

Convergent tapering of xylem conduits in different woody species

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Summary

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- A recent theoretical model (the West, Brown and Enquist, WBE model) hypothesized that plants have evolved a network of xylem conduits with a tapered structure (narrower conduits distally) which should minimize the cost of water transport from roots to leaves. Specific measurements are required to test the model predictions.
- We sampled both angiosperms and gymnosperms (50 trees) growing in different environments with heights ranging from 0.5 to 44.4 m, measuring variations of the xylem–conduit diameter from tree top to stem base.
- In all trees measured, mean hydraulically weighted conduit diameters (Dh) at the tree top were narrower than those at the stem base. In actively growing trees, the longitudinal variation of Dh showed a degree of tapering in agreement with WBE predictions, while trees close to their maximum height showed slightly lower conduit tapering. Comparing different species, a very good correlation was observed between degree of xylem tapering and tree height ($r^2 = 0.88$; $P < 0.0001$) independently of any other variable (age, site, altitude, etc.).
- As predicted by WBE, sampled trees seemed to converge towards similar xylem conduit tapering. However, trees approaching their maximum height had a nonoptimal tapering which appeared insufficient to compensate for the progressive increase in tree height.

Key words: anatomy, evolution, hydraulic constraints, tapering, tree height, xylem conduits.

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Introduction

Trees convey water to the leaves through a long pathway of xylem conduits. While the cohesion–tension theory explaining water ascent is now widely accepted (Tyree, 2003; Angeles *et al.*, 2004), other plant hydraulic topics remain highly controversial. One intriguing issue is the structure the water transport system should have in order to compensate for the increase in length as trees grow taller (Midgley, 2003). Investigations on the tallest trees in the world (Koch *et al.*, 2004) showed that leaves at the treetop underwent severe water stress caused by gravity and path-length resistance. This might support the idea that, as they grow taller, hydraulic resistance would progressively increase, leading to a decline in assimilation and performance as stated by the hydraulic limitation hypothesis (Ryan & Yoder, 1997). Basically, the argument arises from the Hagen–

Poiseuille law, which predicts that resistance to flow in cylindrical conduits increases linearly with conduit length, so the cost of drawing water would increase with tree height. Homeostatic mechanisms could be adopted by plants to compensate for the path-length effect, such as decreasing the leaf area/sapwood area ratio (McDowel *et al.*, 2002) or increasing the allocation in fine roots (Magnani *et al.*, 2000), but these strategies seem to allow only a partial hydraulic compensation or, in any case, to reduce tree growth.

A recent theoretical model (West *et al.*, 1999a: the West, Brown and Enquist, WBE model), through a counterintuitive approach, proposes that hydraulic resistance in plants is almost constant as trees grow taller and independent of path length, provided that xylem conduits taper properly (narrower conduits distally). The degree of xylem conduit tapering predicted by WBE represents the minimum value

of tapering ensuring the independence of flow resistance from path length (Becker *et al.*, 2000; Becker & Gribben, 2001). This anatomical feature is proposed as being universal because it is hypothesized that natural selection would have resulted in a vascular network minimizing resource transport costs (Enquist, 2002). This vascular structure, coupled with maximization of the surface area where resources are exchanged with the environment, would lead to specific allometric scaling exponents in plants (quarter power allometric relationships). The WBE approach (and derived consequences) has been strongly debated (Zianis & Mencuccini, 2004) and also criticized (Bokma, 2004; Kozłowski & Konarzewski, 2004; Zaehle, 2005), thus highlighting its extraordinary scientific interest. In the recent comprehensive review of hydraulic architecture in trees by McCulloh & Sperry (2005), it appeared that in-depth analyses of the longitudinal structure of xylem conduits of the whole tree (the first step required to evaluate the WBE model) are surprisingly uncommon (Becker *et al.*, 2000; Zaehle, 2005) if we exclude the data reported by Zimmermann (1983) and a few others (Gartner, 1995; Spicer & Gartner, 2001; Becker *et al.*, 2003; James *et al.*, 2003).

The main objective of this work was to test whether the structure of the vascular network predicted by the WBE model matches that of real trees. We have not considered many consequences of the WBE model (e.g. different aspects of hydraulic architecture such as sapwood ratio or scaling relationships), just focusing our attention on two fundamental questions. (1) In a single annual tree ring, do xylem conduits taper towards the tree top as proposed by the WBE model? (2) Is the degree of conduits tapering similar in different species, that is, can the degree of tapering be proposed as universal?

We also suggest that, after an in-depth analysis of the WBE model, and comparing it with real xylem conduits patterns, most of the reported discrepancies between the two hypotheses on hydraulic limitations of tree height (Midgley, 2003) seem to disappear.

In order to test the WBE predictions, an in-depth reanalysis of the proposed relationships is needed. Our approach is described in detail in the Appendix.

