AXIAL AND RADIAL VARIATIONS IN XYLEM ANATOMY OF ANGIOSPERM AND CONIFER TREES IN YUNNAN, CHINA

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SUMMARY

The model of West, Brown and Enquist (WBE model) showed that lumen hydraulic resistance in trees can be independent of path length, provided that vascular conduits widen basipetally and sufficiently, and the number of functional conduits is constant from twigs to trunk. To test the anatomical realism of this model, we investigated axial and radial changes in xylem characteristics of six angiosperm tree species (fourteen trees, 15–25 m tall) and three coniferous tree species (seven trees, 16–45 m) in Yunnan, China. Conduit lumen diameter increased linearly with distance from the top of the bole to its base in six trees. In all but one of the fifteen remaining trees, lumen diameter increased from the top to near the base of the crown but remained constant or increased more slowly below the crown. Similar, but inverse patterns were found for axial variation in vessel density of the angiosperms, which indicated that the number of conducting vessels increases from trunk to twig as they become narrower. Vessel diameters increased almost linearly with cambial age for the first 20 to 40 years, and then stabilized or increased more slowly in eight trees of Fagaceae. Axial trends in conduit lumen diameter and number were consistent with only partial buffering of hydraulic resistance from path-length effects, generally confined to the crown region. Neither conduit taper nor number was consistent with the WBE model.

Key words: Chinese trees, hydraulic architecture, tapering, WBE model, xylem anatomy.

INTRODUCTION

Water transport through the xylem is essential for replacing water loss during transpiration, delivering nutrients, and enabling continued photosynthesis (Kramer & Boyer 1995). Xylem anatomical characteristics have important effects on long-distance transport in vascular plants, and have shaped the evolution of many attributes of plant form and function. An optimal water transport system in plants minimizes the investment of carbon in the vascular system while maximizing hydraulic conductance, which is

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proportional to CO_2 uptake (Hubbard *et al.* 2001). This optimum network has wide conduits at the base that feed an increasing number of narrower conduits distally, as prescribed by Murray's law (Murray 1926; McCulloh *et al.* 2003).

The model of West, Brown and Enquist (West *et al.* 1999; Enquist 2003; hereafter WBE model) showed that if conduits widen basipetally and sufficiently, then the lumen resistance of a tube (representing a linear series of vessels) from the base of the trunk to a petiole becomes independent of total tube length. Becker *et al.* (2003) noted that this independence of hydraulic resistance from path-length effects does not depend theoretically on branching architecture or cross-sectional conductive area of the stem. However, the effect of taper does depend on how the number of functional conduits changes from trunk to twig (McCulloh & Sperry 2005). In particular, if there are a greater number of parallel pipes in the twig ranks relative to the trunk, this would in-crease conduit taper needed for minimizing the length-dependent decline in hydraulic conductance. This pattern of taper combined with an increase in conduit number has nevertheless been shown to increase the hydraulic efficiency of the network (McCulloh *et al.* 2003). Increasing efficiency in this way may be more important adaptively than buffering any effects of path length on conductance.

Conduit diameter increases basipetally in both trunks and branches, usually being greatest in the root (Tyree & Ewers 1991; McElrone *et al.* 2004). Longitudinal vari-ation of mean conduit diameter showed a degree of tapering in agreement with WBE predictions in actively growing trees (Anfodillo *et al.* 2006; Weitz *et al.* 2006); however, conduit tapering declined as trees approached their maximum height (Anfodillo *et al.* 2006; Coomes *et al.* 2007; Petit *et al.* 2008). A meta-analysis of available data indicated that the degree of conduit tapering generally declines with distance from the tree apex, and also declines with the increasing of tree size (Mencuccini *et al.* 2007). Reports on radial variation again indicate that conduit lumen diameter eventually stabilizes with distance from the stem center (Spicer & Gartner 2001; references cited in Becker *et al.* 2003). These observations raise doubts about the continuous tapering of conduit diam-eter, which is one of the critical assumptions of the WBE model. Furthermore, none of these studies considered the equally important WBE assumption of an equal number of functional conduits per growth increment from trunk to twig.

To further characterize spatial trends in conduit diameter and number in a wider range of species, we measured axial and radial variation in xylem anatomy of six angiosperm and three conifer tree species in southwestern China.

