Tapering of xylem conduits and hydraulic limitations in sycamore (Acer pseudoplatanus) trees

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Summary

- Vertical conduit tapering is proposed as an effective mechanism to almost eliminate the increase in hydraulic resistance with increased height. Despite this potential role, very little is known about its changes during ontogeny.
- Here, conduit tapering and stem morphology of young/small and old/tall individuals of Acer pseudoplatanus in the field, as well as 3-yr-old grafted trees from both age classes, were analysed. The distribution of hydraulic resistance along stems was also determined in a subsample of trees.
- Substantial conduit tapering was found in small trees (field-grown and grafted from both age classes), whereas values were lower in tall trees, indicating that tapering was a size-related, not an age-related process. Apical conduit diameters were larger in tall trees and were inversely correlated with the degree of tapering. Hydraulic resistance increased less than linearly with distance from the apex. Its scaling against distance was indistinguishable from that predicted from anatomical measurements.
- Conduit tapering was an effective but partial mechanism of compensation for the increase in hydraulic resistance with tree height. Size-related changes in tapering and in apical conduit diameters may be explained by the combined need to reduce the build-up of hydraulic resistance while minimizing the carbon costs of building vessel walls.

Key words: conduit tapering, hydraulic limitation hypothesis, hydraulic resistance, plant allometry, WBE model, wood anatomy.


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Introduction

The life history of trees is characterized by the enormous changes in body mass occurring during ontogeny. For example, the body mass of a giant sequoia may increase by 12 orders of magnitude from seedling to large tree. The structural and physiological modifications that allow trees to achieve these dimensions while maintaining metabolism are currently the subject of research (Mencuccini, 2002; Midgley, 2003; Niklas & Cobb, 2006). Trees typically display different rates of growth in height across ontogeny: the stem elongates rapidly during the first years or decades and thereafter its growth rate declines progressively (Sachs, 1965; Lappi, 1997). Recently, the old debate on whether the decline of growth rates of individual trees and that of forest net primary productivity is age-related or size-related has received renewed attention (Yoder et al., 1994; Gower et al., 1996; Mencuccini & Grace, 1996; Bond, 2000; Binkley et al., 2002; Barnard & Ryan, 2003; Phillips et al., 2003; Ryan et al., 2006; Martínez-Vilalta et al., in press). While Day et al. (2001) suggested that reduced growth in ageing red spruce was primarily age-related, more recent papers (Matsuzaki et al., 2005; Mencuccini et al., 2005, 2007; Bond et al., 2007) have instead presented evidence in favour of size-mediated effects. For instance, Mencuccini et al. (2005) showed that relative above-ground mass growth rates, net assimilation rates and several measures of leaf physiology and biochemistry declined in the field in trees of increased age and size, while the same parameters did not change significantly when measured across grafted
seedlings of varying age but similar size. Because the grafts were obtained by grafting apical shoots taken from the same donor trees in the field onto a common rootstock, they putatively maintained the same meristematic age as the donor trees.

According to the hydraulic limitation hypothesis (Ryan & Yoder, 1997; McDowell et al., 2002b), as the hydraulic resistance of a tube is proportional to its length (Hagen-Poiseuille formula; Tyree & Ewers, 1991), whole-plant hydraulic conductance should decrease as trees grow taller, because of the increased path length of water flow from roots to leaves. This would either result in lower water potentials, which would cause water stress conditions, or elicit stomatal closure to prevent water stress. In either case, increased path length and resistance would lead to a reduced growth rate. Koch et al. (2004) suggested that the maximum height of 120–130 m achieved by coastal redwoods (Sequoia sempervirens) is likely to be determined by the physical constraint of lifting water from roots to the top of the crown. Most tree species do not reach those heights, yet it is possible that hydraulic constraints play an important role in limiting their growth in height (Ryan & Waring, 1992; Mencuccini & Grace, 1996; Ryan et al., 1997).

Nevertheless, mechanisms of compensation are known to exist that help minimize the build-up of resistance with size, such as increasing allocation to fine roots (Magnani et al., 2000) decreasing leaf area/sapwood area ratios (McDowell et al., 2002a), or increasing sapwood permeability with age or size (Pothier et al., 1989).

According to Zimmermann’s segmentation hypothesis (Zimmermann, 1978, 1983), to preserve the whole organism from a hydraulic collapse, xylem conduits decrease in size from the stem base to the apices and are narrower at nodal zones in order to confine any embolism to the peripheral organs, which account for the most of the total hydraulic resistance and are subjected to the lowest xylem tension in the plant.