Materials and Methods

Plant material and sampling

Sampling strategy differed in relation to the two main objectives. In order to study in depth the longitudinal variation of xylem conduit diameter in the same tree ring, we selected four trees: three conifers and one ring-porous species (Table 1). Trees grew in mountain sites at different altitudes (between 1100 and 1600 m asl) in north-eastern Italy. We considered sites where almost the tallest trees in Europe (approx. 50 m) are to be found. Stands were usually managed by selective logging and natural regeneration. No particular method or strategy was used to select trees because, assuming a universal degree of xylem

Table 1 Main dendrometric parameters of four trees selected for measuring the longitudinal (tree top to stem base) variation of hydraulically weighted conduit diameters (D_h)

Tree code	Species	Age (yr)	Tree height (m)	dbh (cm)
FE15	<i>Fraxinus excelsior</i> L.	21	14.5	29.5
LD27	<i>Larix decidua</i> Miller	47	27.1	34.0
LD40	<i>L. decidua</i> Miller	302	39.9	52.4
PA44	<i>Picea abies</i> (L.) Karsten	198	44.4	79.0

conduit tapering, specific (individual) growth conditions should have no effect. We therefore just used plants in normal vegetative conditions (compared with other trees in the same stand) with no evident biotic or abiotic damage to stem or branches.

Trees were cut between 2001 and 2003 and several discs collected from the tree top to stem base along the main bole: the distance between samples ranged from 0.1 to 4 m depending on tree height. The distance of each wood disc from the tree top (l) was carefully measured using a tape-meter. In each wood disc the diameter, number of tree rings (age) and ring widths were measured in order to estimate the rate of longitudinal growth of each tree. Apexes were sampled at the top of the 2-yr-old shoots ($N - 1$) to avoid the developmental lag between cambial reactivation and secondary xylem development in 1-yr-old shoots (Joyce & Steiner, 1995), while basal wood discs were taken above the basal flare of the root collar, where conduits are narrower because of mechanical stresses (Spicer & Gartner, 2001).

In order to study the xylem structure extensively on different species, we also sampled 50 woody plants (including the four above-mentioned trees) with heights (l) ranging from 0.5 to 44.4 m (about half the absolute maximum tree height observed in nature) of several conifer and angiosperm species (ring- and diffuse-porous species) (Table 2). Trees were sampled between 2001 and 2004 on different sites in Italy from lowland to subalpine stand, aiming to measure as many species as possible. As above, sampling was simply to collect trees of different heights, so no other criteria (competition, soil fertility, water availability) were considered. Growth rates differed among selected trees, but no single variable (excepted tree height) was supposed to be relevant in determining tapering variation of xylem conduits. In these trees only two stem discs were collected: at the apex ($N - 1$) and at the base, using the procedure described above.

Anatomical measurements

Microscopy analysis was done on each collected stem disc (for both sampling strategies) by sampling four different positions of the same tree ring (from growing years 2001–04), avoiding areas with reaction wood, injuries and scars. Apical discs, because of their small dimensions, were analysed thoroughly.

Table 2 Dendrometric parameters, site characteristics, base (Dh_0) and apical Dh_{N-1} hydraulic diameter samples are ordered by Δl (distance between the two samples)