MATERIALS AND METHODS

Plant material and sampling

Fourteen felled angiosperm trees (15–25 m tall) of *Castanopsis wattii* (King) A. Camus, *Lithocarpus chintungensis* Hsu & Qian, *Lithocarpus xylocarpus* Markgr., *Cyclobalanopsis (Quercus) stewardiana* (A. Camus) Y. C. Hsu & H. W. Jen (Fagaceae, with ring-porous wood), *Schima noronhae* Reinw. *ex* Blume, and *Hartia sinensis* Dunn (Theaceae, with diffuse-porous wood) were sampled from a montane moist evergreen forest in the Ailao mountains (24° 32' N, 101° 01' E, elevation 2400 m), Yunnan, China.

Seven newly fallen trees (16–45 m tall) of *Picea brachytyla* (Franch.) E. Pritz., *Larix potaninii* Batalin, and *Abies georgei* Orr. with intact sapwood were sampled from a subalpine coniferous forest in the Bita Lake Natural Reserve (27° 49' N, 99° 59' E, elevation 3590 m) in the same province. For each tree, two 3- to 5-cm-deep sapwood cores were taken from the same side of the stem at measured intervals of 1 to 2 m along the trunk to study axial variation in xylem anatomy. Sampling was continued near the actual top (0–1 m below) of the main trunk or vertical branch for some angiosperms whose apical dominance was not obvious. The distance of each sampling point from the tree base was carefully measured using a tape-measure. Cross-sectional discs were cut from the base, middle and top of eight trees of Fagaceae to study radial variation in xylem anatomy. Wood samples were softened by soaking in a solution of glycerin and ethanol (1 : 1 by volume) for three to four months (angiosperms) or one month (conifers).

Xylem anatomical analyses

One transverse section (50–80 µm thick) was made with a sliding microtome from each wood sample from either stem cores or discs, and then stained with safranin and embedded in neutral balsam. Lumen diameters and density of conduits were measured with the aid of a microscope and an ocular micrometer calibrated with a stage micrometer. For the core samples of angiosperms, two or three image fields were chosen in the earlywood of the outermost two to three rings. For disc samples, three image fields were chosen in the earlywood at intervals of five to eight growth rings. The vessels of *Schima noronhae* and *Hartia sinensis* were almost circular, so the diameters of 90–120 vessels in total from six image fields were measured at 200× magnification. The vessels of the remaining angiosperms were approximately elliptical in shape, so the major and minor axes were measured at 100× magnification for 40–100 vessels in total from four image fields. For coniferous core samples, the two widest radial files of tracheids in the earlywood of the outermost one to three rings were selected in each of five image fields and the diameters of the first five tracheids in each file were measured. The tracheids were almost rectangular, so the two sides were measured at 400× magnification for 50 tracheids in total from five image fields.

Based on the equations for flow in noncircular conduits, ellipse and rectangles were converted to equivalent-flow circles. For an ellipse, the effective hydraulic diameter equals (White 1991):

$$d_h = \left(\frac{32\,(ab)^3}{(a^2 + b^2)} \right)^{\frac{1}{4}},$$ (1)

where a and b are the major and minor axis dimensions, respectively.

For rectangle, the effective hydraulic diameter equals (Lewis 1992):

$$d_h = \frac{2\,ab}{a + b},$$ (2)

where a and b are the full lengths of the two sides.

Hydraulically weighted average conduit diameters were calculated using the formula (Tyree & Zimmermann 2002):

$$\bar{d} = \left(\sum \frac{d_h^4}{n} \right)^{\frac{1}{4}}, \tag{3}$$

where diameters are summed over all conduits at a specified axial or radial position.

Statistical analyses

Visual inspection of graphical plots (conduit diameter/density *vs.* distance from the tree base) indicated that xylem characteristics varied axially in most trees, often with two apparently linear segments of different slope. To objectively determine whether a segmented regression provided a better fit than simple linear regression, data were fit by the model (Bacon & Watts 1971):

$$Y = a_0 + b_1(X - X_0) + b_2(X - X_0) * \tanh(X - X_0), \tag{4}$$

where Y is the dependent variable, the hydraulically weighted mean lumen diameter or vessel density, X is the independent variable, the distance from the tree base, X_0 is the estimated transition zone or breakpoint, and b_2 is the change in slope of the two quasi–linear segments. If b_2 was significant (p = 0.05), then a segmented regression provided a better fit than a simple linear regression (D.G. Watts, Queen's Univ., personal communication). Simple, linear least-square regressions were then fitted to the segments above and below the estimated transition zone X_0 to determine the significance of their respective slopes. If b_2 was not significant, then a simple linear regression was fit to all the data for the tree, and its significance was determined.