Recently, the architecture of the water transport system received renewed attention after the introduction of a theoretical model clarifying potential significance of the increase of conduit size from the apex to the stem base (West et al., 1999: West, Brown and Enquist or WBE model). According to the WBE model, evolution forced all plants to adopt a fractal-like body architecture to minimize the limitations imposed on water transport and to maximize their exchange surfaces with the external environment (Enquist, 2003). The ideal WBE plant is composed of successive ideal branching levels and, as a consequence of its fractal-like geometry, its anatomical characteristics, such as conduit diameter (\(d\)), branch diameter (\(D\)) and branch/ conduit length (\(L\)), scale among successive levels, \(k\) (proximal) and \(k + 1\) (distal) as:

\[
\frac{d_{k+1}}{d_k} = n^{-3/2} \quad \text{Eqn 1}
\]

\[
\frac{D_{k+1}}{D_k} = n^{-3/2} \quad \text{Eqn 2}
\]

\[
\frac{L_{k+1}}{L_k} = n^{-1/3} \quad \text{Eqn 3}
\]

where \(a\), \(a\) and \(n\) are specific parameters independent of level \(k\) (see Table 1 for principal abbreviations). By simply assuming that (1) the network is volume-filling (West et al., 1997); (2) the terminal branching unit is size-invariant; (3) the biomechanical constraints are uniform; and (4) the energy dissipated in fluid is minimized, the model predicts many general allometric scaling equations, which can be applied to all plants. Particularly, as the total hydraulic resistance (\(Z\)) is:

\[
Z = \sum_{k=0}^{N} Z_k = \left[ \frac{1 - \left(\frac{(n^{-1/3} - 1) \cdot L / l_0}{n^{(1/3) - 2a}}\right)^{1/(1-2a)}}{1 - n^{(1/3) - 2a}} \right] Z_0
\]

\[
Z = \sum_{k=0}^{N} Z_k = \left[ \frac{1 - \left(\frac{(n^{-1/3} - 1) \cdot L / l_0}{n^{(1/3) - 2a}}\right)^{1/(1-2a)}}{1 - n^{(1/3) - 2a}} \right] Z_0
\]

\[
L = \frac{l_0}{1 - n^{-1/3}} \quad \text{Eqn 5}
\]

where \(L\) is total length of the connected \(k\) levels and \(l_0\) are the length and hydraulic resistance (calculated using the Hagen-Poiseuille formula; Tyree & Ewers, 1991) of the terminal unit tube, it can be demonstrated mathematically that, for \(L >> l_0\) the hydraulic resistance critically depends on \(a\) and becomes a nearly constant value independent of path length with \(a\) equal to or higher than 1/6 (Becker et al., 2000). Moreover, approximating:

\[
L = \frac{l_0}{1 - n^{-1/3}} \quad \text{Eqn 5}
\]

where \(l_0\) is the length of the basal level, the WBE model predicts:

\[
d \propto L^{3a/2} \quad \text{Eqn 6}
\]

\[
L \propto D^{2/3} \quad \text{Eqn 7}
\]
The scaling exponents of equations 6 and 7 are known to be rather variable. Anfodillo et al. (2006) demonstrated that the estimates for these scaling exponents depended critically on tree height, while Niklas (1995) reported the exponent for equation 7 to vary during ontogeny with the value of 2/3 typically found only in actively growing, mature trees.

Xylem conduits have often been reported to increase in size from the apex downwards and from the stem pith outwards (Zimmerman, 1983; Gartner, 1995; Meinzer et al., 2001; Nijssse et al., 2001; Martinez-Vilalta et al., 2002; McElrone et al., 2004; McCulloh & Sperry, 2005), but it has been found only recently that the tapering of xylem conduits follows a similar trajectory in plants of different species (Anfodillo et al., 2006). This study, as well as others (Weitz et al., 2006; Coomes et al., 2007), have demonstrated that the degree of conduits tapering is, at least for juvenile trees, very similar to that predicted by the WBE model. What happens in older trees is less clear. Anfodillo et al. (2006) suggested that there may be a decline in the degree of conduit tapering with increased height. In other words, they suggested that the tapering coefficient $a_{\text{WBE}}$ may decline from its optimal value of 0.167 in juvenile trees to smaller values in older trees. Particularly, at least for trees with columnar posture, the deviation from the optimal conduit tapering is typically given by a flattening of the profile of conduit dimensions towards the stem base (Becker et al., 2003; James et al., 2003), maybe a consequence of the achieved maximum conduit size (Anfodillo et al., 2006).

This is an interesting possibility, as it would provide a theoretical linkage between the hydraulic limitation hypothesis (Ryan & Yoder, 1997) and the WBE model (West et al., 1999), whereby hydraulic constraints would begin to affect tree growth once the tapering of xylem conduits is reduced, such that negative effects of increased path length cannot be avoided any longer.