ID	Species	Height (l) (m)	Age (yr)	Base D (cm)	Altitude (m asl)	Dh_0 (μm)	Dh_{N-1} (μm)
1	<i>Sorbus aucuparia</i> L.	0.5	5	0.5	1900	28.71	24.46
2	<i>Rhododendron ferrugineum</i> L.	0.9	28	1.0	1900	20.76	18.06
3	<i>Pinus sylvestris</i> L.	1.2	11	3.7	1100	23.89	17.96
4	<i>Acer pseudoplatanus</i> L.	1.3	5	3.0	1300	56.27	48.24
5	<i>Arbutus unedo</i> L.	1.5	15	1.2	10	15.58	13.78
6	<i>Juniperus sabina</i> L.	1.7	22	3.2	10	7.61	6.22
7	<i>Populus nigra</i> L.	2.0	6	5	20	58.41	47.46
8	<i>Salix purpurea</i> L.	2.4	4	2.0	1000	53.14	31.92
9	<i>Pinus mugo</i> Turra	2.4	16	5.0	1100	25.34	16.25
10	<i>Prunus avium</i> L.	2.6	7	3.5	650	42.72	29.10
11	<i>Picea abies</i> (L.) Karsten	2.9	9	5.0	1500	28.37	19.03
12	<i>S. purpurea</i> L.	3.2	7	3.5	1100	45.34	29.70
13	<i>Prunus spinosa</i> L.	4.3	8	3.0	700	44.89	25.76
14	<i>Erica arborea</i> L.	4.7	37	11.0	10	21.78	11.92
15	<i>Fagus sylvatica</i> L.	4.9	15	4.0	700	49.79	25.47
16	<i>Phillyrea latifolia</i> L.	5.1	28	14.0	10	17.10	9.05
17	<i>Salix eleagnos</i> Scop.	5.2	17	4.5	1000	65.11	33.21
18	<i>Pinus nigra</i> Arnold	5.7	29	9.8	650	31.44	18.60
19	<i>Juniperus oxycedrus</i> L.	5.1	32	6.6	10	11.22	5.37
20	<i>Fraxinus excelsior</i> L.	5.9	22	6.5	700	182.06	100.11
21	<i>Ilex aquifolium</i> L.	6.0	29	13.0	10	14.36	7.44
22	<i>Corylus avellana</i> L.	7.5	13	5.0	700	48.68	27.67
23	<i>Ostria carpinifolia</i> Scop.	8.0	22	10.0	700	77.59	37.52
24	<i>Alnus incana</i> (L.) Moench	8.5	11	7.5	1300	50.47	29.24
25	<i>Larix decidua</i> Miller	8.5	15	15.0	700	36.55	18.02
26	<i>Juglans regia</i> L.	8.8	25	14.5	700	168.89	80.64
27	<i>Sorbus aucuparia</i> L.	9.1	40	41.0	1300	50.27	24.17
28	<i>Fraxinus ornus</i> L.	9.5	35	13.5	700	106.28	63.12
29	<i>Carpinus betulus</i> L.	9.5	19	5.5	700	53.57	24.68
30	<i>Quercus ilex</i> L.	10.9	40	24.0	10	42.91	18.83
31	<i>Populus nigra</i> L.	11.2	30	22.0	20	85.74	47.46
32	<i>Fraxinus excelsior</i> L.	14.4	21	29.5	1100	103.80	43.62
33	<i>L. decidua</i> Miller	18.2	32	27.6	1100	50.64	19.89
34	<i>L. decidua</i> Miller	18.5	27	18.0	1000	39.30	18.02
35	<i>P. abies</i> (L.) Karsten	19.8	34	20.0	1100	40.04	20.78
36	<i>Hedera elix</i> L.	20.0	21	9.0	10	53.93	24.75
37	<i>P. nigra</i> L.	21.2	35	50.2	10	113.79	47.46
38	<i>L. decidua</i> Miller	26.6	40	34.0	1100	47.85	19.30
39	<i>P. abies</i> (L.) Karsten	27.5	51	40.0	1000	39.51	16.41
40	<i>Abies alba</i> Miller	29.9	179	48.0	1600	31.42	14.95
41	<i>P. abies</i> (L.) Karsten	32.2	125	42.0	1550	33.71	14.55
42	<i>P. abies</i> (L.) Karsten	32.2	126	42.0	1550	38.61	15.50
43	<i>P. abies</i> (L.) Karsten	33.5	143	52.0	1550	37.41	15.61
44	<i>P. abies</i> (L.) Karsten	36.5	125	43.0	1550	33.78	13.46
45	<i>L. decidua</i> Miller	39.9	302	52.4	1600	43.96	16.26
46	<i>P. abies</i> (L.) Karsten	40.0	137	56.0	1550	32.53	13.61
47	<i>P. abies</i> (L.) Karsten	40.0	165	55.0	1550	41.48	14.32
48	<i>P. abies</i> (L.) Karsten	42.2	145	57.0	1550	40.74	15.50
49	<i>P. abies</i> (L.) Karsten	43.5	160	60.0	1500	43.76	15.61
50	<i>P. abies</i> (L.) Karsten	44.4	223	78.0	1600	43.27	14.27

Woody samples were then cut and embedded in paraffin (Anderson & Bancroft, 2002), and transverse sections of 8–10 μm were cut with a rotary microtome, stained with safranin (1% in water) and fixed permanently with Eukitt. The sections were observed under a light microscope (Leitz, Laborlux S), the images (at 100–250 \times) digitalized, and the

lumen area measured automatically with specific software (WINCELL, Régent Instruments Inc., Sainte-Foy, QC, Canada). In each section of the four different positions on the stem disc, at least five cell rows (Pittermann & Sperry, 2003) from early to late wood were measured, thus analysing from *c.* 20–50 cell rows in each disc. The diameter of each cell was then calculated,

considering the lumen to be circular. All the N_c measured cells (from 200 to *c.* 4000 each stem disc, i.e. sampling position) were then selected. Only those with a lumen diameter greater than half the diameter of the largest conduit in each tree ring were chosen, in order to eliminate conduits that may have been tapering, as suggested by James *et al.* (2003). Only the selected cells were then included in the calculation of the weighted average of hydraulic diameters (Dh) as frequently proposed (Mencuccini *et al.*, 1997) as

$$Dh = \frac{\sum_{n=1}^N d_n^5}{\sum_{n=1}^N d_n^4}$$

where d_n is the diameter of the n cell (Sperry *et al.*, 1994) which weights hydraulic diameters of single cells according to hydraulic conductance.

The Dh values of the apical conduit (Dh_{N-1}) and those at the stem base (Dh_0) were used to compute the conduit-tapering ratio (T) as:

$$T = Dh_0 / Dh_{N-1}$$

separately for each tree. This allows us to compare different species, which evidently have different conduit dimensions.

