Changes in vessel anatomy in response to mechanical loading in six species of tropical trees

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Summary

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- It is well known that trees adapt their supportive tissues to changes in loading conditions, yet little is known about how the vascular anatomy is modified in this process.
- We investigated this by comparing more and less mechanically loaded sections in six species of tropical trees with two different rooting morphologies. We measured the strain, vessel size, frequency and area fraction and from this calculated the specific conductivity, then measured the conductivity, modulus of elasticity and yield stress.
- The smallest vessels and the lowest vessel frequency were found in the parts of the trees subjected to the greatest stresses or strains. The specific conductivity varied up to two orders of magnitude between mechanically loaded and mechanically unimportant parts of the root system.
- A trade-off between conductivity and stiffness or strength was revealed, which suggests that anatomical alterations occur in response to mechanical strain. By contrast, between-tree comparisons showed that average anatomical features for the whole tree seemed more closely related to their ecological strategy.

Key words: hydraulic architecture, hydraulic-mechanical trade-off, mechanical adaptation, rooting morphology, tropical trees, vascular anatomy.

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Introduction

The ability of plants to perceive and react to mechanical stimuli is crucial for their growth, survival and reproductive potential. Thigmomorphogenetic responses by which plants react to mechanical loads have been widely described at different scales, from allometric relationships to cellular mechanisms (Telewski, 1995, 2006; Cordero *et al.*, 2007). Ecologically, this process enables trees to maintain mechanical safety against breakage or buckling when subjected to externally imposed forces while minimizing biomass allocation (Fournier *et al.*, 2006). In trees subjected to relatively larger forces, the biomass allocation to the root plate as well as the secondary

thickening of the stem and roots is increased in the direction parallel to the force vector (Telewski, 1995; Nicoll & Ray, 1996; Stokes *et al.*, 1997; Mickovski & Ennos, 2003; Di Iorio *et al.*, 2005). These geometrical changes by themselves play a major role in increasing the mechanical safety of the tree in the flexing direction and so tissue level responses are more variable. Stem wood appears to become less stiff and strong in plants subjected to dynamic bending (Telewski, 1995), but root wood, in contrast, is stiffer and stronger in areas thought to be subjected to greater mechanical loading (Stokes & Mattheck, 1996; Niklas, 1999).

Modifications in wood stiffness and strength could be associated with anatomical adaptations of the xylem. The vascular

efficiency is a determining factor for whole plant conductance, which imposes a limit on the maximal stomatal conductance and so potentially on the photosynthetic rate (Hubbard *et al.*, 2001; Tyree, 2003). Despite the ecological importance of the vasculature and of the extensive work done on the morphological adaptations trees undergo in response to mechanical loading, very little is known on how mechanical load affects the vascular anatomy of wood. However, when comparing self-supporting and nonself-supporting plants within a species, the conductivity of the self-supporting developmental stages is lower and the stiffness higher (Dean, 1991; Gartner, 1991b) because of a reduction in the vessel area fraction (Gartner, 1991a; Isnard *et al.*, 2003).

For the vascular adaptations to be mechanically beneficial there should be a trade-off between the hydraulic efficiency and the mechanical parameters within the tissue. The reduced porosity in tissues with lower conductivity due to smaller and fewer vessels must be associated with an increase in stiffness and strength. A number of studies have given evidence that such trade-offs at tissue level do occur (Schniewind, 1959; Hathaway & Penny, 1975; Beery *et al.*, 1983; Gartner, 1991b,c; Wagner *et al.*, 1998; Jagels *et al.*, 2003), although a few have not (Gartner *et al.*, 2003; Woodrum *et al.*, 2003) and some have even shown that there may be a positive correlation between conductivity and stiffness instead (Mencuccini *et al.*, 1997). The apparent ambiguity of the previous work is not surprising since a number of anatomical parameters affect the mechanical properties of the tissue, many of which show little or no relationship with the hydraulic properties (Gibson & Ashby, 1997; Hofstetter & Eberhardsteiner, 2005). Density, which may be the most important factor affecting the mechanical properties, can be changed not only by reducing the size and number of vessels but also by increasing the fibre wall thickness and so the density of the tissue surrounding the vessels (Woodrum *et al.*, 2003). Further, the stiffness and strength of wood has been found to be modified by changes in the S_2 microfibril angle (Hathaway & Penny, 1975; Bendtsen & Senft, 1986), the relative lignin content (Köhler *et al.*, 2000, 2006; Niklas *et al.*, 2000) and the volume fraction of rays (Schniewind, 1959; Woodrum *et al.*, 2003). Therefore, the presence of a hydraulic-mechanical trade-off cannot be taken for granted.

It has been suggested that comparing closely related species growing side by side could reduce the problem of having to take into account these factors through reducing phyletic and environmental differences (Wagner *et al.*, 1998). If true, this could be the case to an even greater extent if one compares different sections subjected to different mechanical requirements within the same individuals. The stress patterns and relative bending moments to which different parts of the root system are subjected depend on the morphology of the root system. In trees anchored by a plate-root system and numerous sinker roots the force is transferred to the ground relatively close to the stem by the sinkers (Stokes & Mattheck, 1996). It follows that the distal roots can be expected to be of little mechanical

importance whereas the lateral root connecting the sinker roots to the trunk may be subjected to large tensile and bending stresses (Mattheck, 1991; Mattheck *et al.*, 1993). These theoretical predictions have been supported by strain measurements (Clair *et al.*, 2003). Conversely, taproot anchored trees have weak lateral roots (Ennos, 1993) and so tensile and bending stresses are concentrated in the taproot and lower trunk rather than in the laterals (Crook *et al.*, 1997). Any stress transferred to the laterals should be transmitted further along the root because of a lack of sinker roots, as has been confirmed by strain measurements (Crook *et al.*, 1997).

