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# Functional anatomy of five endangered tropical timber wood species of the family Dipterocarpaceae

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**Abstract** Wood anatomy of five dipterocarp species endemic to the Philippines was studied with the goal to explore functional wood traits of ecological significance. Stem wood of 6-year-old trees grown under similar environmental conditions in a plantation (Leyte, Philippines) was used. Wood densities decreased in the following order *Hopea plagata* > *Dipterocarpus kerrii* > *Parashorea malaanoman* > *Shorea almon* ≈ *Shorea contorta*. This was mainly caused by significantly thicker fiber cell walls of *H. plagata* and *D. kerrii* than those of the other three species. Wood density was negatively correlated with the abundance of axial parenchyma cells. Predicted conductance was independent from wood density and lowest in *H. plataga* and highest in *D. kerrii* and *S. contorta*. These results indicate that *H. plagata* and *D. kerrii* is woods have higher constructions costs in term of carbon per unit of biomass, and that *H. plagata* is probably better acclimated to varying soil moisture than the other species.

**Keywords** Dipterocarps · Anatomical traits · Hydraulic system · Xylem

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## Introduction

Most tropical forests in Southeast Asia are dominated by Dipterocarpaceae. The members of this family are especially abundant in lowland forests and most of them are valuable timber species. However, due to the destruction of tropical rain forests, they disappear at an alarming rate (FAO 2007). In the Philippines, only 3% of the land area is still covered by primary forests, and very few natural dipterocarp forests are left, although the islands are one of the most important biodiversity hotspots of the world (Myers et al. 2000). Economically important genera such as *Dipterocarpus*, *Parashorea* and *Shorea* have been classified as critically endangered species (IUNC 2007). Nowadays, a logging ban prohibits cutting of trees on the Philippines and reforestation trials with native species are being made. However, documentation and analysis of success of these measures is scarce (Langenberger 2006), and information on anatomical traits relevant for the ecological requirements of many tree species is lacking.

Tissue traits such as wood density and the hydraulic architecture of plant species are informative for land-plant ecology (Westoby and Wright 2006; Swenson and Enquist 2007). With respect to water transport, wood properties such as vessel dimensions and lumen area are relevant (Preston et al. 2006). Conductivity increases with the fourth power of radius and only linearly with vessel number. Therefore, vessel size is a far more important parameter determining hydraulic characteristics than vessel number (Tyree and Zimmermann 2002). It has been suspected that large vessels are more prone to cavitation than smaller ones; however, this is still unclear. Correlations appear to exist between cavitation resistance and wood density (Hacke and Sperry 2001; Hacke et al. 2001,

2006). In some tropical tree species, conductivity was found to vary with density (Christensen-Dalsgaard et al. 2007a).

Tropical tree species cover a wide range of wood densities from 0.3 to 1.2 g cm$^{-3}$ (Ketterings et al. 2001, Wood density database 2007). However, saplings of shade-tolerant trees may spend years growing slowly in the understory, only to grow into a tall reproductive adult when supplied by a gap in the canopy. The wood anatomy and hydraulic properties of juvenile trees may, therefore, differ from features found in large adults. In emergent tropical trees, thin-walled fibers are more typical for rapidly growing, early succession species and thick-walled fibers are more common in climax species (Swaine and Whitemore 1988). The fibers in the wood matrix appear to contribute directly to biomechanical strength and offer support against implosion (Baas et al. 2004; Berry and Roderick 2005; Jacobson et al. 2005).

Dipterocarps are characterized by a high diversity of wood anatomy (Gottwald and Parameswaran 1966; Lomibao 1973; Ashton 1982; Ella and Meniado 1992; Newman et al. 1996). While members of the tribe Dipterocarpae are characterized by solitary vessels, scattered resin canals and fibers with bordered pits, members of the Shoreae (Hopea, Shorea and Parashorea) have grouped vessels and resin canals in tangential bands (Ashton 1982). Furthermore, abundant parenchyma is typical for tropical forest tree species with high photosynthetic rates (Alves and Angyalossy-Alfonso 2002). The combination of abundant parenchyma with septate fiber gives a huge potential for carbon and water storage in the wood of these species (Baas et al. 2004).