Statistical analyses

All data were first log₁₀-transformed, as traditionally done in contemporary allometric analyses, mainly (i) to comply with the statistical assumptions of normality and homoscedacity; and (ii) to provide a convenient means of examining proportionality that is unaffected by the unit of measurement (Sokal & Rohlf, 1981; Niklas, 1994, 2004). Model type II regression analysis with the reduced major axis (RMA) protocol was used to determine empirically the scaling exponents and allometric constants (regression slope and y -intercept, α_{RMA} and β_{RMA} , respectively) of pairwise comparisons of log₁₀-transformed data. This protocol is recommended when functional rather than predictive relationships are sought among variables that are biologically interdependent and subject to unknown measurement error (Sokal & Rohlf, 1981; Niklas, 1994). Regression coefficients, their significance and 95% confidence and prediction intervals were computed using standard methods (Sokal & Rohlf, 1981) and adopting a bootstrap procedure with 100 000 replications (Efron, 1982; Davison & Hinkley, 1997).

Results

Longitudinal variation of Dh within a tree ring

The variation of the weighted average of hydraulic diameters (Dh) from tree top to stem base along the main stem in the last

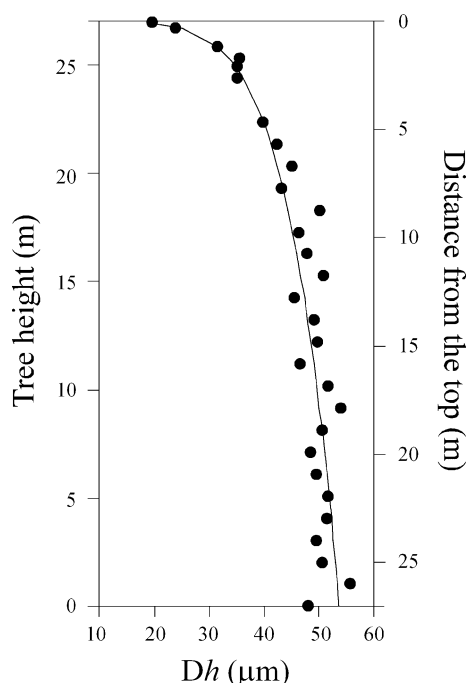


Fig. 1 Longitudinal variation of hydraulically weighted conduit diameters (Dh) in the same tree ring (year 2003) at different tree heights and at different distances from the tree top in *Larix decidua* (tree LD27).

annual ring in the LD27 tree is shown in Fig. 1. For a better understanding of the general trend, no logarithmic scale was used. Dh increased from the apex (19.3 μm) towards the stem base (approx. 50 μm), showing that conduit elements tapered significantly. The tapering degree was not constant with path length l (distance from tree top) as stated by WBE: Dh varied sharply near the apex (at $l = 2$ m, Dh is approx. 38 μm), but very little near the stem base (from 15 m to the stem base Dh varied only by approx. 5 μm). The best fitting is obtained by using a power function ($r^2 = 0.96$, $P < 0.001$; Table 3) in agreement with the WBE model (equation 9).

Using log–log plots, the variations of Dh in the last annual ring as a function of tree height (l) (and the relative deviation from the fitting model) can be assessed (Fig. 2). The four trees showed a similar general pattern, with l explaining 86–96% of the total Dh variance (Table 3). In tree FE15, which is the smallest and youngest, the slope of equation 3 is 0.30, which gives, using equation 9b, $\bar{a} = 0.252$ (95% CI 0.184–0.292), which is significantly above the WBE predicted threshold value (0.167), thus assuring that xylem conduit resistance is substantially independent of tree height. High values of xylem tapering seemed to be coupled with a relatively constant and elevated growth in height (approx. 0.8 m yr^{-1} ; Fig. 2a, box). In LD27 (Fig. 2b), Dh of the tracheids in the last annual ring appeared strongly correlated to l and the calculated slope was 0.168, which gives $\bar{a} = 0.141$ (95% CI 0.131–0.153), which is significantly lower than 1/6. This conduit tapering appeared

Table 3 Regression coefficients, r^2 and confidence intervals of the main relationships used to estimate the WBE conduit tapering parameter (\bar{a} , a and α) in the four selected trees

Tree code	Model	N	Intercept	Slope	r^2	95% CI	
						Intercept	Slope
LD27	log Dh vs log l (eqn 9)	29	1.490	0.168	0.96	1.476 to 1.502	0.156 to 0.182
	log Dh vs log D (eqn 3)	29	1.483	0.158	0.94	1.436 to 1.506	0.139 to 0.199
	log l vs log D (eqn 7)	30	-0.066	0.951	0.97	-0.318 to 0.042	0.864 to 1.168
FE15	log Dh vs log l (eqn 9)	15	1.746	0.300	0.88	1.725 to 1.812	0.219 to 0.348
	log Dh vs log D (eqn 3)	15	1.674	0.416	0.88	1.630 to 1.763	0.297 to 0.492
	log l vs log D (eqn 7)	17	-0.243	1.395	0.99	-0.329 to -0.170	1.297 to 1.495
LD39	log Dh vs log l (eqn 9)	15	1.488	0.177	0.86	1.458 to 1.529	0.138 to 0.211
	log Dh vs log D (eqn 3)	15	1.315	0.274	0.85	1.282 to 1.409	0.199 to 0.314
	log l vs log D (eqn 7)	18	-0.987	1.554	0.99	-1.097 to -0.804	1.410 to 1.631
PA44	log Dh vs log l (eqn 9)	26	1.376	0.195	0.93	1.353 to 1.409	0.162 to 0.220
	log Dh vs log D (eqn 3)	26	0.742	0.228	0.95	0.695 to 0.823	0.192 to 0.251
	log l vs log D (eqn 7)	26	-1.718	1.168	0.99	-1.790 to -1.670	1.144 to 1.201