This hypothesis has not been tested systematically so far. Mencuccini (2002) reviewed published data and concluded that the hydraulic conductance of stem segments of maple and pine trees scaled with their diameter, as stated by the WBE model, while the whole-tree hydraulic conductance of the same species scaled with the diameter at breast height (dbh) with a smaller exponent than the WBE model. Similarly, the hydraulic resistance of stem segments (Yang & Tyree, 1993) was reported to decrease with their distance from the apex, in agreement with the WBE model (Enquist, 2003). In addition to the lack of systematic tests of this hypothesis, complete analyses of the distribution of hydraulic resistance, as well as anatomical characters along stems, are also rare (Zimmermann, 1978; Ewers & Zimmermann, 1984; Tyree, 1988).

In addition to the degree of tapering along a stem down from the apex, the hydraulic efficiency of a vascular system can be affected by additional variables. First, no matter how rapidly conduit diameter changes with distance from the apex, the absolute value of conduit diameter in primis will affect conductance. Second, McCulloh et al. (2003); McCulloh & Sperry (2005) proposed that, to maximize the structural investment in xylem tissues, a network should have a minimum number of wide conduits at the base feeding an increasing number of narrowing conduits distally. These authors showed that conduit furcation occurs in some cases but also that, in cases in which the conduits provide mechanical support to the plant (e.g. in tree stems), conduit furcation is limited or absent.

The aim of this work is to provide an answer to some important questions regarding the tapering of xylem conduits. First, by systematically measuring the conduit diameters in young and old trees, we tested the hypothesis that the degree of conduit tapering does not change during ontogeny in sycamore (Acer pseudoplatanus), a diffuse-porous angiosperm tree. Moreover, to understand whether changes in conduit tapering were size- or age-related, we also compared those donor trees in the field with grafted plants obtained from the same trees and grown outside our greenhouses. Lastly, we combined anatomical and hydraulic measurements to investigate the distribution of conduit diameters and hydraulic resistances along branches and stems to determine whether hydraulic conductance of these organs was primarily affected by conduit tapering, apical conduit diameters, conduit furcation or a combination of the three.

### Materials and Methods

#### Site and plant material

The study area was located at Cramond, Almond Valley, in the western part of Edinburgh, UK (55°58′42″ N, 3°16′09″ W). The study woodland is comprised of two dominant species, sycamore (Acer pseudoplatanus L.) and ash (Fraxinus excelsior L.), and a number of minor species, as well as active regeneration (sycamore and ash) and a dense understorey of shrubs and ground flora. Sycamore trees were located mainly in an area close to the coast at the bottom of the steep slope of the valley.

Nine sycamore trees were selected from the area: five young (age = 5 yr, height = 5 m: S1) and four old (age > 130 yr, height approx. 25 m: S4). Apical shoots of S1 and shoots from lateral branches from the top third of the crown of S4 were grafted onto 2-yr-old rootstocks (GS1 and GS4) in 2003 to separate size- and age-related effects on plant structure and physiology. More details on grafting protocol and growing conditions are given by Mencuccini et al. (2005); Hamid (2006). Trees analysed were coded as by Mencuccini et al. (2005); Hamid (2006).

Wood from S4 trees was sampled by extracting wooden cores along the main stem (two cores from diametrically opposite points every 3.5 m along the stem from the top of the canopy to the tree base), taking care to avoid zones with tension wood and knots. In addition, the whole topmost branch
In addition, the vertical profiles of measured hydraulic diameters of each tree were used to estimate the hydraulic resistance $R_{\text{TOT}}$ of a tapered pipe spanning the height of each tree, but using the actual measured values as opposed to the theoretical scaling exponent derived by WBE. This approach assumes no conduit furcation (McCulloh et al., 2003) and an ideal pipe model system with tapered resistances in series. Because of the nonlinearity in the relationship of conduit diameter (and hydraulic resistance) with distance from the apex, calculations are sensitive to the length of segments employed. Hence segments 0.1 cm long were employed in all cases.

### Hydraulics measurements

We measured the water flow rate out of the apex, $F$ (cm$^3$ s$^{-1}$) of nine plants (two GS1, two GS4, three S1, two S4), while applying a known pressure head, $P$ (MPa) from the base to the cut apex (the cut was made approx. 2 mm below the bud scar). Secondary apices were also cut. Degassed distilled water was made to pass through the xylem under positive pressure, $P$, generated as a water pressure head of 2.5 m above the stem. In order to achieve equal $P$ from the base to every apex, the stem was immersed in a container with the same water level as the water in the balance (cf. Tyree et al., 1991). The hydraulic resistance, $R$ (MPa s cm$^{-3}$) was computed as $P/F$. The variation of $R$ with path length, $L$ (cm) was estimated by progressively shortening the stem from its base after each measurement session and reattaching the tubing to the new base.