The present study investigated whether the vascular anatomy of tropical trees is modified by the mechanical loading the trees are subjected to during development. This was done by testing three hypotheses. (1) There will be an increase in the vessel area fraction and so in the conductivity of the wood distally along the superficial roots that reflects the decrease in strain. (2) Trees with different root system morphology and anchorage mechanics will have contrasting patterns in their vascular anatomy that reflect the patterns in locally supported loads. (3) There will be a trade-off between the hydraulic conductivity and mechanical properties of wood so that an increase in the stiffness and strength of the tissue will be associated with a decrease in the specific conductivity. The investigation was carried out on trees from six different species. Three of these were plate root anchored and developed the characteristic triangular buttress roots at the root–trunk interface; the other three were taproot anchored. Ecological strategy such as shade tolerance and successional status has also been associated with a number of wood traits such as density (ter Steege & Hammond, 2001; Falster & Westoby, 2005) and conductivity (Becker, 2000; Tyree *et al.*, 1998). Early succession species, which typically are fast growing and light-demanding, have lower density and higher conductivity than shade-tolerant late succession species, implying that they may differ in anatomical traits. Hence fast-growing light-demanding as well as slow-growing shade-tolerant species were selected for investigation within each of the two root architectural groups.

Materials and Methods

Field site, species and sampling

The sampling for this study took place at the Paracou Experimental forest in French Guyana (52°56'W, 5°16'N) from October to December 2004 and September to December 2005. The climate at the station is seasonal with an extended dry season from mid-August to late November and an occasional shorter dry season from March to April. The mean annual rainfall is 2896 mm and the mean temperature 25.8°C. The site is described in detail in Gourlet-Fleury *et al.* (2004). The following species were chosen for investigation: *Xylopia nitida* Dunal (Annonaceae) and *Tachigali melinonii* (Harms) Zarucchi & Herend (Caesalpinaceae), which both

are buttressed light-demanding species (Toriola *et al.*, 1998; Flores *et al.*, 2006); *Pradosia cochlearia* (Lecomte) T.D.Penn (Sapotaceae), which is a buttressed shade-tolerant species that will reach the upper canopy (Koestel & Rankin-De Merona, 1998; Valerie & Marie-Pierre, 2006); *Oxandra asbeckii* (Pulle) R.E.Fr. (Annonaceae) and *Micropholis egensis* (A.DC.) Pierre (Sapotaceae), which are both are nonbuttressed shade-tolerant species (Vieiraa *et al.*, 2003; Flores *et al.*, 2006); and finally *Jacaranda copaia* D.Don (Bignoniaceae), which is a nonbuttressed light-demanding species (Thompson *et al.*, 1998). All the trees chosen for this study had a stem diameter at breast-height of 7–13 cm and a height of 8–14 m. Six individuals were sampled from each species except for *M. egensis*, in which only one individual was found.

To confirm expected strain patterns, trees from the four species *X. nitida*, *T. melinonii*, *O. asbeckii* and *J. copaia* were subjected to overturning moments and the resulting strains along the grain in the trunk and superficial roots of 10 of the trees were measured. The equipment and experimental procedure are described in detail elsewhere (Clair *et al.*, 2003). Briefly, strain transducers were pinned into the peripheral wood at the locations shown in Fig. 1. Using a manual winch attached by a steel cable to the base of another tree, a load of 0.2–0.5 kN was applied to the trunk at a height of 2 m. This mimics (though not exactly) the effect of small wind forces on the root system, allowing strains around the root base to be compared. To enable a comparison between trees, the mechanical strain was normalized by the maximum value measured for that particular tree. Trees were pulled in the opposite direction to the side in which the strain gauges were placed. The strain was measured in roots in tension rather than compression because these have been shown to contribute the major part of the anchorage (Ennos, 2000).

The root system was excavated to a distance of 0.7–1.5 m from the trunk and to a depth of 20–50 cm. The tree was felled, and the root system as well as 2-m long sections of the upper trunk and the lower trunk were sampled (Fig. 1). The sections were wrapped in plastic bags to avoid evaporation and immediately transported back to the laboratory. Here, a number of digital images were taken of the root system both in parallel and perpendicular to the trunk to facilitate a morphological investigation of the root system and it was cut into segments. The sections were stored in water at room temperature (*c.* 30°C) until the conductivity measurements were performed. To avoid microbial growth, all measurements were performed no later than 3 d after the tree was felled. That storage for this length of time was acceptable was confirmed by that the conductivity did not fall over this time, but did fall after *c.* 4–5 d.