To compare conduit tapering of the studied trees with theoretical predictions of the WBE model (West *et al*. 1999), the conduit tapering coefficient (ā in the WBE model) was calculated according to the method described by Anfodillo *et al*. (2006). Least squares regression was used to determine empirically the scaling exponents and allometric constant for the $\log_{10}$-transformed data (hydraulically weighted lumen diameter *vs* distance from the tree top). The tapering coefficient (ā) was obtained according to equation 9b in Anfodillo *et al*. (2006).

RESULTS

General xylem characteristics

There were distinct, annual growth rings in the nine tree species. The four species of Fagaceae had ring-porous wood, their earlywood vessel diameters were large with maximum diameter exceeding 240 μm, the earlywood vessel density was 2–8 mm^{-2} (Fig. 1, 3), and the lumens accounted for 2–14% of the sapwood area (data not shown). Both species of the Theaceae (*Schima noronhae* and *Hartia sinensis*) had diffuse-porous wood. Their vessel diameters ranged from 30 to 75 μm with no distinct size classes (Fig. 1), the vessel density was 60–160 mm^{-2} (Fig. 3), and the proportion of vessel lumen area in the sapwood exceeded 20% (data not shown). The tracheid lumen diameters of the three coniferous species were 20–45 μm (Fig. 2).