### Statistical analyses

The scaling parameters of the allometric equations were determined from pairwise comparisons of log$_{10}$-transformed data. Using reduced major axis (RMA) analysis, the scaling exponents and allometric constants were identified as the regression slopes ($a$RMA) and y-intercept ($b$RMA), respectively. Regression coefficients and their 95% confidence and prediction intervals were computed using standard methods (Sokal & Rohlf, 1981) using a bootstrap procedure with 100 000 replications (Davison & Hinkley, 1997). ANOVAs among treatments were carried out using the GLM procedure in SAS 8.02 (SAS Institute, Cary, NC, USA).

### Results

#### Anatomy

Stem morphology was quite variable among plants. The analysis of stem tapering showed that the variation of stem length (distance from the apex, $L$) with stem diameter ($D$) was well described by a power function (Table 2). $L$ explained 80–98% of the total variance of $D$. The scaling exponent ranged from 1.555 to 5.446 and hence was always higher than the commonly reported exponent of $2/3$ (Niklas, 1995). However, in the...
Stem tapering (variation of path length, \( L \)) with stem diameter, \( D \), left and variation of hydraulic diameter (\( Dh \)) with \( D \), right) for each plant from the relation \( Dh = aL^{b} \) at the distance of 0.1 cm from the stem tip. S4 trees significantly differed from GS1 and GS4 but not S1 when the analysis was extended to the whole tree (Fig. 1a, right). Patterns between trees were similar for both \( b \) and \( Dh \).

In addition, \( Dh_{APEX} \) was found to be inversely proportional to \( b \) (Fig. 3), suggesting a trade-off mechanism between tapering of conduits and size of xylem cells at the apex. This relationship remained when actual, measured \( Dh_{APEX} \) data were regressed against \( b \) (data not shown).

Moreover, the estimated \( R_{TOT} \) of the theoretical tapered pipe for the S4 trees was significantly larger than for small trees (GS1, GS4 and S1), which did not differ significantly from one another (Duncan’s grouping test: overall \( ANOVA, F = 21.56, P < 0.001 \)).
Table 3  Scaling features of xylem conduits