Conductivity measurements

For each tree, the conductivity was measured on the sections shown in Fig. 1. The measurements were performed broadly as in Sperry *et al.* (1988) and are described in detail elsewhere

Fig. 1 Schematic overview over the sampling protocol for the individual tree. The sapwood area is marked with light grey in the transects except for the transect of the taproot, in which it was impossible to measure sapwood area. On all trees, areas marked in medium grey would be sampled for conductivity measurements. In addition to this, in a selection of trees tissue would be sampled for anatomy investigations in the areas marked with a small black circle. In the roots, where the circles are difficult to see, they are indicated by arrows. In other trees, comprehensive mechanical investigations were carried out in addition to the conductivity measurements. In the spots marked by small black bridges, strain would be measured in the direction opposite to that of the force. Rectangular beams would be cut from the larger sections on which conductivity was measured as indicated with black bars. Elasticity and yield stress would be measured on the beams or on the entire roots if these had a diameter of < 1 cm (those in which no beams are marked, marked with black cross-hatching instead). At least two whole roots were sampled in all trees (of which only one is marked on the Fig.). The sampling for the nonbuttressed trees was analogous.

(Christensen-Dalsgaard *et al.*, 2006). The ends were re-cut to remove embolized or damaged vessel ends and sawdust. The stumps of the sinker roots of the buttresses were sealed of using several layers of parafilm. Following a 5 min flushing at 0.1 MPa to remove embolisms, a known pressure gradient (ΔP , MPa) was applied over the sections and the flow rate of water (q , kg s⁻¹) through the section was measured. Since many of the sections in this study had asymmetrical cross-sections soft, flexible attachment collars were used for attaching the segments to the pressure head.

The sapwood area of the trunk sections was visualized using ink dissolved in water. Black India ink is known to clog up vessels and be incapable of crossing pits and so blue ink was chosen. The ink was found to reduce the conductivity by 0–17% over a half-hour period and penetrated 1.3- to 2-m long stem segments, though air subsequently was found not to do so. Hence, although ink may not be a good stain for trees in general, in the species studied here it was capable of crossing the pits and only to a limited extent reduced the conductivity. The sapwood area (A_s) was measured digitally using IMAGEJ image

analysis software (freeware, available: <http://rsb.info.nih.gov/ij/index.html>). In the roots the sapwood was assumed to constitute the entire cross-sectional area of the section, an assumption that was supported by preliminary tests. The conductivity (K , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) and specific conductivity (K_s , $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) of a section with length l was calculated from the postflushing flow rates as:

$$K = \frac{ql}{\Delta P} \quad \text{Eqn 1}$$

$$K_s = \frac{k}{A_s} \quad \text{Eqn 2}$$

The sections were then flushed with air to check for the presence of open vessels without vessel ends.

Anatomy

Tissue samples for anatomy studies were extracted as shown in Fig. 1. The samples were rehydrated and softened by repeated cycles of boiling and cooling over a minimum of 24 h. Using a Leica rotary microtome (Leica Microsystems Ltd, Milton Keynes, UK) fitted with disposable microtome blades, the samples were sectioned perpendicular to the grain at a thickness of 20 μm and stained with Toluidine blue. Images were captured of the anatomy sections at $\times 50$ magnification using a Leica DMR fluorescent microscope (Leica Microsystems Ltd) and photographed with a Spot RT digital camera (Image Solutions, Wigan, UK). three to six images were taken of each anatomy section so that at least 200 vessels were captured. The images were calibrated with a slide-mounted micrometer.

The images were analysed using the IMAGEJ image analysis software. About 230–1620 vessels were analysed per transect. Minor axis and major axis diameters, the number of vessels and the vessel area fraction were measured. The hydraulically weighed mean diameter (HMD), was calculated as in Ewers *et al.* (1997):

$$\text{HMD} = \sqrt[4]{\frac{\sum d^4}{N}} \quad \text{Eqn 3}$$

(d is the average between the major and minor axis diameter of the vessel and N the number of vessels for the section).

The cross-section of the vessels was approximated as being elliptical, and the theoretical specific conductivity (C_s) for each sample was calculated as in Calkin *et al.* (1986) using Poiseuille's law modified for tubes with elliptical cross-sections:

$$C_s = \frac{\sum \frac{\pi r_1^3 r_2^3}{4\eta(r_1^2 + r_2^2)}}{A} \quad \text{Eqn 4}$$

(r_1 and r^2 are the major and minor axis radius, respectively, of all the individual vessels captured from the sample; η is the dynamic viscosity of water; A is the area of the imaged part of the sample).

Mechanical measurements

Mechanical measurements were performed on 11 trees of the species *T. melinonii*, *X. nitida*, *O. asbeckii* and *J. copaia* immediately following the conductivity measurements while the wood was still fresh. The samples for the measurements were taken as shown in Fig. 1. As in numerous previous studies (Niklas, 1999), the mechanical properties of the root and beam samples were measured in a three-point bending test. A MecMesin PFI-200N force gauge (Mecmesin Limited, Slinfold, UK) attached to the centre of the sample was pulled back perpendicularly to the axis of the sample by a screw-mechanism at a velocity of no greater than 50 $\mu\text{m s}^{-1}$. The force and displacement (displacement measurer: Mitutoyo 543-250B, precision 3 μm ; Mitutoyo, Paris, France) was recorded every 100–400 μm in the first 1–2 mm of displacement, depending on the rigidity of the segment, and every 500 μm thereafter.

On eight uncut roots, the second moment of area (I) was calculated from digital scanning images by fitting 10 trapezoids spanning the width of the section to the cross-section of the root. I was then calculated as:

$$I = \sum \int_{y_i}^{y_{i+1}} y^2 w(y) dy \quad \text{Eqn 5}$$

(y is the distance from the neutral axis; $w(y)$ the width of the relevant trapezoid as function of y ; y_i and y_{i+1} are the distances from the neutral axis to the bottom and top of the trapezoid, respectively).