Axial and radial xylem characteristics

Four of the fourteen sampled angiosperm trees and two of the seven conifer trees exhibited a uniform linear increase of lumen diameter with distance from the top to
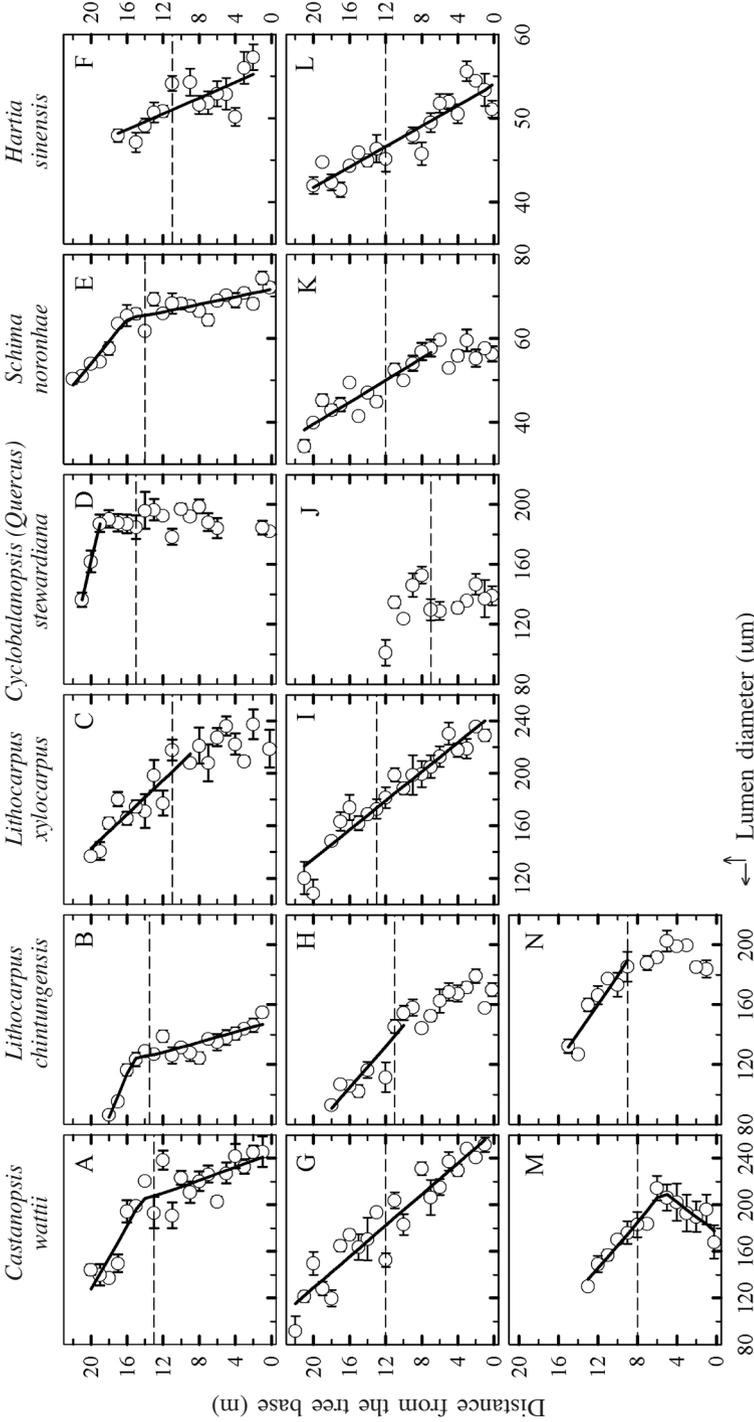
Figure 1. Variation in hydraulically weighted mean lumen diameter in the outermost 2–3 growth rings along the main stem of six angiosperm tree species. The full names of the species are given in the text. Each panel represents one tree, and the dashed line indicates the base of the live crown. Data are means ± SE, n = 4–6 image fields. Error bars covered by data points are not shown. Based on segmented or simple regression