In the present study, we investigated wood anatomy of five dipterocarp species endemic to the Philippines grown in an experimental plantation. The main goal was to explore wood traits important for the hydraulic system. The species studied here represent three timber groups, i.e., Apitong (Dipterocarpus kerrii), Yakal (Hopea plagata), and Philippine mahagony (Parashorea malaanoman, Shorea almon, Shorea contorta), which differ in wood densities and utilization purposes (Newman et al. 1996). Despite anatomical work on many dipterocarps (Gottwald and Parameswaran 1966), quantitative anatomical analyses indicative for wood functions are still lacking. In the Philippine lowland forests, dry periods occur annually and are particularly severe and long-lasting during El Niño events. These events threaten the establishment of restoration plantations (Slik 2004). To obtain information with respect to potential differences in hydraulic properties and water requirements, we investigated functional wood anatomy in young plantation trees.

## Materials and methods

### Field site and sampling

A plantation with five dipterocarp species (Dipterocarpus kerrii King Damar, H. plagata (Blanco) S. Vidal, Parashorea malaanoman (Blanco) Merr, Shorea almon Foxw and Shorea contorta Vidal) was installed at the western foothills of Mt. Pangasugan, within the forest reserve of the Leyte State University (Leyte, Philippines, 9°55′N to 11°48′N and 124°17′E to 125°18′E). The local climate data from a weather station of the Philippines Atmospheric, Geophysical and Astronomical Service Administration (PAGASA, 7 m.a.s.l.) on the campus of the Leyte State University showed a mean annual temperature of 27.4°C and mean sum of annual precipitation of 2,586 mm (Langenberger 2003). The wettest months are November–January with a mean monthly precipitation of about 290 mm. The driest months are March–May with an average monthly precipitation of 95–133 mm (Langenberger 2003).

Five individual trees of each of the five species were felled after 6 years with the following mean heights: Dipterocarpus kerrii (8.6 ± 0.9 m), H. plagata (9.6 ± 1.1 m), Parashorea malaanoman (7.2 ± 0.8 m), Shorea almon (4.1 ± 0.5 m), Shorea contorta (9.8 ± 1.3 m). Two stem disks (thickness about 3 cm each) were immediately excised from each tree at 1.3 m above ground: one was sealed in plastic and later stored air dried, and the other was preserved in 70% ethanol for anatomical analyses. Wood densities were determined by the Archimedes' principle (Hacke et al. 2000) by transferring samples (half disks without bark or pith) that had been stored sealed in plastic during transportation to a water-containing vessel placed on a balance. The weight change recorded during submersion corresponded to the mass of water displaced. The volume was calculated as: displacement weight/$D$ where $D$ = density of water at 20°C (0.998 kg m$^{-3}$).

### Wood anatomy

Since the wood was very hard to section, especially that of H. plagata, small samples were taken in the mid between pith and cambium from ethanol preserved disks and softened as described by Wagenführ (1966). The pieces were boiled for about 90 min in 30% glycerine. H. plagata wood was boiled for 150 min. Afterwards, the samples were kept in a solution of 30% glycerol, 30% ethanol in water for at least 30 min before sectioning.

For anatomical studies, 30-μm-thick cross sections and 30-μm-thick radial sections were cut with a sledge microtome (Reichert-Jung, Heidelberg, Germany). Sections were stained for 10 min with 0.05% toluidine blue (pH 7.0),

washed with Na-phosphate buffer (0.1 M) (Robinson et al. 1987), and then mounted in 60% glycerol for microscopy. Well stained sections and a micrometer scale were photographed under a light microscope (Axioplan, Zeiss, Oberkochen, Germany) with a digital camera (Nikon CoolPix 990, Nikon, Tokyo, Japan). In cross sections of *D. kerrii* and *H. plagata* but not in those of the other species, parenchyma cells were detected after toluidine blue staining by a dark coloration that distinguished these cell types from fibers or vessels. Since parenchyma cells of all species contained starch grains, new cross sections were stained with IKI (Johansen 1940; Eschrich 1976). By this method, parenchyma cell were localized due to the presence of starch and could be quantified (see below). In addition, the presence of thin-walled cells was also used for identification of parenchyma cells.

Microphotographs of wood were analyzed with the image processing program ImageJ (Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA; http://rsb.info.nih.gov/ij/) for the following parameters: mean diameter of vessel lumina (excluding the cell wall), mean lumen area per vessel, mean lumen area per fiber, fiber cell wall thickness defined as the thickness of the double wall between the lumina of two adjacent fiber cells, and area of ray parenchyma cells. To determine vessel density an area of 3.7431 mm$^2$ was chosen and the number of all vessels in this area was counted. Fiber cross sectional lumen area was determined in an area of 0.0148 mm$^2$ to avoid inclusion of vessels. The cell wall area was determined by ImageJ, and fiber cross sectional area was calculated as follows:

$$\text{Fibre lumen area}(\%) = [(\text{total area} - \text{cell wall area})/ \text{total area}] \times 100$$

The wood anatomical terms are used in accordance with the IAWA Committee (1989).