To generalize results obtained from the eight roots studied in detail, I was fitted to the general equation:

$$I = \frac{D_1 D_2^3}{k} \quad \text{Eqn 6}$$

(D_1 and D_2 are the diameters in the direction perpendicular and parallel to the force vector, respectively, and k the constant determined by the shape of the cross-section). For the following uncut roots, the value of k derived from the above was used in the calculation of I . In the case of the beams, the cross-section was uniformly rectangular (and so $k = 12$). From I , the slope of the force-displacement curve in the elastic range ($S = F/d$), and the length of the sample between the two supports (l), the modulus of elasticity in bending, E , was calculated:

$$E = \frac{Sl^3}{48I} \quad \text{Eqn 7}$$

The yield stress (YS) for a section with a cross-sectional height (h) in the direction parallel to the force was calculated as the maximum bending stress at the point where an increase in displacement caused no further increase in force (F_{max}):

$$YS = \frac{F_{\text{max}} l h}{8I} \quad \text{Eqn 8}$$

Table 1 Ratios between vessel parameters in different sections of buttressed compared with nonbuttressed trees

		Buttressed species	Nonbuttressed species	Significance
Vessel frequency	RTI/VR	0.74 ± 0.08	2.19 ± 1.12	*
HM diameter	LT/RTI	1.65 ± 0.30	0.923 ± 0.07	*
Vessel area fraction	RTI/DSR	0.13 ± 0.02	0.42 ± 0.08	**
	RTI/VR	0.93 ± 0.07	2.07 ± 0.31	**
	LT/RTI	1.98 ± 0.40	0.46 ± 0.07	**
	UT/LT	1.80 ± 0.74	2.9 ± 0.55	*
C_s	RTI/DSR	0.047 ± 0.018	0.30 ± 0.08	**
	LT/RTI	5.22 ± 2.97	0.38 ± 0.04	*
	UT/LT	2.59 ± 1.68	6.26 ± 1.59	*

HM, hydraulic mean; C_s , calculated specific conductivity; RTI, roots at the root–trunk interface; VR, vertical roots; DSR, distal superficial roots; LT, lower trunk; UT, upper trunk.

***, $P < 0.05$ and $P < 0.01$, respectively. Values are means ± SD.

Table 2 Ratios between vessel parameters in different sections of light-demanding compared with shade-tolerant trees

		Light-demanding species	Shade-tolerant species	Significance
Vessel frequency	UT/LT	1.03 ± 0.08	1.70 ± 0.26	**
Area fraction	UT/DSR	0.35 ± 0.06	0.63 ± 0.05	**
	UT/LT	1.56 ± 0.39	3.11 ± 0.22	**
C_s	UT/DSR	0.30 ± 0.075	0.98 ± 0.20	**
	UT/LT	2.21 ± 1.24	6.44 ± 1.18	**

C_s , calculated specific conductivity; DSR, distal superficial roots; LT, lower trunk; UT, upper trunk.

**, $P < 0.01$. Values are means ± SD.

Data analysis

All data analysis was carried out using SIGMAPLOT software (SYSTAT Software Inc., London, UK). In the case of the buttressed species the relationships between relative strain, the size or frequency of the vessels or the vessels area fraction and the distance from the root–trunk interface (RTI) were typically both linear and fulfilled the normality and constant variance test, or could be made to do so by log-transforming the data. However, for the values of C_s in the buttressed species and all values in the nonbuttressed species this was not the case. Therefore, to use the same procedure with respect to all measurements from both groups, the data for the statistical calculations were instead grouped after distance from the trunk. The RTI root samples were defined as samples taken 0–5 cm from the RTI, intermediate root samples as samples taken 10–30 cm from the RTI and distal root samples as samples taken > 50 cm from the RTI. Paired t -tests were carried out to investigate if there were significant differences between the RTI roots and the intermediate roots and between the intermediate and the distal roots. In the case of C_s , where the data set was skewed by outlying large values, the nonparametric Wilcoxon paired comparison test had to be used instead.

To quantify how the anatomical pattern throughout the trees differed between the plate root anchored buttressed trees and the taproot anchored nonbuttressed trees, the ratio between values for the anatomical traits were calculated for the

different parts of each tree. For example, the vessel frequency ratio in the trunk was calculated as the vessel frequency of the upper trunk divided by that of the lower trunk for each individual tree. For comparative purposes the data was pooled in groups. The ratio values for a given part of the tree (e.g. the upper trunk : lower trunk ratio) of all buttressed trees were compared with those of all nonbuttressed trees. Subsequently, the data for all light-demanding trees were compared with those of all shade-tolerant trees. In the comparison, a Students t -test was used, and all ratios for which significance levels of $P < 0.05$ or less were found were recorded (see Tables 1 and 2). Similarly, Students t -tests were carried out to determine if the absolute values for the vessel characteristics for a given section of the tree (e.g. the vessel frequency of the upper trunk) differed between buttressed and nonbuttressed species or between light-demanding and shade-tolerant species.

The relationship between K_s and C_s as well as between K_s and E was investigated using linear regressions after relevant log-transformations of the data so that they conformed to the requirements for the tests.