<table>
<thead>
<tr>
<th>ID</th>
<th>n</th>
<th>$r^2$</th>
<th>$a$</th>
<th>$b$</th>
<th>95% CI</th>
<th>$a$</th>
<th>95% CI</th>
<th>$D_{h_{\text{APEX}}}$ (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GS1–3</td>
<td>10</td>
<td>0.974</td>
<td>1.306</td>
<td>0.193</td>
<td>0.175/0.241</td>
<td>0.162</td>
<td>0.147/0.202</td>
<td>24.416</td>
</tr>
<tr>
<td>GS1–6</td>
<td>8</td>
<td>0.980</td>
<td>1.355</td>
<td>0.159</td>
<td>0.140/0.175</td>
<td>0.173</td>
<td>0.134/0.182</td>
<td>26.486</td>
</tr>
<tr>
<td>GS1–7</td>
<td>9</td>
<td>0.916</td>
<td>1.316</td>
<td>0.168</td>
<td>0.104/0.242</td>
<td>0.180</td>
<td>0.147/0.202</td>
<td>24.279</td>
</tr>
<tr>
<td>GS4–9</td>
<td>11</td>
<td>0.968</td>
<td>1.294</td>
<td>0.168</td>
<td>0.155/0.207</td>
<td>0.174</td>
<td>0.130/0.174</td>
<td>22.651</td>
</tr>
<tr>
<td>GS4–98</td>
<td>10</td>
<td>0.906</td>
<td>1.224</td>
<td>0.236</td>
<td>0.107/0.281</td>
<td>0.199</td>
<td>0.090/0.236</td>
<td>21.252</td>
</tr>
<tr>
<td>GS4–99</td>
<td>10</td>
<td>0.905</td>
<td>1.377</td>
<td>0.144</td>
<td>0.119/0.212</td>
<td>0.121</td>
<td>0.100/0.178</td>
<td>25.355</td>
</tr>
<tr>
<td>S1–4</td>
<td>6</td>
<td>0.946</td>
<td>1.359</td>
<td>0.156</td>
<td>0.110/0.218</td>
<td>0.131</td>
<td>0.092/0.183</td>
<td>29.788</td>
</tr>
<tr>
<td>S1–5</td>
<td>12</td>
<td>0.915</td>
<td>1.300</td>
<td>0.182</td>
<td>0.099/0.210</td>
<td>0.152</td>
<td>0.083/0.176</td>
<td>22.444</td>
</tr>
<tr>
<td>S1–6</td>
<td>8</td>
<td>0.949</td>
<td>1.318</td>
<td>0.153</td>
<td>0.131/0.201</td>
<td>0.129</td>
<td>0.110/0.169</td>
<td>27.770</td>
</tr>
<tr>
<td>S1–7</td>
<td>11</td>
<td>0.893</td>
<td>1.429</td>
<td>0.143</td>
<td>0.116/0.203</td>
<td>0.120</td>
<td>0.097/0.170</td>
<td>28.950</td>
</tr>
<tr>
<td>S1–8</td>
<td>15</td>
<td>0.942</td>
<td>1.316</td>
<td>0.168</td>
<td>0.119/0.189</td>
<td>0.152</td>
<td>0.100/0.159*</td>
<td>23.034</td>
</tr>
<tr>
<td>S4–7</td>
<td>21</td>
<td>0.930</td>
<td>1.413</td>
<td>0.129</td>
<td>0.111/0.145</td>
<td>0.108</td>
<td>0.093/0.122*</td>
<td>24.794</td>
</tr>
<tr>
<td>S4–7 (below junction)</td>
<td>7</td>
<td>0.994</td>
<td>1.138</td>
<td>0.221</td>
<td>0.206/0.235</td>
<td>0.186</td>
<td>0.173/0.197</td>
<td>24.794</td>
</tr>
<tr>
<td>S4–7 (branch 1)</td>
<td>15</td>
<td>0.871</td>
<td>1.446</td>
<td>0.106</td>
<td>0.071/0.126</td>
<td>0.089</td>
<td>0.060/0.106*</td>
<td>30.790</td>
</tr>
<tr>
<td>S4–7 (branch 2)</td>
<td>16</td>
<td>0.975</td>
<td>1.438</td>
<td>0.101</td>
<td>0.094/0.111</td>
<td>0.085</td>
<td>0.079/0.093*</td>
<td>21.762</td>
</tr>
<tr>
<td>S4–9</td>
<td>23</td>
<td>0.857</td>
<td>1.372</td>
<td>0.124</td>
<td>0.101/0.150</td>
<td>0.100</td>
<td>0.085/0.126*</td>
<td>30.790</td>
</tr>
<tr>
<td>S4–9 (below junction)</td>
<td>7</td>
<td>0.887</td>
<td>1.219</td>
<td>0.179</td>
<td>0.142/0.327</td>
<td>0.150</td>
<td>0.119/0.275</td>
<td>30.790</td>
</tr>
<tr>
<td>S4–9 (branch 1)</td>
<td>17</td>
<td>0.715</td>
<td>1.438</td>
<td>0.081</td>
<td>0.059/0.103</td>
<td>0.068</td>
<td>0.050/0.086*</td>
<td>22.666</td>
</tr>
<tr>
<td>S4–9 (branch 2)</td>
<td>11</td>
<td>0.888</td>
<td>1.421</td>
<td>0.105</td>
<td>0.070/0.123</td>
<td>0.088</td>
<td>0.059/0.103*</td>
<td>29.244</td>
</tr>
<tr>
<td>S4–98</td>
<td>14</td>
<td>0.924</td>
<td>1.391</td>
<td>0.132</td>
<td>0.117/0.161</td>
<td>0.111</td>
<td>0.098/0.135*</td>
<td>32.763</td>
</tr>
<tr>
<td>S4–98 (below junction)</td>
<td>7</td>
<td>0.856</td>
<td>1.416</td>
<td>0.212</td>
<td>0.113/0.267</td>
<td>0.178</td>
<td>0.095/0.224</td>
<td>29.244</td>
</tr>
<tr>
<td>S4–99</td>
<td>14</td>
<td>0.963</td>
<td>1.403</td>
<td>0.148</td>
<td>0.133/0.168</td>
<td>0.126</td>
<td>0.112/0.141*</td>
<td>32.763</td>
</tr>
<tr>
<td>S4–99 (below junction)</td>
<td>6</td>
<td>0.775</td>
<td>1.332</td>
<td>0.172</td>
<td>0.040/0.247</td>
<td>0.145</td>
<td>0.034/0.207</td>
<td>32.763</td>
</tr>
<tr>
<td>S4–99 (branch)</td>
<td>9</td>
<td>0.964</td>
<td>1.435</td>
<td>0.126</td>
<td>0.110/0.150</td>
<td>0.106</td>
<td>0.092/0.126*</td>
<td>32.763</td>
</tr>
</tbody>
</table>

Variation of hydraulically weighted diameter ($D_{h}$) with path length ($L$): estimates for the log10-transformed scaling parameters $a$ and $b$, the WBE parameter $a$ and 95% CI for $b$ and $a$. $D_{h}$ of the most distal section is also reported.