To determine the lengths of vessel elements and fibers, the same stem segments used for cross sections were chosen. About 1-mm width of wood next to the cambium was discarded to avoid young xylem cells, and the residual wood was cut longitudinally into pieces for chemical maceration in 30% $H_2O_2$ (Merck, Darmstadt, Germany) and acetic acid (Merck, Darmstadt, Germany) mixed 1:1 (after Franklin 1945 in Jansen et al. 1998). After 5 days of maceration at 60°C, it was possible to separate the different wood elements. The macerate was then preserved in 70% ethanol for further analysis. For microscopy, the macerated wood was mounted in 60% glycerol, either unstained or stained with 0.05% toluidine blue (pH 7.0). The short lengths of vessel elements (the short distance between the perforations) were measured after the definition of Chalk and Chattaway (1934).

## Predicted specific hydraulic conductance

Vessels were attributed to diameter classes with a step width of 10 μm. Predicted specific conductance ($K_h$) was determined as $K_h = \Pi \sum r^4 / 8\eta A$, where $A$ = measuring area (mm$^2$) and $\eta$ = viscosity of water at 20°C (Pa s) (Tyree and Zimmermann 2002). Relative contribution (%) of vessel diameter classes to the predicted conductance (PC) was calculated as:

$$\text{PC}(\%) = \frac{[\sum r^4 (\text{number of vessels per diameter class}) \times 100]}{\sum r^4 (\text{number of all vessels})}$$

## Statistical analysis

Statistical analysis was performed with SAS (version 9.13, SAS Institute Inc. 2004, Cary, NC, USA) using analysis of variance (ANOVA), followed by Duncan's multiple range test. Data were indicated as means ± SD. Differences between means were considered significant when the $P$ value of the ANOVA Duncan's multiple range test was less than 0.05. Different letters indicate significant difference. Pearson correlation coefficients were determined with the program Statgraphic Plus (Statistical Graphics Corporation, St. Louis, MO, USA).

# Results

## Wood density and anatomical properties

The five dipterocarp species analyzed in this study differed in wood densities in the following order *H. plagata* > *D. kerrii* > *P. malaanoman* > *S. almon* ≈ *S. contorta* (Table 1). These differences were caused by pronounced structural differences in wood anatomy (Fig. 1). The fibers of *D. kerrii* (Fig. 1a) and *H. plagata* (Fig. 1b) were very thick, almost without any lumen. Quantitative analysis showed that the fiber walls of these species were three- to four-times thicker than those of *P. malaanoman* or those of the two *Shorea* species (Table 1). The vessel densities of *H. plagata* were higher and the vessel diameters were smaller than those of the other species (Table 1). Correlation analysis showed that significant positive relationships existed between wood density and thickness of the fiber walls or vessel density, and a negative relationship with vessel diameter (Table 2).

Significant differences among the five species were found for vessel element lengths and fiber lengths (Table 1). *D. kerrii* had the longest fibers and vessel elements compared with the other species (Table 1). *H. plagata* also displayed long fibers, but relatively short vessel lengths compared with *D. kerrii* (Table 1). Analysis