Results

Root morphology

The morphology of the roots corresponded well to that predicted for the two different anchorage types. The

Fig. 2 Strain as function of distance from the root–trunk (RT) interface. The strain is normalized by the maximum value for the individual tree, so that the development becomes comparable between trees. The roots are marked by negative distance, the trunk by positive distance. (a) The buttressed species *Xylopia nitida* (squares and dashed lines) and *Tachigali melinonii* (circles and solid lines). (b) The nonbuttressed species *Jacaranda copaia* (upward-pointing triangles, solid lines) and *Oxandra asbeckii* (downward-pointing triangles, dashed lines.).

buttressed trees had well-developed lateral roots positioned at the surface of the soil. The buttressed part of the roots, which extended to 0.3–0.7 m from the trunk, was supported by between three and seven sinker roots with a radius of > 0.5 cm as well as a number of thinner roots. Distally from the buttress, there was only one or no sinker roots. Lateral branching of the root system was often found towards the tip of the buttress as well as further out. The diameter of the taproot 10 cm below the soil was $< 30\%$ of the diameter at breast height (d.b.h.), and the taproot was < 45 cm long.

The nonbuttressed trees had thinner lateral roots positioned between 1 and 20 cm below the surface of the soil. In these trees no sinker roots were found. Only *c.* 20% of the roots showed side branching, though in *O. asbeckii* and *M. egensis* some roots were associated with a number of long filamentous roots (diameter < 1.5 mm) protruding from the surface. The diameter of the taproot 10 cm below the surface of the soil was greater than 70% of the d.b.h. and > 45 cm long. In *O. asbeckii* and *M. egensis* the taproot was $> 100\%$ of the d.b.h. and the length impossible to determine since they could not be pulled out of the soil.

Changes in strain along the superficial roots

As expected, the greatest strain in the buttressed trees occurred right above or on the buttress root close to the RTI; thereafter it fell rapidly along the root reaching or approaching zero between 0.5 and 0.7 m from the trunk (Fig. 2a). In the nonbuttressed species (Fig. 2b), the strain was greatest either in the lower part of the trunk or right at the RTI. Further along the root, there was an initial drop in strain, but following this, the pattern was not clear. The values appeared to oscillate, in some cases between positive and negative values. The absolute value of the strain showed an initial decrease to between 0.25 and 0.5 of the maximum value, and then appeared to level off.

Anatomical changes distally along the superficial roots

There were anatomical changes along the superficial roots that were inversely related to the changes in strain. In the buttressed species there was a continuous increase in vessel frequency, vessel area fraction and C_s away from the bole (Fig. 3). Further, there was an increase in vessel diameter from the RTI to a distance of 0.5–0.7 m from the trunk. After this point, the vessel diameter levelled off in several of the roots, and so there was no further significant difference ($P = 0.59$). In all three buttressed species, the increase in vessel area fraction was approximately linear.

In the nonbuttressed species, the differences in vascular anatomy were less uniform (Fig. 3) as were the changes in strain (Fig. 2). The anatomical differences were also less marked. For example, whereas the area fraction increased by, on average, a factor of 8.14 (SD 1.96) in the roots of the buttressed species, it increased only by a factor of 2.42 (SD 0.66) in the nonbuttressed species corresponding to the more moderate drop in strain seen in the latter. As was seen for strain the increase in size and frequency of the vessels occurred close to the RTI, and there was little change further along the roots. The differences between the roots close to the RTI and roots at a distance of 10–30 cm from the trunk was significant for all parameters (vessel diameter $P = 0.037$; frequency $P = 0.027$; area fraction $P = 4.5 \times 10^{-4}$; C_s $P < 0.01$). There were no differences when comparing the roots at a distance of 10–30 cm from the trunk and the distal-most roots (vessel frequency $P = 0.99$; vessel diameter $P = 0.80$; vessel area fraction $P = 0.97$; C_s $P > 0.1$).

Patterns in the vascular anatomy of trees with different root system morphology

The pattern of anatomical change differed between the plate root anchored buttressed trees and the taproot anchored nonbuttressed trees (Fig. 4, 5). To quantify these differences,

Fig. 3 Frequency, hydraulic mean diameter (HMD) area fraction and calculated specific conductivity (C_s) of the xylem vessels of the roots of the buttressed (left) and nonbuttressed (right) species as function of the distance from the trunk. C_s is calculated from the hydraulic mean diameter and the frequency using Poiseuille's equation. The lines connect sections taken along the same roots. Different symbols within the same colour represent different individuals within the same species. White and light grey are used for light-demanding species, dark grey and black for shade-tolerant species. Buttressed species: light grey symbols and dash-dot lines, *Tachegali melinonii*; open symbols and solid lines, *Xylopia nitida*; closed symbols and dashed lines, *Pradosia cochlearia*. Nonbuttressed species: dark grey symbols and dashed lines, *Micropholis egensis*; open symbols and solid lines, *Jacaranda copaia*; closed symbols and dash-dot lines, *Oxandra asbeckii*. Error bars indicate 1 SE.

the ratio between values for the anatomical traits were calculated for the different parts of each tree (see the section on Data Analysis). The ratios that differed significantly between buttressed and nonbuttressed species can be seen in Table 1.