analyses and significance tests as described in Materials and Methods, a solid line indicates that the dependent variable (X-axis) varied significantly with height over the corresponding region of the data. A solid line with a uniform slope over the entire data set indicates that a segmented regression did not provide a better fit than a simple linear regression.
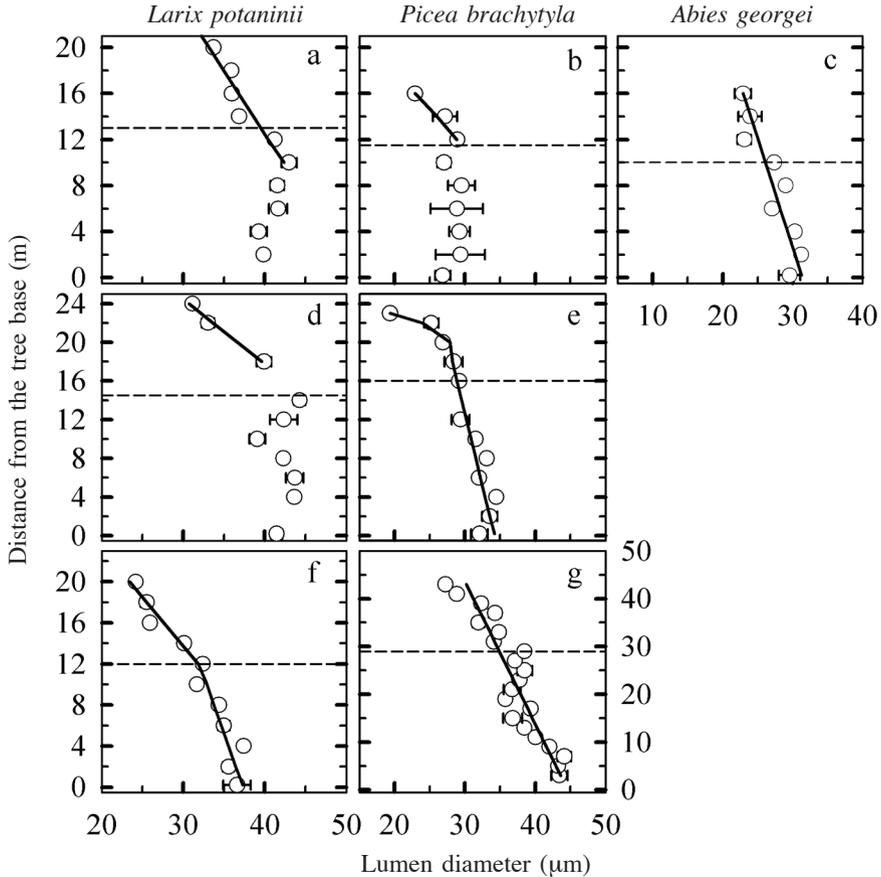
Figure 2. Variations in hydraulically weighted mean lumen diameter in the outermost 2–3 growth rings along the main stem of three conifer tree species. Data are means ± SE; n = 5 image fields. Regression analyses and other conventions follow those in Figure 1.