**Table 1** Wood density and anatomical characteristics of vessels and fiber of five dipterocarps

| Species | Wood density ($g\ cm^{-3}$) | CW thickness ($\mu m$) | V density (number $mm^{-2}$) | V diameter ($\mu m$) | V length ($\mu m$) | F length ($\mu m$) | Predicted $K_h$ ($mm^2\ Pa^{-1}\ s^{-1}$) |
|---|---|---|---|---|---|---|---|
| *D. kerrii* | 0.70 ± 0.06 c | 13.77 ± 2.89 b | 9.9 ± 2.5 a | 157.9 ± 20.2d | 459.0 ± 29.6 c | 778.0 ± 57.1 c | 11.93 ± 3.12 d |
| *H. plagata* | 0.97 ± 0.01 d | 13.94 ± 1.28 b | 19.1 ± 3.7 b | 96.0 ± 8.7a | 378.1 ± 62.2 ab | 692.5 ± 71.4 b | 3.92 ± 1.36 a |
| *P. malaanoman* | 0.45 ± 0.03 b | 4.19 ± 0.51 a | 8.2 ± 1.3 a | 134.7 ± 17.6bc | 338.4 ± 33.5 a | 527.3 ± 31.5 a | 6.88 ± 2.28 bc |
| *S. almon* | 0.38 ± 0.03 a | 2.93 ± 0.20 a | 8.9 ± 1.6 a | 118.8 ± 6.4 c | 369.4 ± 26.7 ab | 465.9 ± 44.2 a | 6.14 ± 1.68 ab |
| *S. contorta* | 0.40 ± 0.02 a | 4.03 ± 0.72 a | 9.0 ± 1.6 a | 151.4 ±10.8 cd | 402.5 ± 48.1 b | 624.8 ± 51.6 b | 9.46 ± 2.23 cd |

In each individual tree the following number of replicates was measured: vessel density $n = 5$, vessel diameter $n = 14$, vessel lengths $n = 25$, fiber length $n = 25$, and cell wall thickness $n = 10$, respectively. The values followed by different letters in the same column indicate significant differences at $P \leq 0.05$. Data indicate means of $n = 5$ per species ($\pm SD$)

*CW* cell wall measured between the lumina of two adjacent fiber cells, *V* vessel, *F* fiber

of Pearson's correlation coefficients for fiber and vessel lengths with tree height revealed a positive relationship for fiber length ($P = 0.001$), but not for vessel element length ($P = 0.1361$). This is understandable, as total vessel length and not the length of the individual element is the functional character. The structure of perforation plates of the vessels may also influence water conduit. All species contained only simple perforation plates (not shown).

A closer inspection of the cross sections revealed the presence of resin canals in all species. The canals were characterized by surrounding epithelial cells, which were not lignified (see example in Fig. 1f). Their contribution to the total cross sectional area of wood was low in all species (<1%); however, their distribution varied. In *D. kerrii,* they were relatively homogeneously interspersed in the secondary xylem, whereas they formed tangential bands in the other species (Rana 2008).

The wood was also composed of axial and ray parenchyma cells (Fig. 1). The axial parenchyma was observed in radial sections by vertically arranged cell files (not shown) but could also be detected in cross sections (Fig. 1c–e). In *H. plagata* wood, the axial parenchyma cells were mainly found surrounding the vessels (Fig. 1b), whereas in other species they formed wing-like structures occasionally connecting groups of vessels (Fig. 1a, c–e).

To analyze the wood structural composition quantitatively, the relative portions of cell wall area, vessel lumen area, fiber lumen area, ray parenchyma area and axial parenchyma area were determined. Canals were neglected because of their low abundance. The fraction of wood area occupied by ray parenchyma cells formed three groups in the five species (Fig. 2): it was high in *D. kerrii*, low in *P. malaanoman* and *S. contorta* and intermediate in *H. plagata* and *S. almon* (Fig. 2). The axial parenchyma fraction of *H. plagata* was significantly lower than in the other species. The area occupied by axial parenchyma showed a negative correlation coefficient with wood density (Fig. 2; Table 2).

In *H. plagata*, the species with the highest wood density, the largest area was occupied by cell walls compared with the other species (Fig. 2). For all species together, the correlation of cell wall area and wood density was highly significant (Table 2).

The secondary xylem of *D. kerrii* had the largest portion of vessel lumen area, which was significantly different from that of the remaining four species (Fig. 2). The high vessel density but low vessel diameter of *H. plagata* resulted in vessel lumen areas similar to those of *P. malaanoman*, *S. almon* and *S. contorta* (Table 1; Fig. 2).

The fiber lumen fractions in *D. kerrii* and *H. plagata* were significantly smaller than those from the other three species (Fig. 2) due to their very thick fiber walls (Table 1; Fig. 1). Fiber lumen area was negatively correlated with wood density (Table 2).

Distribution of vessel diameter classes and predicted conductance

The vessel diameters of 5 dipterocarps were classified into 15 classes of 10-µm steps starting with the diameter class 60–70 µm and the relative contribution of each diameter class to the predicted specific conductance was calculated (Fig. 3). There was considerable variation in the distribution of vessel diameter classes among the five species (Fig. 3). *D. kerrii* and *P. malaanoman* had a large range of vessel diameter classes from 60 to 210 µm and from 60 to 200 µm, respectively (Fig. 3b, d). In contrast, the diameter ranges of *H. plagata*, *S. almon* and *S. contorta* were smaller, each showing only one diameter class 100–110, 120–130 and 170–180 µm, respectively, with maximum contribution to the predicted specific conductivity (Fig. 3a, c, e).