In the buttressed species, the buttress and sinker roots had a smaller vessel area fraction and lower specific conductivity than anywhere else in the tree. The distal superficial roots, which play little or no mechanical role, had a larger vessel area fraction than found elsewhere and a specific conductivity up to two orders of magnitude higher than that of the buttress roots, owing to differences both in size and frequency of the vessels (Fig. 5). The bole, which is supported by the buttresses (Young & Perkocha, 1994; Woodcock *et al.*, 2000), had a higher vessel area fraction and a higher conductivity than the RTI roots, due mainly to differences in the size of the vessels. In the nonbuttressed species the vessel area fraction and

specific conductivity were lowest in the taproot and in the lower part of the trunk, the areas in which the greatest stress accumulation are found. Hence, in contrast to the buttressed trees, the nonbuttressed trees had a higher area fraction and conductivity in the RTI roots than found in the lower trunk and taproot, due mainly to a difference in vessel frequency. The nonbuttressed trees also had a greater difference between the vessel area fraction in the upper and the lower part of the trunk, and consequently a greater difference in specific conductivity.

Effects of growth strategy on the observed changes

There were few significant differences in anatomical ratios between light-demanding and shade-tolerant species (Fig. 4, 5, Table 2). When comparing the upper trunk and the distal

Xylopia nitida *Micropholis egeensis*

DS root

RTI root

Vertical root

Lower trunk

Upper trunk

Fig. 4 Anatomy sections of different parts of a tree of the buttressed species *Xylopia nitida* and the nonbuttressed species *Micropholis egeensis*. Bar (upper right corner), 1 mm and is valid for all sections. DS roots, distal superficial roots taken 1 m from the root–trunk interface; RTI roots, superficial roots close to (3–5 cm from) the root–trunk interface; vertical roots, taproot in the case of the nonbuttressed species, tap- or sinker roots in the case of the buttressed species (the section here is from a sinker root. There were no systematic differences between taproot and sinker roots within a tree). All root sections within a species are from the same root with the exception of the taproot in *M. egeensis*. Lower trunk, 1.3 m above soil level; upper trunk, 6 m above soil level.

Table 3 Parameters that differ significantly between similar sections in light-demanding and shade-tolerant species

		Light-demanding species	Shade-tolerant species	Significance
Frequency (vessels mm ⁻²)	DSR	21.1 ± 7.1	68.3 ± 12.4	**
	LT	5.9 ± 0.2	16.6 ± 1.7	**
	UT	6.1 ± 0.2	28.2 ± 3.9	**
HM diameter (µm)	DSR	133.19 ± 14.50	59.93 ± 5.03	**
	LT	112.68 ± 13.36	53.23 ± 4.94	**
	UT	132.19 ± 2.19	75.22 ± 2.63	**
<i>C</i> _s (kg m ⁻¹ s ⁻¹ MPa ⁻¹)	DSR	123.67 ± 33.95	18.04 ± 2.40	**
	LT	19.83 ± 8.54	2.81 ± 1.03	*
	UT	34.60 ± 2.76	17.33 ± 2.76	**

HM, hydraulic mean; *C*_s, calculated specific conductivity; DSR, distal superficial roots; LT, lower trunk; UT, upper trunk.

*, **, *P* < 0.05 and *P* < 0.01, respectively. Values are means ± SD.

superficial roots the difference in area fraction and calculated specific conductivity was greater in the case of the light-demanding than the shade-tolerant species. When comparing the upper and lower trunk, however, the difference in vessel area fraction and specific conductivity was greater in the case of the shade-tolerant than the light-demanding species, and was largely due to differences in vessel frequency.

By contrast, the absolute characteristics of the individual segments seemed more closely related to ecological strategy than rooting morphology (Fig. 5, Table 3). Light-demanding species had fewer but larger vessels in the distal superficial roots, lower trunk and upper trunk than shade-tolerant species. In the superficial roots of buttressed trees, on average 42% (SD 16.35%) of the increase in vessel area fraction along

the roots was due to an increase in vessel frequency and 58% was due to an increase in vessel size in the light-demanding species *X. nitida* and *T. melinonii*. In the shade-tolerant species *P. cochlearia*, however, the increase in area fraction was to a much greater extent (73%, SD 7%) due to an increase in frequency. The differences in conductivity calculated for the two light-demanding species were correspondingly up to one order of magnitude greater than those calculated for *P. cochlearia*. There were no significant differences between the two groups in the vessel characteristics of the vertical roots or the RTI roots.

The effects of ecological strategy and rooting morphology appeared superimposed on each other (Table 4). Shade-tolerant species, for example, had a greater difference in conductivity

Fig. 5 An overview over the characteristics of the xylem vessels for the six species studied in the key areas: Distal superficial (DS) roots, vertical roots (sink- and tap roots), roots at the root-trunk interface (RTI roots, e.g. buttress roots), lower trunk and upper trunk. indicates light-demanding species; the remaining species are shade-tolerant. Error bars indicate 1 SE.