Number of samples in each tree along the main stem is also shown (N). Dh , weighted average of hydraulic diameters; l , plant height; D , stem diameter. Parameters are referred to plots of Fig. 2. $P < 0.0001$ in all cases. The assumption of normality of residuals, tested through the Shapiro-Wilks W -test, was met for all models except log l vs log D in LD27.

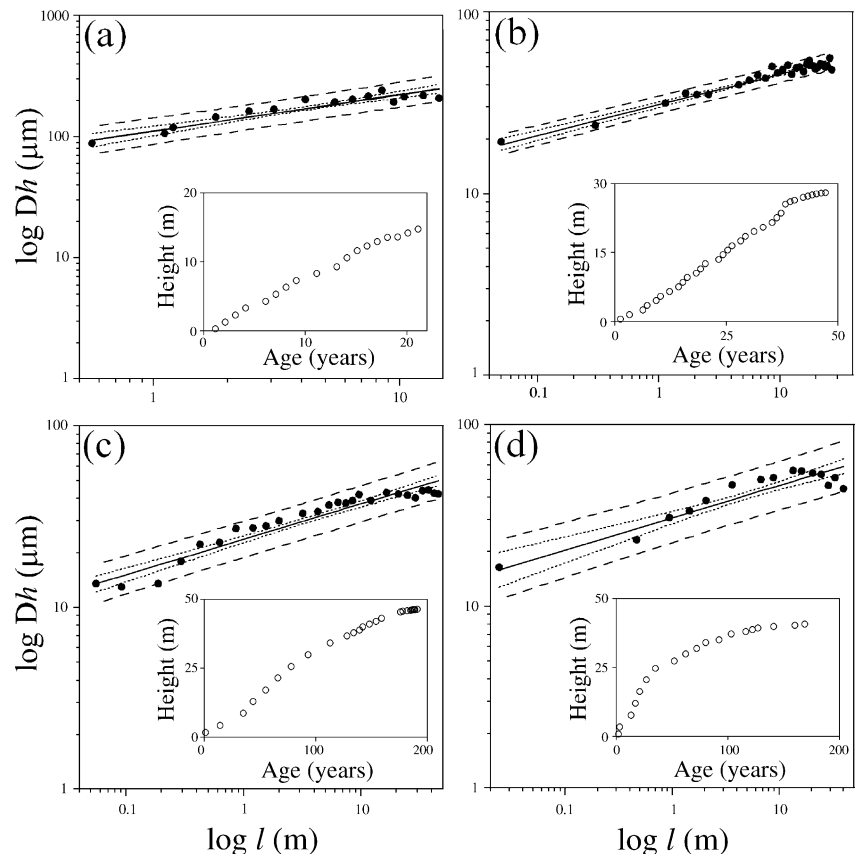


Fig. 2 Variation of hydraulically weighted conduit diameters (Dh) as a function of the distance from the tree top (l) for trees (a) FE15; (b) LD27; (c) PA44; (d) LD40 (see Table 1 for details). Insets represent the tree height : age relationship. Dotted lines, 95% prediction (wider) and confidence bands (narrower). Regression coefficients are reported in Table 3.

to be associated with a relevant decrease in the longitudinal growth rate: during the first 40 yr LD27 showed an average longitudinal increment of 70 cm yr⁻¹, whereas the last annual apical shoot was only 6 cm in length. In the tallest trees sampled (PA44 and LD40) parameter \bar{a} was 0.164 (95% CI

0.137–0.185) and 0.149 (95% CI 0.116–0.177), respectively (\bar{a} lower than 1/6 but not statistically different from 1/6). Both PA44 and LD40 showed an evident decrease in annual longitudinal growth during the past decades (Fig. 2c,d, boxes). In particular, LD39 grew by only 3 m in height in the