Using these vessel diameter class distributions, the cumulative predicted conductance was calculated for each species and scaled relative to *D. kerrii*, which showed maximum predicted specific conductance (Table 1). The resulting curves indicate important differences in the water conduit systems of the five species. *H. plagata*, the species with the highest wood density, had the lowest predicted
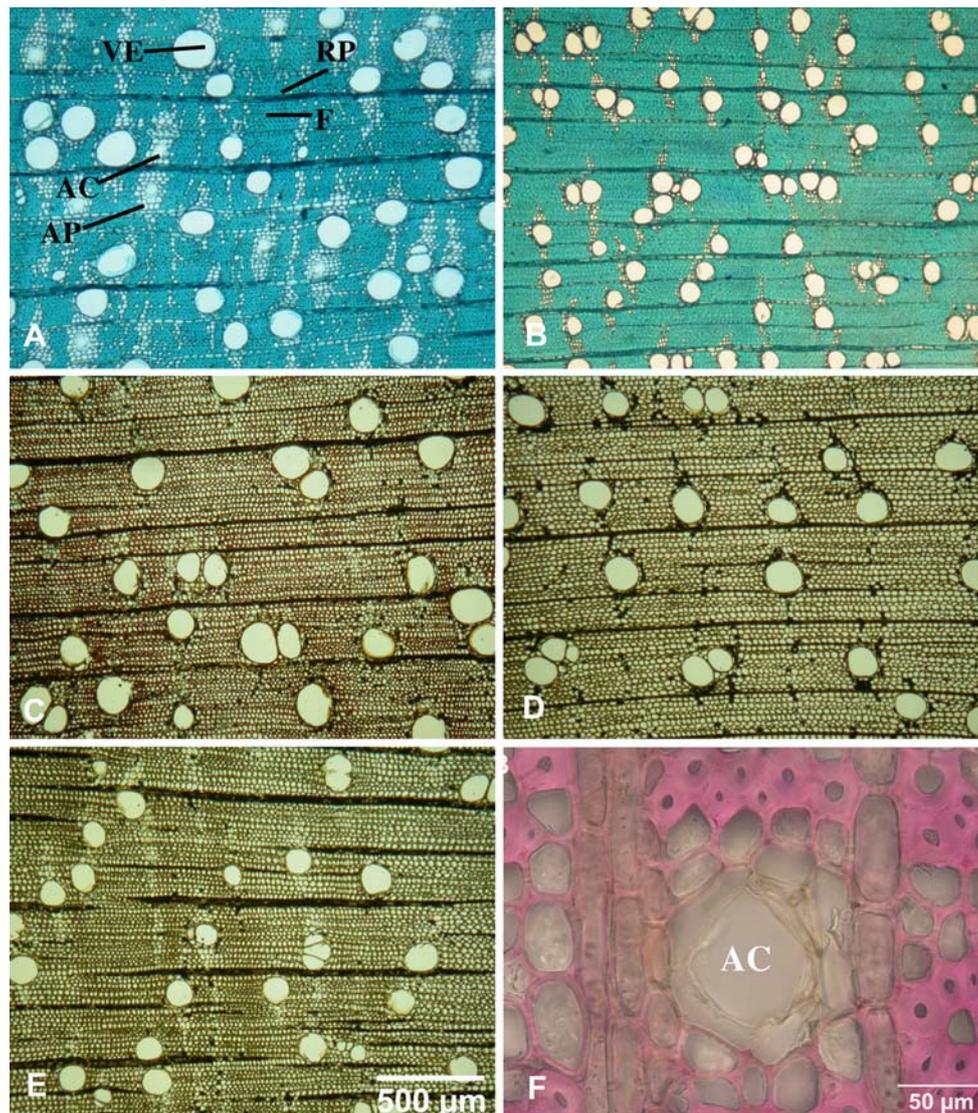
**Fig. 1** Stem cross sections of five dipterocarp species. *D. kerrii* (**a**), *H. plagata* (**b**), *P. malaanoman* (**c**), *S. almon* (**d**) and *S. contorta* (**e**). The sections were stained with toluidine blue (**a**, **b**) or with IKI (**c**, **d**,