Table 4 Ratio between theoretical specific conductivity in upper trunk vs lower trunk

Species			Ratio
Light-demanding	Buttressed	<i>Xylopia nitida</i>	1.33
		<i>Tachegali melinonii</i>	1.48
	Nonbuttressed	<i>Jacaranda copaia</i>	4.02
Shade-tolerant	Buttressed	<i>Pradosia cochlearia</i>	4.96
	Nonbuttressed	<i>Micropholis egenis</i>	7.31
		<i>Oxandra asbeckii</i>	7.47

Fig. 6 The measured conductivity (K_s) of sections as function of the calculated specific conductivity (C_s) calculated from the size and number of vessels using the Poiseuilles equation. Open symbols, values for trunk section; closed symbols, values for root sections. Squares, *Tachigali melinonii*; circles, *Xylopia nitida*; upward-pointing triangles, *Pradosia cochlearia*; downward-pointing triangles, *Oxandra asbeckii*; diamonds, *Jacaranda copaia*. The results are plotted in log-log space to make it possible to visualize data spanning two orders of magnitude. Since the relationship was linear, the slope of the log-transformed data was approx. 1. In both the roots and trunk the slopes in linear space is approx. 0.4.

between upper and lower trunk than light-demanding species and nonbuttressed trees showed a greater difference than buttressed trees. Hence, species that were buttressed as well as light-demanding showed very little difference and species that were nonbuttressed as well as shade-tolerant showed a large difference. The two species that were buttressed and shade-tolerant or nonbuttressed and light-demanding had values that fell in between.

Connections between calculated and measured specific conductivity

As predicted, there was a strong positive linear relationship ($R^2 = 0.85$) between the measured specific conductivity and that calculated from the anatomy section based on Eqn 4 (Fig. 6). The slope of the linear relationship was 0.44 for

Fig. 7 Trade-off between specific conductivity (K_s) and modulus of elasticity in bending (E) across the four species *Tachigali melinonii* (circles), *Xylopia nitida* (squares), *Jacaranda copaia* (upward-pointing triangles) and *Oxandra asbeckii* (downward-pointing triangles). Values for the roots are shown with closed symbols, values for the trunk with open symbols. The plot is log-linear since the data for the roots are obviously skewed. The trade-off was significant both for the trunk (linear regression, for the roots: $P < 0.001$; for the trunk: $P < 0.05$).

the roots and 0.42 for the trunk. The differences in the slopes for the roots and trunk were not significant. In the roots, it was impossible to obtain sections long enough to avoid open vessels in which no vessel ends were present. In the trunk, however, the sections were sufficiently long to avoid open vessels in all species but *T. melinonii*, in which the longest vessels exceeded the 2.5 m of the longest section studied.

Hydraulic-mechanical trade-offs

The yield stress (YS) was linearly related to the modulus of elasticity in bending (E), and so correlations with YS were similar to correlations with E . Conclusions drawn on trade-offs between K_s and stiffness are therefore also valid for strength. Since no systematic deviations were found in the relationship between E and K_s as opposed to YS and K_s , only the results for E are presented.

There were trade-offs between K_s and E as well as YS both within and between the four species studied (Fig. 7), though because of equipment failure it was not possible to obtain a large enough number of data points for the trade-off within *O. asbeckii* and *J. copaia* by themselves to be significant. The regressions for the roots after log-transforming K_s gave R^2 values of 0.74 for *X. nitida*, 0.75 for *T. melinonii* and 0.61 for all four species pooled. All of the above regressions were highly significant ($P < 0.01$). There was an apparently linear trade-off between species within the trunk, but it was less significant than that of the roots ($R^2 = 0.25$, $P < 0.05$).

Discussion

Relationships between vascular anatomy and specific conductivity

There was a strong linear correlation between K_s and C_s and so the calculated values for C_s can be used as a good indicator of the actual specific conductivity K_s of the wood (Fig. 6). The measured values were approx. 40% of the calculated ones in agreement with the results of previous studies (Chiu & Ewers, 1992; Wheeler *et al.*, 2005). The discrepancy can largely be attributed to the resistance of the pits (Chiu & Ewers, 1992; Wheeler *et al.*, 2005). Other factors may also affect the conductivity, such as the presence of vessel perforation plates (Ellerby & Ennos, 1998), that the cross sections of the vessels are not perfectly elliptical, and that the vessel walls are not perfectly smooth. In the roots as opposed to the trunk there were open vessels with no pits present. However, since the length distribution of vessels is strongly skewed (Sperry *et al.*, 2005), it is likely that only a small fraction of the vessels were open. This is supported by the fact that there were no significant differences between the roots and trunk in the slope of the regression.

Anatomical differences within trees related to patterns in strain or stress

The anatomical changes observed in the roots showed a good agreement with the hypotheses. There were clear anatomical changes distally along the superficial roots resulting in an increase in C_s of up to two orders of magnitude. These reflected the patterns in strain; the vessel area fraction and so the calculated specific conductivity increased as the strain decreased. The anatomical changes were greater in the case of the buttressed trees, corresponding to the greater changes in strain observed for these trees compared with the nonbuttressed species. Analogously, trees with different root system morphology did have contrasting patterns in their vascular anatomy that reflected the patterns in locally supported loads. In the buttressed trees, the lateral roots represent the main rigid element resisting the bend moments generated in the trunk and transfer the tensile forces to the sinker roots and into the ground (Mattheck, 1991; Ennos, 1993; Mattheck *et al.*, 1993). In the nonbuttressed species the main rigid element is in the taproot, and the lateral roots function as guy ropes keeping the taproot in place (Crook *et al.*, 1997; Ennos, 1993). Accordingly, the lowest vessel area fraction and calculated specific conductivity was found in the RTI roots of the buttressed species but in the taproot and bole of the nonbuttressed species.