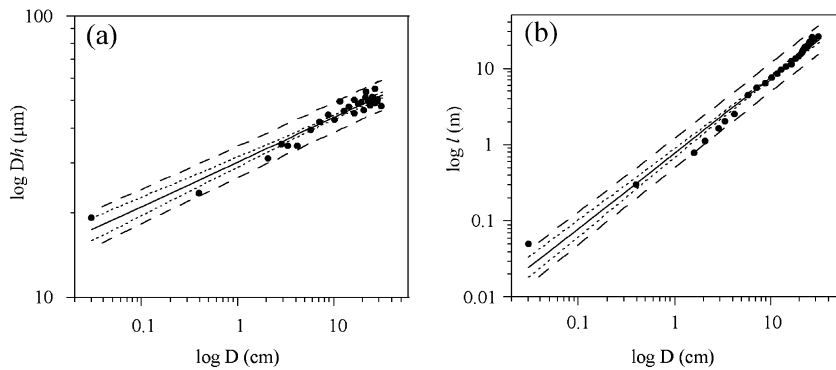


Fig. 3 Relationships between hydraulically weighted conduit diameters (Dh) vs D (stem diameter) at the same sampling height (a), and distance from the tree top (l) vs D (b) in the LD27 (*Larix decidua*) tree.

past 70 yr. The Dh of wood discs collected in the basal part of the stem (up to 15 m from the ground) even showed an inverse trend basipetally (a slight decrease) (Fig. 2d).

As predicted by the WBE model (equation 3), Dh and the corresponding stem diameter at different height (D) appeared strongly correlated (Fig. 3a; Table 3) and D accounted for more than 85% of Dh variation in all sampled trees. Parameter \bar{a} can be calculated from this relationship (see Appendix) using a measured degree of stem tapering (α). The slope of this relationship gives the parameter \bar{a}/a for each tree (e.g. for LD27 = 0.158). Thus, knowing α (0.951) and its correction (0.951×0.794) from equation 7b (Fig. 3b; Table 3), parameter a can be obtained ($a = 0.883$) and consequently $\bar{a} = 0.1575 \times 0.883 = 0.139$. Values calculated in this way were equal, in any tree, to those using equation 9b.

Interspecific tapering ratio (T)

The calculated Dh_0 and Dh_{N-1} both varied widely (from 5.37 to 182.06 μm) in the sampled trees (Table 2): marked differences were observed among species and within the same species in different environments. However, within the same plant, Dh_0 was always larger than Dh_{N-1} , proving the well known general pattern (Zimmermann, 1983; Meinzer *et al.*, 2001) of decreasing conduit dimensions distally.

The difference between Dh_0 and Dh_{N-1} increased with tree height, and the tapering ratio (T) appeared to be highly correlated to l ($r^2 = 0.88$; $P < 0.001$), independently of species, age, site features, altitude, stand structure, etc. (Fig. 4). A semi-epiphytic woody species (ID 36, Table 2), with different biomechanical constraints, also fits the relationship.

The exponent of the experimental relationship was 0.221 (Table 4), thus giving an interspecific averaged $\bar{a} = 0.186$ (95% CI 0.168–0.203) that is larger than $1/6$. The general relationship was also maintained, splitting the sampled trees into two groups: angiosperms and gymnosperms (Table 4). The angiosperms showed slightly higher tapering ($\bar{a} = 0.208$, 95% CI 0.175–0.249), probably because the very tall plants in our data set are all conifers (which separately have $\bar{a} = 0.184$, 95% CI 0.163–0.214). However, tapering between

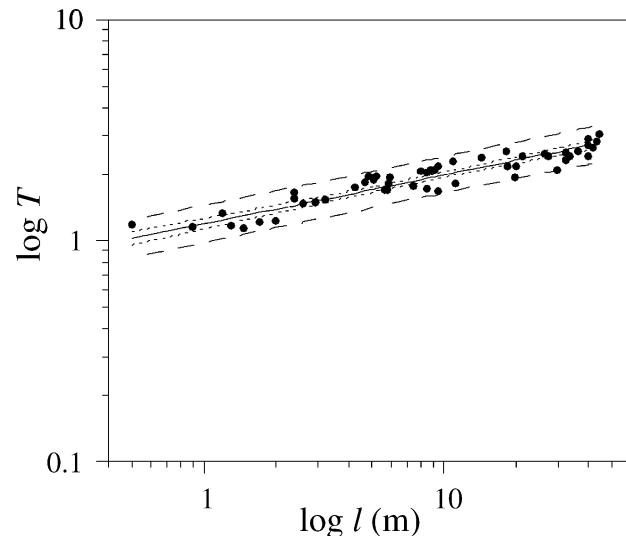


Fig. 4 Relationship between tapering ratio (T) and distance from the tree top (l) relative to the sampled trees of Table 2. Dotted lines: 95% prediction (wider) and confidence bands (narrower). Regression coefficients are reported in Table 4.

the two groups was not significantly different. The relationship in Fig. 4 allows us to estimate how T should change with tree height: the minimum value of T should be approx. 1 ($l = 0.45$ m), because for $T < 1$ there would be unrealistic reverse tapering. This would mean that for a plant with $Dh_{N-1} = 10$ μm , the dimension of xylem elements at the stem base (Dh_0) should be 15 μm at $l = 3$ m, 20 μm at $l = 10$ m, and approx. 28 μm at $l = 50$ m. Trees growing taller than 50 m should increase the dimension of xylem conduits by only 5 μm more (up to 33 μm) in order to be able to maintain optimal tapering up to a height of 100 m. Hence our sampled trees, with a height range from 0.5 to approx. 45 m, span over 85% of the Dh maximum variation.