**e**). **f** Shows an axial canal in a cross section of *D. kerrii* after lignin staining with phloroglucinol/HCl. *AC* axial canal, *AP* axial parenchyma, *F* fiber, *RP* ray parenchyma, *VE* vessel element

conductance (Fig. 3f). As the vessel diameters were shifted to higher classes in the different species, the predicted conductance increased (Fig. 3f). This relationship was highly significant (Table 2); however, the predicted specific conductance did not correlate with wood density (Table 2) because *D. kerrii*, a species with high and *S. contorta*, a species with low wood density both displayed the highest predicted conductance. The calculated maximum conductance of *S. almon* was similar to that of *P. malaanoman* (Table 1). However, for *S. almon* this value was already obtained at a smaller vessel diameter class than in *P. malaanoman* (Fig. 3f). The reason was that in *S. almon* a large number of small vessels in only two classes contributed already 27 and 24% to the predicted conductance (Fig. 3c), whereas in *P. malaanoman* the contribution

of each vessel class to total predicted conductance was always much smaller (Fig. 3d). Although predicted conductance was high in both *S. contorta* and *D. kerrii*, the latter reached high predicted values mainly by similar contributions of seven vessel classes from 130–200 μm (Fig. 3d). In contrast, in *S. contorta* high predicted conductance was achieved by larger numbers of smaller vessels in only four classes (80–120 μm) (Fig. 3c).

## Discussion

In the present study, we show that ecologically important wood traits of five selected Dipterocarpaceae differed significantly among the species. Our data on wood densities

**Table 2** Pearson correlation coefficient (PCC) between each pair of variables and estimated $P$ value

|  | CW | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
|  | $V$ density | $V$ diameter | Thickness | CW area | VL area | FL area | RP area | AP area | $K_h$ |
| W Density PCC | 0.8220 | −0.4033 | 0.8902 | 0.9762 | 0.2481 | −0.8942 | 0.4815 | −0.7320 | −0.1866 |
| $P$ value | **0.0000** | **0.0456** | **0.0000** | **0.0000** | 0.2318 | **0.0000** | **0.0148** | **0.0000** | 0.3718 |
| V Density PCC |  | −0.6395 | 0.5798 | 0.7443 | 0.0845 | −0.6137 | 0.3372 | −0.7285 | −0.4067 |
| $P$ value |  | **0.0006** | **0.0024** | **0.0000** | 0.6882 | **0.0011** | 0.0993 | **0.0000** | **0.0437** |
| V diameter PCC |  |  | −0.1333 | −0.3338 | 0.3807 | 0.1619 | −0.1119 | 0.4633 | 0.8498 |
| $P$ value |  |  | 0.5253 | 0.1029 | 0.0604 | 0.4394 | 0.5944 | **0.0197** | **0.0000** |
| CW thickness PCC |  |  |  | 0.9205 | 0.3480 | −0.9494 | 0.6774 | −0.4771 | 0.0445 |
| $P$ value |  |  |  | **0.0000** | 0.0882 | **0.0000** | **0.0002** | **0.0159** | 0.8327 |
| CW area PCC |  |  |  |  | 0.2560 | −0.9352 | 0.4990 | −0.6803 | −0.1527 |
| $P$ value |  |  |  |  | 0.2167 | **0.0000** | **0.0111** | **0.0002** | 0.4663 |
| VL area PCC |  |  |  |  |  | −0.4849 | 0.3888 | 0.0347 | 0.6875 |
| $P$ value |  |  |  |  |  | **0.0140** | 0.0547 | 0.8691 | **0.0001** |
| FL area PCC |  |  |  |  |  |  | −0.6900 | 0.4269 | −0.0542 |
| $P$ value |  |  |  |  |  |  | **0.0001** | **0.0333** | 0.7969 |
| RP area PCC |  |  |  |  |  |  |  | −0.0548 | 0.0921 |
| $P$ value |  |  |  |  |  |  |  | 0.7946 | 0.6616 |
| AP area PCC |  |  |  |  |  |  |  |  | 0.2926 |
| $P$ value |  |  |  |  |  |  |  |  | 0.1557 |