Fig. 1 ANOVA of slope $b$ of the relation $\log_{10} D_{h} = \log_{10} a + b \log_{10} L$ (left-hand side) and $D_{h}$ at the apex (calculated from the same equation for a distance of 0.1 cm from the tip, right-hand side). Two different analyses were carried out: (a) considering the whole $D_{h}$ profiles of all plants of all treatments ($n = 19$; $P(b) = 0.037$; $P(D_{h_{\text{APEX}}}) = 0.053$); (b) considering only the $D_{h}$ profiles of the first 3 m of distance from the apex: whole profile for plants of treatments GS1, GS4 and S1; $D_{h}$ profiles of the top six branches in S4 ($n = 21$; $P(b) < 0.001$; $P(D_{h_{\text{APEX}}}) < 0.001$). Duncan’s grouping is shown for both analyses; groups with different letters differ significantly at 95%. 

Hydraulics

The whole-shoot hydraulic resistance ($R$) increased from the apex to the stem base. Most of the resistance was located towards the apex, where xylem conduits tapered more sharply. Consequently, $R$ increased less than linearly with path length ($L$), and the best function describing this variation was again a power function (Fig. 4). $L$ explained 83–98% of the total $R$ variance and the scaling exponents ranged from 0.293 to 0.644, that is, they were significantly lower than 1.00 (Table 4). The increase of $R$ with $L$ was reduced below isometry by tapering of conduits: the increased tapering of xylem conduits resulted in an increase of $R$ with $L$ lower than isometric (Fig. 5).

Moreover, we estimated the theoretical variation of $R$ with $L$ for an ideal tube (composed of successive 0.1-cm-long levels) with anatomical features obtained from the empirical measurements in the plants analysed ($Dh_{APEX}$ and $\bar{d}$). The scaling exponents ($\alpha'$) of the fitting curve for the hydraulic measurements matched well the scaling exponents ($\alpha''$) of the fitting curve for the theoretical $R$ of ideal tubes of known anatomical characteristics (Fig. 6). The RMA slope of the linear relationship between predicted and measured scaling of resistances was 0.831 (with confidence limits including 1.00).

Discussion

Age vs size

The results revealed that, in sycamore ($A. pseudoplatanus$), the scaling of xylem anatomical features did not change as a consequence of increased tree age per se, as the scaling found in GS4 did not differ from that found in GS1, but was significantly different from that of S4. In other words, the scaling relationships for the small trees (S1, GS1 and GS4) did not differ from one another despite differences in growing conditions (forest for S1 vs common garden for GS1 and GS4) and meristematic age (young for S1 and GS1 vs putatively old for GS4), whereas the scaling in GS1 and GS4 was found to be significantly different from that recorded in S4, suggesting that either size or environment, but not age, was responsible for these differences. When the analyses were limited to the distance of approx. 3 m from the apex, a distance similar to the total height/length of the field saplings, the grafted seedlings and the length of a major branch in the old trees, conduit tapering was found to be similar among all the plants analysed except for the S4 top branches, in which conduit tapering was significantly slower than in the small plants, irrespective of their meristematic age and whether grown in the field or common gardens. Moreover, S4 trees also had larger apical conduits than small trees. However, because the tall/old trees showed increased conduit tapering along the main stem, these differences tended to decrease when the analyses were carried out for the whole tree. The significance of this rather unusual tapering pattern is discussed below.

Moreover, S4 trees showed greater stem tapering compared with the other treatments, probably as a consequence of the increased mechanical constraints with height (Niklas, 1995).

Compared with S1 and GS1, GS4 trees showed similar scaling relations but also displayed higher variability in the estimated $\bar{d}$ (Figure 1). This was probably a result of the variability in recovery time from grafting stress, which has been reported to affect growth and physiological processes after grafting (Mencuccini et al., 2007; Vanderklein et al., 2007).

Conduit tapering in tall trees

The analyses of conduit dimensions suggested that the tapered nature of the xylem transport system was common among all
plants studied. Nevertheless, while previous studies found conduit tapering similar to WBE predictions ($a \approx 0.167$), in these trees $a$ was generally $< 0.167$, with the lowest values estimated for S4 trees. Despite this variability, values of $a$ were significantly different from WBE predictions in only seven trees (four of which were S4) out of the 19 analysed. Previous authors attributed this reduction in tapering in the tall trees to the potential problems determined by excessive widening of xylem conduits at the stem base (Anfodillo et al., 2006), as the profile of conduit dimensions has often been found to form a plateau at the base of the trunk (Becker et al., 2003; James et al., 2003; Anfodillo et al., 2006; Coomes et al., 2007). However, our large trees (S4) showed a different $Dh$ profile, with a point of discontinuity a few metres below the tree top, around the junction of the top branches with the main trunk. Below this point, conduit tapering was similar to the predicted WBE value, $a \approx 0.167$, whereas in the top branches it was much lower ($0.068 < a < 0.106$). It is interesting to observe that the treatment (S4) with reduced xylem tapering was also characterized by a different canopy architecture (sympodial with little apical dominance as opposed to monopodial with high apical dominance, as in the other cases). The significance of these differences is presently unclear but, as discussed below, it may be that, in the absence of apical dominance, lateral branches tend to widen their apical conduits (which consequently reduces conduit tapering further down the branch; trade-off in Fig. 3) to reduce the build-up of hydraulic resistance while maintaining a segmented architecture (discontinuity of $Dh$ profile) that would confine potential embolism to the peripheral–top branches (Zimmermann, 1978, 1983). This hypothesis contrasts with the WBE assumption of the