Clearly, plants with wider apical conduits (ring-porous species) will have proportionally wider basal conduits (e.g. for $Dh_{N-1} = 80$ μm , Dh_0 will be 160 μm at $l = 10$ m). As predicted by WBE, the experimental relationship gives $T \approx 3$ (3.3) in the tallest trees (approx. 100 m). Notably, variation of

Table 4 Regression coefficients, r^2 and confidence intervals relative to relationship of Fig. 4

Model	N	Intercept	Slope	r^2	95% CI	
					Intercept	Slope
All	50	0.077	0.221	0.88	0.199–0.243	0.200–0.242
Angiosperm	27	0.067	0.248	0.82	0.027–0.101	0.208–0.297
Gymnosperm	23	0.069	0.219	0.90	0.017–0.101	0.194–0.255

Regression coefficients were also calculated dividing the measured trees into gymnosperms and angiosperms. All regressions have $P < 0.0001$. The assumption of normality of residuals, tested through the Shapiro–Wilks W -test, was met for all models.

conduit diameters per unit increase in tree height is much greater when the plant is relatively small ($l < 10$ m).

Discussion

Longitudinal variation of Dh within a tree ring

The analysis of xylem anatomy within a tree ring from tree top to stem base (and eventually also in the roots) could be the first step in testing the predictions of different models dealing with hydraulic architecture of trees.

Our measurements (Figs 1, 2) showed that, in a single tree ring, xylem conduits taper decreasing their diameter distally: this general trend is in agreement with many other reports (Zimmermann, 1983; Tyree & Ewers, 1991; Gartner, 1995; Joyce & Steiner, 1995; Aloni, 2001; Meinzer *et al.*, 2001; McCulloh & Sperry, 2005). This would definitely suggest that the structure of xylem conduits considered as 'cylindrical pipes' cannot be realistic and should be updated according to these findings.

Notably, tapering of xylem conduits appeared to be strictly dependent on distance from the tree top (Table 3), thus suggesting that, in a real tree, scaling of conduit tapering occurs in a stem with no visible furcations. This would demonstrate that the WBE prediction of how conduit tapering can be tested using the path length (tree height) instead of the macroscopic structure of branching, as often reported (McCulloh & Sperry, 2005), which evidently does not correspond to the 'WBE segments'. This would expand application of the WBE model to real plants.

The main question to be answered, however, is whether or not the observed tapering can fully compensate for growing in height. The most important quantitative prediction of the WEB model is that full compensation would occur if the conduit tapering parameter (\bar{a}) is above or, in the limiting case of very tall plants, equal to 0.167 (1/6). This sharp mathematical limit of optimized vascular network ($\bar{a} = 1/6$) cannot easily be compared for assessing the tapering in real trees, because the empirical degree of tapering always has a certain confidence interval and, more importantly, the variation of xylem tapering when plants grow taller occurs continuously. It is therefore reasonable to consider three different cases.

(1) Empirical \bar{a} significantly higher than 1/6 means full agreement with WBE predictions and suggests that the vascular network is optimized. (2) Empirical \bar{a} not different from 1/6 (the confidence intervals of empirical exponents include values even lower than 1/6) means that the vascular network structure is beginning to move from optimality towards conditions very close to optimality (suboptimal conditions). In this specific case, empirical \bar{a} must be considered again in agreement with the WBE predictions, even if a moderate increase in hydrodynamic resistance cannot be excluded in principle. (3) Empirical \bar{a} significantly lower than 1/6 means that the vascular network is not optimized and that the upper parts of the tree should experience water-stress conditions.

Trees with elevated height increment (FE15) showed \bar{a} significantly above the predicted threshold. This 'over-tapering' conduit structure leads, in addition to the resistance of the entire path being almost independent of tree height, to the total hydraulic resistance being lower (Becker *et al.*, 2000) than when tapering is at the lowest threshold. Notably, the WBE model indicates *minimum* tapering, so it could be even higher, but taller plants would tend to minimize tapering as much as possible (Enquist, 2002). Interestingly, as a direct consequence of the WBE model, it can be noted that in order to maintain an optimized vascular network, a growing tree must progressively increase the dimensions of the xylem elements at the stem base.

Instead, trees approaching their maximum height, PA44 and LD40 (Fig. 2c,d), showed that near the base (right side of the plot) Dh appeared rather constant (points below the regression line), determining a suboptimal xylem structure, thus decreasing the value of the estimated exponent (\bar{a} not different from 1/6). James *et al.* (2003) also observed a higher conduit diameter variation near the tree top but, in some trees, a relatively constant diameter through the lower part of the trunk.

In both cases the empirical \bar{a} , even if not different from 1/6, seems to suggest that trees are in transition from suboptimal to nonoptimal conditions, and this is associated with a relevant reduction of longitudinal increments in the past decades.