the base of the trunk (Fig. 1 F, G, I, L; Fig. 2 c, g). Lumen diameter did not vary axially in one angiosperm (Fig. 1 J). In the remaining fourteen trees, conduit lumen diameter increased basipetally from the top of the crown and then stabilized near the base of the crown (Fig. 1 C, D, H, K, N; Fig. 2 a, b, d), or increased more slowly downwards (Fig. 1 A, B, E; Fig. 2 e, f), or decreased (Fig. 1 M). Thus, conduit taper (*sensu* West *et al*. 1999) diminished basipetally, and usually exhibited intra-specific variation in this pattern. For fourteen trees in which a segmented regression provided a better fit than simple linear regression, the transition zone occurred near the base of the live crown (Y = 2.59, X = 0.93, R^2 = 0.82, P < 0.001; where X and Y are the distances of the crown base and the transition zone relative to total tree height, respectively).

Vessel density usually increased with height on the trunk, especially inside the crown (Fig. 3). Assuming that the collective cross-sectional area of the branches is approxi-
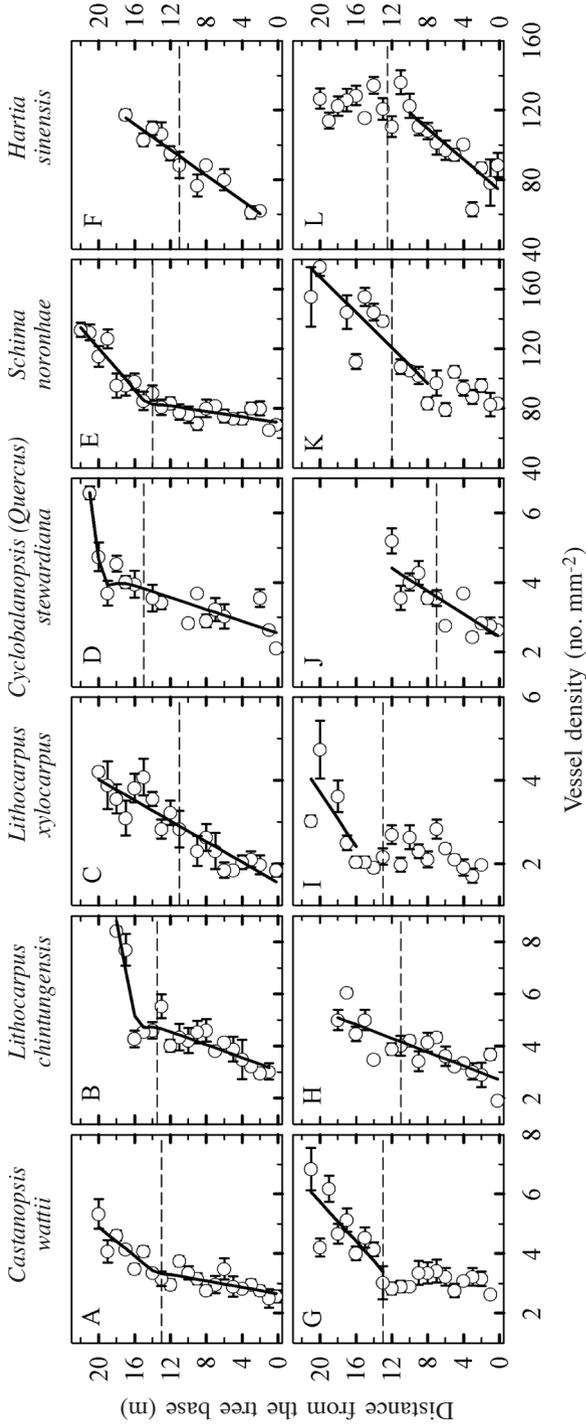
Figure 3. Variations in vessel density (no. mm^{-2}) along the main stem in the six angiosperm tree species. Data are mean ± SE, n = 4–6 image fields. Regression analyses and other conventions follow those in Figure 1.
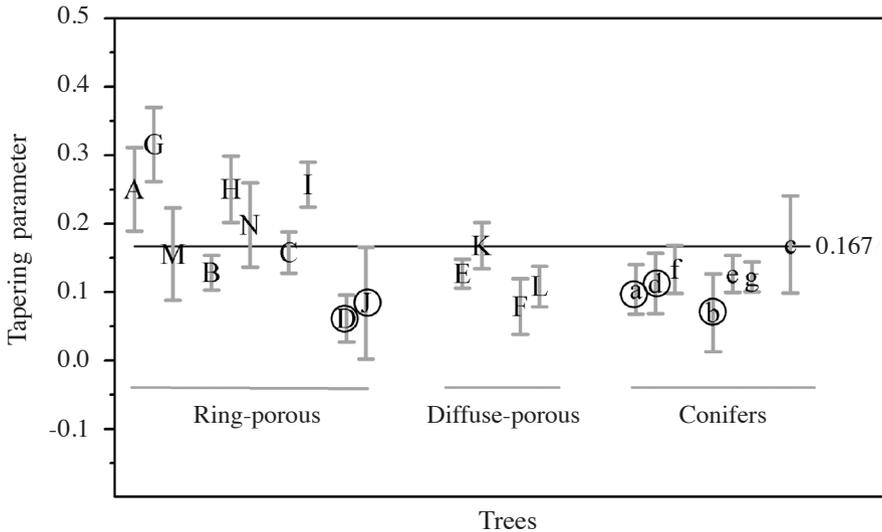
Figure 4. The tapering coefficient (ā) and its 95% confidence intervals (gray bars) for three anatomical groups, namely, ring-porous (A, G, M, B, H, N, C, I, D, J), diffuse-porous (E, K, F, L) and conifers (a–f). The trees match the coding in Figure 1 (upper case) and Figure 2 (lower case). The predicted value of the conduit tapering coefficient to ensure independence of hydraulic conductance from path-length effects (0.167 in WBE model, solid line) is shown. The regressions on log10-transformed data were not significant (p = 0.05) for the circled trees.