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In the last column, estimates are given of the scaling exponent $d$ for the hydraulic resistance of the same branches and stems estimated from anatomical measurements. Resistance was estimated assuming ideal tubes made by successive 0.1-cm-long levels, with $a$ and $Dh$ at the apex as measured in the sample plants.
size-invariance of the terminal units (West et al., 1999), although it is consistent with the principle that all plants are forced to adopt a transport network that minimizes the total hydraulic resistance (Enquist, 2003).

Comparison of anatomical and hydraulic measurements

The hydraulic measurements confirmed that conduit tapering can compensate for the potential linear increase of hydraulic resistance with path length (Fig. 5). In fact, for theoretical tubes with the same tapering characteristics of the conduits of our plants, we estimated hydraulic scaling exponents against distance from the apex effectively identical to those obtained from direct hydraulic measurements (Fig. 6). While the scaling exponents were almost identical, the scaling constants of these relationships could not be compared directly, as anatomical characteristics such as number of conduits and end wall resistance will probably have varied from plant to plant (Sperry et al., 2005). Despite this, the close agreement between the two scaling exponents against distance from the apex brings about two important conclusions. First, the pathway conducting water to the top apex was not significantly affected by the presence of open pathways into the lateral branches kept at identical water potential. This suggests that, under these conditions, the water-carrying capacity of each pathway was independent from the others, as also found by others (Larson et al., 1994; Brooks et al., 2003). Second, it is very unlikely that conduit furcation (sensu McCulloh et al., 2003) was present in our system. In other words, if pipes were not independent, but were joined into fewer and fewer conduits basally (an aorta as opposed to a pipe model type of system), the relationship between the two scaling exponents would have diverged systematically from the 1 : 1 line. This result agrees well with previous conclusions by McCulloh & Sperry (2005), whose data set also included a maple (Acer negundo), a diffuse-porous species. The maple stem showed no evidence of furcation and its degree of tapering was fairly close to the predicted WBE exponent, as also found here.

The scaling exponents for measurements of hydraulic resistance vs distance from the apex were always < 1.0 (Fig. 4), suggesting a progressive saturation in the rate of increase in hydraulic resistance with distance from the apex. However, the length of the branches used for hydraulic measurements was too short to find a plateau in the hydraulic resistance profile along the stem (Becker et al., 2000). To determine whether conduit tapering completely compensated for the increased segment length (Zaehle, 2005), that is, if the hydraulic resistance tended to become independent of path length after a certain length, would have required directly measuring the variation of hydraulic resistance with path length along entire big trees, obviously not a straightforward operation.

Relationship \( D_{h,APEX} \) vs \( \bar{a} \)

Another novel finding of this work was that conduit tapering \( \bar{a} \) was inversely related to the dimension of the apical conduits. This was not theoretically surprising, given the sensitivity of hydraulic conductance to conduit diameter, but this trade-off has not been demonstrated empirically before, while the WBE model explicitly assumes size-invariance of the apical elements (West et al., 1999). Element size is not only related to hydraulic conductance (Tyree & Ewers, 1991), but also has significant implications with regard to safety from embolism (Wheeler et al., 2005) and structural carbon investment (McCulloh & Sperry, 2005). Hence many different aspects are likely to be involved in this trade-off. Although tentative, we evaluated possible implications of this phenomenon for hydraulic properties and carbon costs. We calculated (1) the build-up of the total hydraulic resistance and (2) the total carbon costs of the pipe walls, for different lengths (tree heights) and different combinations of \( D_{h,APEX} \) and \( \bar{a} \).

These combinations were chosen to represent the trade-off shown in Fig. 4 (representative only for small plants) for an ideal pipe, composed by successive cylindrical sections (1 cm long), the wall thickness of which was estimated based on its resistance to implosion against xylem embolisms (Hacke et al., 2001). For a realistic range of apical conduit diameters between 10 and 25 µm (corresponding to tapering rates varying from 0.231 to 0.106, respectively), both total hydraulic resistance and total carbon costs were shown to be quite variable in small trees, although always much lower than in tall trees. This would suggest, as it should be, that neither the total hydraulic resistance nor the amount of carbon investment can limit growth in small trees.
growing in a favourable environment such as our field site and our greenhouses.