Significant $P$ values with $P \leq 0.05$ have been indicated with bold letters. For data see Table 1 and Fig. 2. The variables are vessel ($V$) density and diameter, double fiber cell wall (CW) thickness, the relative portions of cell wall, vessel lumen, fiber ($F$) lumen, ray parenchyma (RP) and axial parenchyma (AP) per cross sectional area and predicted conductance ($K_h$)
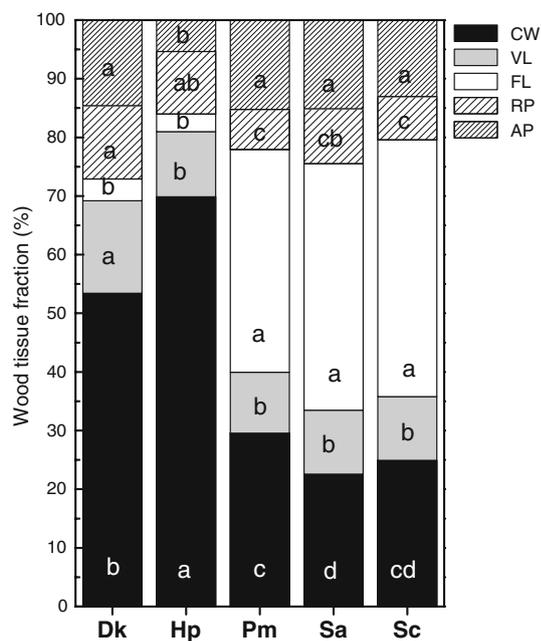


**Fig. 2** Relative portion of cell wall area (*CW*), vessel lumen area (*VL*), fiber lumen area (*FL*), ray parenchyma (*RP*) and axial parenchyma area (*AP*). Different letters in bars indicate significant differences at $P \leq 0.05$

were in the same range as those previously reported for these species. 0.7–1.1 g cm$^{-3}$ for *D. kerrii*, 0.8–1.2 g cm$^{-3}$ for *H. plagata*, 0.5 g cm$^{-3}$ for *P. malaanoman*, and about 0.45 g cm$^{-3}$ for the two *Shorea* species (Newman et al. 1996). Since carbon constitutes about 50% of the woody biomass, it can be concluded that in terms of photosynthetically assimilated carbon, the construction costs of *H. plagata* and *D. kerrii* per unit of wood volume must have been about twice those of *P. malaanoman, S. almon* and *S. contorta.* The high carbon demand of wood formation probably contributes to the slower growth rates of *D. kerrii* and *H. plagata* compared with the other species (Ashton 1982; Newman et al. 1996). Slow-growing species are characterized by thick-walled fibers, whereas the reverse is true for the fast-growing species (Swaine and Whitemore 1988). Similarly, van Gelder et al. (2006) showed that shade-tolerant tropical woody species had dense and tough wood to enhance survival in the understory, whereas pioneer species had low-density wood and low safety margins to enhance growth in gaps.

Resin canels have been detected in all species analyzed. In general, resins act as deterrent or have fungicidal properties (Richardson et al. 2005; Onuorah 2000), and are therefore important in shaping interactions with higher trophic levels.