The close relationship between loading patterns and vascular characteristics supports the hypothesis that wood anatomy is adapted inside the tree in response to mechanical loading. Hence the results of previous studies showing that roots of

trees have larger vessels than the trunk (Ewers *et al.*, 1997; McElrone *et al.*, 2004) were, in the present species, only uniformly true when comparing the lower part of the trunk with the distal superficial roots. The anatomical pattern for the buttressed trees conform well to that described by Stahel (1971), but not to that described by ter Steege *et al.* (1997). In the latter study, however, the trees grew on very loose soil and the trees were thought to be anchored largely by the thick trailing roots rather than by sinker roots.

Our results suggest that tree growth and development may be affected by mechanical loading not only through the allocation of larger amounts of biomass to nonphotosynthesizing tissues, but also through a modification of the vascular anatomy. An increase in resistance due to localized areas of lower conductivity could reduce the photosynthetic rate through limiting the stomatal conductance (Hubbard *et al.*, 2001; Tyree, 2003). The two may well occur in parallel. Trees could compensate for a reduction in conductivity by locally increasing the amount of sapwood, thus also increasing the rigidity. In two of the buttressed species investigated here, it has been shown that the decrease in total sapwood area distally along the roots by a factor 10 only partially compensates for the increase in conductivity of a factor 40. Hence the total conductivity of all distal roots was around four times higher than that of all buttress roots (Christensen-Dalsgaard *et al.*, 2006). Whether this local increase in resistance at the RTI has much of an effect on the overall resistance of the tree, however, is questionable. Further, the effect may vary between trees or climatic regions since it has been found that mechanical adaptations in poplars do not reduce the conductance of the tree (Kern *et al.*, 2005).

It is often assumed that the size of the vessels and consequently the specific conductivity of the wood increases from the tip of the branches and towards the roots (West *et al.*, 1999). In the present study all the trees showed a decrease in vessel size and typically also in frequency towards the base of the trunk and in the proximal parts of the roots. Hence it appears that hydraulic models of the vascular system would benefit from taking into account the mechanical requirements on the wood in specific areas of the tree and the anatomical changes that may result from these, as also shown in McCulloh *et al.* (2004).

Differences between species reflecting growth strategy

The differences observed between growth forms accorded well with those described in the literature. It is well known that the vascular anatomy of woody growth forms is influenced by the conditions under which the plant grows and by the growth strategy (Carlquist & Hoekman, 1985; Preston *et al.*, 2006). The higher conductivity of light-demanding compared with shade-tolerant species measured in this study seems to be a general pattern in tropical forests (Tyree *et al.*, 1998; Becker, 2000). As in previous studies, this was associated with a lower

density of the tissue (data not shown). The differences in conductivity occurred because light-demanding species had fewer but larger vessels than shade-tolerant species. Since conductivity is related to the fourth power of diameter but only linearly related to frequency, this resulted in a higher conductivity.

The vessel area fraction, though highly variable within the tree, was not significantly different between groups of species. Differences in the size of vessels were largely counterbalanced by differences in frequencies. These results support previous work that show a trade-off between vessel size and frequency not because of packing, but so that the vessel area fraction is maintained in a range where the tissue is strong enough to provide support but porous enough to provide conductance (Preston *et al.*, 2006). The deviation from this trend seemed to be mainly in localized areas of the trees where the need for support outweighs the need for conductivity, or where the mechanical requirements on the tissue are minimal and so conductance can be optimized.

Trade-offs between the mechanical and hydraulic properties at the tissue level

Both within and between the species studied, a negative relationship between hydraulic and mechanical parameters were found, most clearly so in the roots of the individual buttressed species but also across the four species. The regression was poorer within the trunk, which could imply that here other trends in nonconductivity-related anatomical parameters are superimposed on the vascular trends, thus cancelling out the vascular effects on the mechanical parameters. This could explain the ambiguous results of previous work, which has been focused on the trunk and branches. Anatomical changes may affect the mechanical properties of the tissue even in cases where there is no apparent trade-off between hydraulic and mechanical parameters, since the mechanical properties are simultaneously a function of nonconductivity-related tissue characteristics. Differences in other anatomical parameters superimposed on the vascular patterns could obscure the relationship. The relevant question when evaluating the mechanical effect of vascular adaptations is what mechanical properties the same tissue with the same microfibril angle, fibre wall thickness, etc., would have had with different vascular characteristics. This is very difficult to determine. The general trade-off between the K_s and the mechanical properties of the tissue in these trees as well as in numerous previous studies, however, indicates that it is reasonable to assume that the vascular modifications observed may have a function in reinforcing stressed tissues.

Conclusion

The results of this survey showed inverse associations between mechanical strain and hydraulic anatomy. The anatomical changes along the superficial roots reflected the distal fall

in strain. Similarly, the differences in anatomical patterns between the two rooting morphologies reflected the differences in expected mechanical loading patterns. Therefore, vessel anatomy within individual trees does seem to change in response to mechanical loading. Since we found a trade-off between hydraulic efficiency and mechanical properties, these changes appear to be an adaptation towards reinforcing mechanically loaded areas. Ecological studies generally focus on mean specific values of traits such as wood density along the major axis of growth strategies. In our study, the differences between the rooting morphologies locally reduced or eliminated differences due to growth strategy, indicating that it might also be important to take into account morphological differences between trees. Using anatomical ratios and measuring mechanical and hydraulic properties independently gives new insights into the diversity of wood functional roles. Among other things, this may explain the enhanced anatomical diversity seen in climatic regions such as tropical forests that promotes a number of morphologies as well as provides a range of microhabitats.

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