For tall trees, instead, the scenario was slightly different. Because of their segmented $Dh$ profile and hence their unclear coupling of $Dh_{\text{APEX}}$ and $b$, the trade-off in Fig. 4 did not include S4 trees. However, whether we consider the whole tree profile or only the top branch, S4 trees showed high values of $Dh_{\text{APEX}}$ combined with reduced rates of conduit tapering ($b$), as predicted by the trade-off mechanism. Therefore, in taller trees, total hydraulic resistance built up at rates inversely dependent on conduit tapering (that is, low rates of tapering significantly increased the build-up of resistance; Fig. 7a, West et al., 1999; Becker et al., 2000), although at very low rates of tapering ($b < 0.09$) the total build-up of hydraulic resistance was somehow compensated by having wider apical conduits. Moreover, wall carbon costs built up at rates directly dependent on conduit tapering (steep tapering significantly increased the build-up of carbon costs; Fig. 7b), whereas for low rates of tapering, carbon costs varied much less. Therefore, while in small trees carbon costs did not appear to be affected by the different combination of $Dh_{\text{APEX}}$ and $b$, in tall trees fairly low rates of tapering, coupled with large apical diameters ($b \approx 0.10$; $Dh_{\text{APEX}} \approx 25 \mu m$) appeared to produce the most efficient use of wall material for a similar hydraulic return, given the shape of the relationship in Fig. 4.

The observed size-related decreases in $b$ and increases in $Dh_{\text{APEX}}$ (Fig. 2; cf. $x$ in Fig. 8) can probably be explained on the basis of a decline of hydraulic efficiency, perhaps driven by the need to maintain the efficiency in carbon investment (McCulloh et al., 2003). First, it is likely that S4 trees reached their possible maximum conduit dimension at the stem base. In this case, maintaining an ‘optimal conduit tapering’ while growing taller would have required a reduction in the dimension of apical conduits, a biologically unrealistic situation that would have determined a very high total hydraulic resistance ($C$ in Fig. 8a), approx. 1.5 times higher than real trees experienced (+ in Fig. 8a). Moreover, if S4 trees retained the small dimensions of apical conduits typical of the younger trees, and given the trade-off of Fig. 4, the conduits at the trunk base would have been very large (e.g. at 20 m, for a $Dh_{\text{APEX}}$ of 10 µm, $Dh_{\text{BASE}}$ would be approx. 100 µm; in our tall trees, 22–26 m high, it never exceeded 79 µm). In addition to the large increases in carbon costs (Fig. 8b), this would probably also affect their vulnerability to cavitation (Hargrave et al., 1994; Pittermann & Sperry, 2003).

Finally, it might be speculated that our tall trees (S4), because of their sympodial branching, developed lateral top branches with larger apical conduits and lower conduit tapering in order to grow still a few metres taller, and this new, segmented $Dh$ profile did not appear to have a negative impact on the total amount of carbon investment (Fig. 8b).

However, given the slopes in Fig. 8, it appears that the best strategy for a tree to grow taller is to structure the water transport network to best compensate for the build-up of hydraulic resistance with the increased height: the conduit tapering must be optimized.

We conclude that the observed size-related increase in hydraulic resistance in sycamore trees is likely to result from a late optimization of xylem structure in trees approaching their maximum height, mediated by a principle of efficiency of carbon allocation to conduit walls.

As noted (Fig. 8a), our large trees experienced a higher hydraulic resistance than the small trees (approx. 1–2 m tall), and this is probably why their physiological performances differed (Mencuccini et al., 2005; Hamid, 2006). Importantly, a tapered xylem structure for a 24-m-tall tree, for example,
limited the increase in total hydraulic resistance to only three
to five times that of a 1-m-tall tree, as opposed to a factor of
24 in the case of an unpruned xylem structure. This means
that the tapering of xylem conduits is probably the most
important compensating factor reducing the effect of the
build-up of hydraulic resistance with increased tree height.

In conclusion, we note that this study extends our knowledge
on the mechanisms of compensation for the increase in
hydraulic resistance during tree development and supports the
notion that tapering of xylem conduits plays a crucial role
in this respect. We have demonstrated that vessel tapering
accounted for the less-than-linear increase in measured branch
hydraulic resistance with length, and have shown that these
results indicate that vessel fukation was unlikely to occur in
our branches. In addition, we have shown the existence of a
trade-off between vessel tapering and size of apical vessels, the
significance of which needs to be explored further in the context
of the carbon costs of vessel walls.

The decline in tree performance reported previously
(Mencuccini et al., 2005; Hamid, 2006) was found to be
accompanied by structural changes in the xylem driven by the
need to minimize the increase of hydraulic resistance under
limited carbon resources, a result independent of direct,
age-mediated processes and probably a function of size-related
processes. Finally, while the observed ontogenetic trends were
not entirely consistent with the WBE model, they highlight
the significance of the basic principles of this model for a better
understanding of the hydraulic limitations on tree height.

Acknowledgements

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