**Fig. 3** Relative contribution of vessel diameter classes (step width 10 μm) to predicted conductance of the xylem of **a** *Hopea plagata* (*Hp*), **b** *Dipterocarpus kerrii* (*Dk*), **c** *Shorea almon* (*Sa*), **d** *Parashorea malaanoman* (*Pm*), **e** *Shorea contorta* (*Sc*), **f** cumulative predicted conductance. For species comparison, the calculated predicted conductance of *D. kerrii* (30.44 × 10$^{-3}$ mm$^{-2}$) was set as 100% and those of the other species were calculated relative to this maximum using the data from Table 1. *Bars* indicate means (±SD)
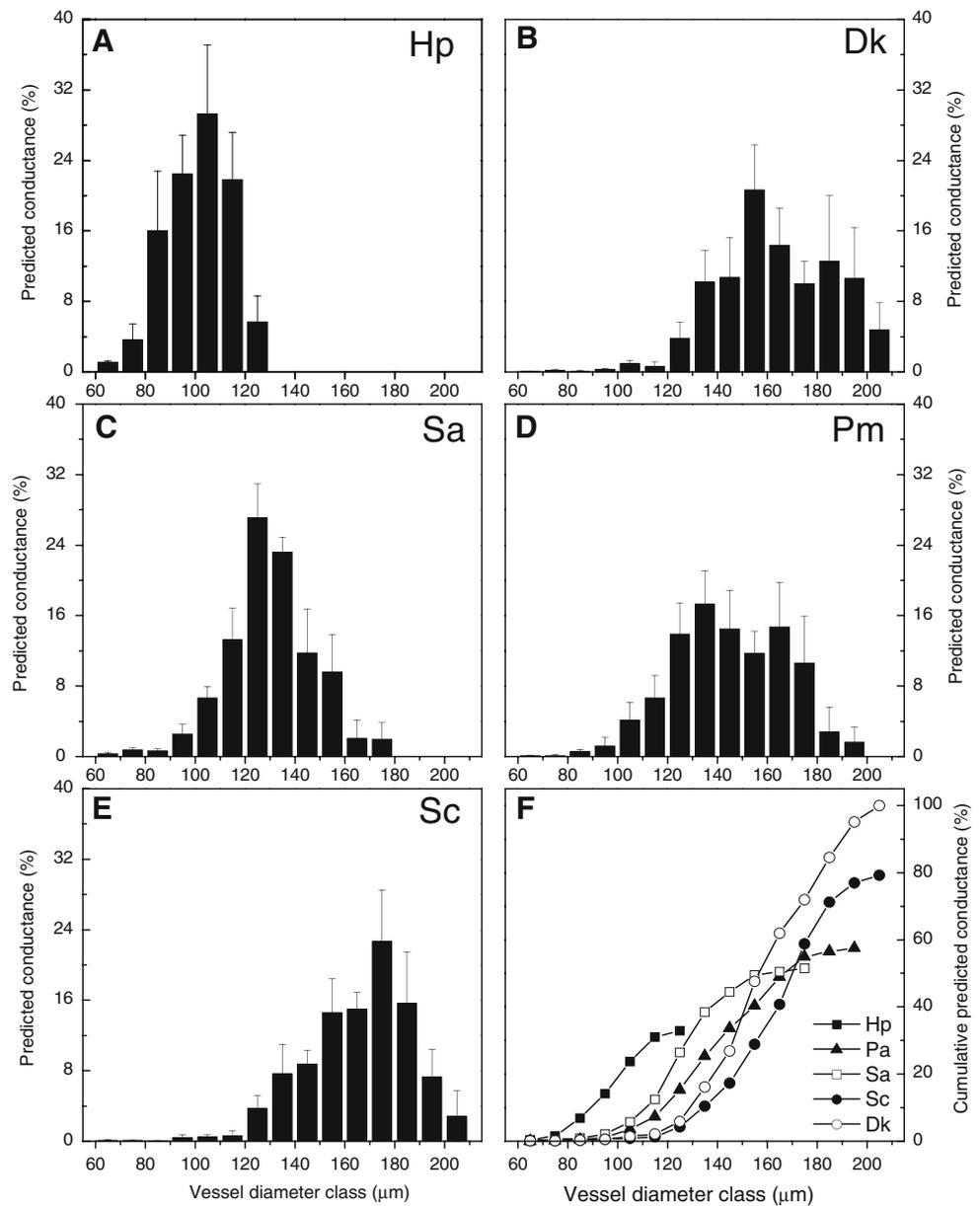


In accordance with other studies including tropical and temperate trees (Tyree et al. 1998; Hacke et al. 2000; Hacke and Sperry 2001; Swenson and Enquist 2007), wood densities were strongly correlated with occupation of the cross sectional wood area with cell walls or cell wall thickness and negatively with fiber lumen area (Tables 1, 2). A novel observation of our study was that wood densities also showed correlations with cross sectional area of parenchyma cells. Ray parenchyma which are responsible for radial nutrient transport are usually strongly lignified, may be the reason for the unexpected positive correlation coefficient between wood densities and ray cell area (Table 2). In contrast axial parenchyma, which function mainly as storage reservoir, were very thin-walled (Fig. 1).

Their cross sectional area showed a negative correlation with wood density (Table. 2). It is likely that this may decrease the mechanical strength of the wood.

Vessel diameters determine the potential hydraulic conductivity, but do not necessarily influence wood density or cavitation susceptibility (Hacke and Sperry 2001). In our study, vessel diameter was negatively correlated with wood density. Negative correlations between conductivity and wood density have previously been shown in other fast-growing light-demanding as well as slow-growing shade-tolerant tropical trees species (Christensen-Dalsgaard et al. 2007a). The light requirements of the species of our study and their influence on growth and wood properties are not known. In general, growth of Dipterocarps displays high

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