mately conserved moving from trunk to twigs, consistent with the Da Vinci area-preserving rule (Horn 2000); the increase in vessel density indicates a strong increase in the number of functional conduits distally, in association with their narrower diameter. This pattern is diametrically opposite the one assumed by the WBE model, of an equal number of conduits per growth ring from trunk to twig.

Our data showed that the tapering coefficient (ā) equaled or exceeded the value (0.167) predicted by the WBE model to eliminate path-length effects on hydraulic conductance in most of the ring-porous trees, but not in diffuse-porous and coniferous trees (Fig. 4). It should be noted that the regression method of Anfodillo *et al*. (2006), and as followed here, failed to take account of the segmented behavior of conduit taper.

Lumen diameter increased with cambial age for the first 20–40 years in the four Fagaceae species, and then leveled off or increased more slowly. There was generally no difference in lumen diameter for growth rings originating from the same aged cambium at different heights above the ground (Fig. 5).

DISCUSSION

Our measurements (Fig. 1 & 2) showed that the lumen diameter of xylem conduits decreased distally in agreement with previous reports (Tyree & Ewers 1991; James *et al*. 2003). This pattern can be interpreted as the trade-off between hydraulic efficiency and vulnerability to cavitation (Tyree *et al*. 1994; Domec & Gartner 2002). Narrow
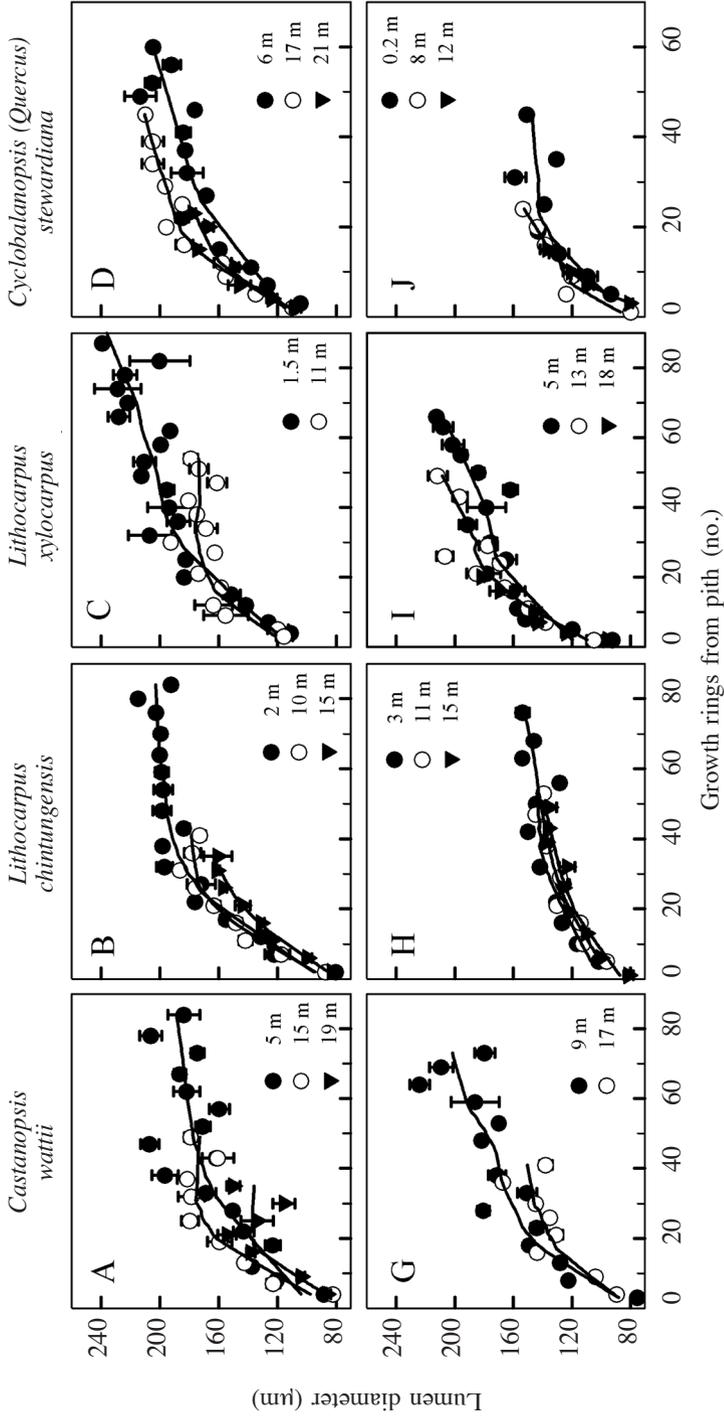
Figure 5. Variations in hydraulically weighted mean lumen diameter with cambial age (number of annual growth rings from pith) at different heights (see legends) above ground in four Fagaceae. Each panel represents one tree, and the tree codes match those in Figure 1. Data are means ± SE, n = 3 image fields. The curves were fitted by lowess (locally weighted, piecewise, linear regression) with smoothing factor f = 0.6–0.9, using SigmaPlot (v. 8.0).

conduits are less vulnerable to freezing-induced cavitation (Hacke & Sperry 2001), and conduit size parallels the vertical trend in xylem water potential which decrease with tree height due to gravity (*e.g.* Koch *et al*. 2004). Meanwhile, conduit taper plays a complementary role in controlling conductivity, and thus minimizing differences in conductance to leaves at different distances from the base of the trunk (Enquist 2003). Low conductivities at the downstream end result in similar values of total root-leaf conductance despite different path length (Zimmermann 1978; McCulloh & Sperry 2005).

For a constant conduit number, the WBE model predicts the minimum value of conduit taper to ensure the complete independence of flow resistance from path-length effects, but partial buffering of path-length effects can occur with even moderate taper (West *et al*. 1999; Becker *et al*. 2000; Zaehle 2005). Although axial trends in lumen diameter within the crowns of angiosperm and conifer trees were consistent with such buffering, conduit lumen diameter remained relatively constant or increased quite slowly below the live crown in ten of the fourteen angiosperm trees and five of the seven conifer trees (Fig. 1 & 2).

There was a marked increase (1.5–3.2 times) in the vessel density (the number of vessels per wood area) moving from trunk to twig in the eight angiosperms (Fig. 3). To maintain the mechanical stability, trees tend to conserve the cross-sectional area of wood with branching level to avoid being top-heavy, at least within their crowns (Horn 2000; Enquist 2003). If the vessel numbers within each rank were constant, the total cross-sectional wood area would have to decline 1.5–3.2 times from trunk base to the tree apex accordingly, which is inconsistent with the observation of area-preserving branching (*e.g.* McMahon & Kronauer 1976; Song *et al*. 2005). Da Vinci's area-preserving rule implies that the increase of vessel density distally results in an increase of conduit number from trunk to twig, as they became narrower (Fig. 3). The observed absence of conduit taper below the crown in many trees, and the increase in conduit number distally, does not support the model of West *et al*. (1999).

The number of conduits is as important as their taper for influencing path resistance and the conductance per investment in the vascular system (McCulloh *et al*. 2003; Sperry *et al*. 2008). Because most conduits are much shorter than the plant, the number of conduits running in parallel is not necessarily constant with height. By applying the Murray's law to plants, McCulloh *et al*. (2003, 2004) reported that maximum conducting efficiency was achieved with an increase of conduit number and decrease of conduit size in parallel along the branch rank distally. These patterns were confirmed for various free-standing trees, and especially for vines and compound leaves whose xylem conduits are not significantly involved in structural support (McCulloh *et al*. 2004).

The absence or reduction of conduit taper below the crown may be due to biomechanical constraints. The optimal area profiles for hydraulics *vs* mechanics of free-standing trees are in direct conflict (McCulloh *et al*. 2004). The increase in vessel density distally (*i.e.*, increasing proportion of fibers in the proximal direction) provides greater mechanical strength to resist the greater load in the lower stem (Wagner *et al*. 1998). The strong negative relationship between vessel diameter and density (R = -0.67 and -0.81, p < 0.001, for ring-porous and diffuse-porous respectively) confirmed this trade-off

in our study species. By concentrating conduit taper in the crown, trees may maintain mechanical stability while lessening conflict for water supply within the crown, where equalization of gas exchange potential is important.

The empirical determination of conduit tapering among the three anatomical groups indicated that the observed degree of tapering in diffuse-porous and coniferous trees was much smaller than that of the WBE prediction (Fig. 4). Compared with the ring-porous wood, the xylem conduits in diffuse-porous and coniferous wood play a significant role in structural support, as well as fluid transport, and their wall thickness per unit of conduit diameter must be larger for a given vulnerability to cavitation, therefore leading to larger carbon costs (Sperry *et al*. 2006). However, their hydraulic efficiency can be maximized by packing large numbers of small conduits per unit of volume (McCulloh & Sperry 2005; Mencuccini *et al*. 2007). Also, as remarked above, distally increasing conduit number will increase the conduit taper required to minimize path-length effects at the whole-tree level (McCulloh & Sperry 2005). Because of the limitations in conduit dimension of tracheid-bearing trees, tracheid- and vessel-bearing trees may differ importantly in the extent to which they can compensate for path-length effects on hydraulic resistance through conduit taper (Becker *et al*. 2003).

Vessel diameter increased two to three times with cambial age for the first 20 to 40 years, and then stabilized or increased more slowly in the four Fagaceae (Fig. 5). The radial changes observed in vessel size may reflect the processes of cambial maturation, which results in ever larger vessels until relatively uniform wood, so called "mature wood", is produced (Di Lucca 1989; Bao *et al*. 2001; Spicer & Gartner 2001). On the other hand, the juvenile-mature wood transition in the radial profile (Fig. 5) indirectly reflects the patterns observed in axial conduit taper, which is mostly confined to that portion of the bole within the live crown (Fig. 1 & 2). Some studies have found that the juvenile-mature transition zone was associated with the location of the live crown, *i.e*., trees produce juvenile wood within the crown and mature wood below that level (Larson *et al*. 2001; Gartner *et al*. 2005). An abrupt change from juvenile to mature wood was observed after pruning the lower crown branches (Di Lucca 1989).

CONCLUSIONS

Although theoretical models have been proposed to explain the structure and allometry of plant vascular systems (West *et al*. 1999; McCulloh *et al*. 2003), analysis of the spatial variation in xylem anatomy is surprisingly uncommon (Zimmermann 1978; James *et al*. 2003; Zaehle 2005; Anfodillo *et al*. 2006; Weitz *et al*. 2006; Coomes *et al*. 2007). Using data from multiple individuals spanning a wide range of species, including ring-porous and diffuse-porous angiosperms and tracheid-bearing gymnosperms, we tested two critical assumptions (constant conduit taper and number) of the WBE model (West *et al*. 1999). The bi-phasic conduit tapering and distally increasing conduit densities contradicted key assumptions of the WBE model (West *et al*. 1999). The relative lower potential of conduit tapering in the diffuse-porous trees and conifers indicated that other factors, such as biomechanical support, may affect the hydraulic design in those trees.

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