The longitudinal Dh profiles of tree LD27 (Fig. 2b, box) showed a tapering parameter \bar{a} below the minimum predicted

by WBE (the vascular network is not optimized). This can occur because each different tree species, in a given environment, is characterized by a maximum lumen dimension that basically depends on trade-off between hydraulic efficiency and vulnerability to cavitation (Zimmermann, 1983; Tyree, 2003). Whatever the environmental factor driving the selection of a given maximum conduit dimension, such as freezing events (Pittermann & Sperry, 2003) or water deficit during drought (Martínez-Vilalta *et al.*, 2002), any individual tree has a limited capacity to increase conduit dimensions at the stem base compared with that of apical conduits. The achievement of a maximum lumen area leads to the well reported plateau of conduit dimension, in a transverse section, when plotted against cambial age from the inner growth ring in old trees (Mencuccini & Magnani, 2000; Mencuccini, 2002).

When vascular network is not optimized (empirical $\bar{a} < 1/6$), hydraulic resistance should increase with tree height, that is, the tree cannot fully compensate for the increase in path length. It can therefore be speculated that very tall trees, for example those measured by Koch *et al.*, 2004), in analogy with some of our trees, should have nonoptimal conduit tapering that could be consistent with the lower stomatal conductance and assimilation rate measured in the needles at the tree top.

This suggests that the WBE model deals only with actively growing plants when there are no limitations in increasing the dimension of xylem conduits at the stem base. In a natural situation, this condition is fulfilled during the juvenile stage when height increment is near maximum (Bond, 2000). After this stage, the vascular system can turn from a suboptimal to a nonoptimal structure, leading to an increase in path resistance and a decrease in tree performance.

This would also mean that the whole-plant hydraulic conductance decreases nonlinearly as the plant grows taller (as noted by Midgley, 2003), because resistance would be maintained relatively constant in a juvenile stage, in agreement with Barnard & Ryan (2003) who found no differences in whole-tree conductance comparing only young *Eucalyptus* trees.

Indeed, many papers aimed at supporting the hydraulic limitation hypothesis (Ryan & Yoder, 1997) reported differences in measured parameters (hydraulic conductance, leaf-specific hydraulic conductance, assimilation, etc.) between two age classes, namely young and old trees (optimal vs suboptimal) (Hubbard *et al.*, 1999). When more than two age classes are considered, the differences very often appeared significant only between the oldest and the others, with no clear trend (Delzon *et al.*, 2004).

Notably, trees can withstand suboptimal and nonoptimal conditions in a given site (empirical $\bar{a} = 0.167$) for many years or centuries (as the oldest trees in the world suggest). Moreover, the decrease in tree performance with ageing should be species-specific, for example, depending on the

capacity to osmoregulate, or to drop leaf water potential, or to change the cell-wall modulus of elasticity, or depending on other types of acclimation.

An awareness that the WBE model can be applied strictly (when dealing with an ontogenetic perspective) only to a juvenile stage (e.g. there are no limitations in enlarging conduits at the stem base and corresponding elevated increments in height are possible) suggests that the hydraulic limitation hypothesis and the WBE model are not in opposition, but rather are two different perspectives of the same general phenomenon.

Interspecific tapering ratio (T)

One of the most important consequences of the WBE model is the perspective that evolution by natural selection has acted to minimize hydrodynamic constraints through the vascular network (Enquist, 2003). This, importantly, would mean that all plants should have converged towards the same structure of conduit tapering to minimize water-transport costs. Our measurements of tapering ratio (T) showed that plants of different species in different sites seemed to converge towards the same degree of tapering (Fig. 4). The estimated \bar{a} (0.186) fully supports the WBE predictions, even if the model does not take into account all the complexities of the transport network in real plants. For example, it does not consider the effect of horizontal flow between parallel tubes (resistance of the pits). A recent paper (Sperry *et al.*, 2005) showed that cell-wall resistance is an almost constant fraction (approx. 50%) of the lumen resistance, which is accounted for by the WBE model. This would mean that no effects on the exponent values are expected when considering both the cell wall and lumen resistance.

Notably, the relationship $T-l$ (Fig. 4) must not be considered within an ontogenetic perspective (unlike relationship $Dh-l$ of Fig. 2), but within an interspecific (phylogenetic) perspective, which is very similar to the approach of West *et al.* (1999a). They considered an ideal 'plant' actively growing (or similarly, a series of different species with different heights all in a juvenile stage); by sampling different species of different heights we have studied many individuals, most of them probably actively growing and thus fully representative of the conditions in the WBE model.

A common and possibly universal structure of conduit tapering in the stems of woody plants has been demonstrated empirically, suggesting that a simple compensation strategy (increasing sapwood permeability by increasing lumens of xylem conduits at the stem base) seems to have evolved in order to minimize total hydrodynamic resistance: without such compensation, trees seem to be unable to grow taller because the topmost leaves would experience water-stress conditions.

Moreover, as tapering is demonstrated to be strictly path length-dependent, it should be expected that Dh increases

progressively also towards the rootlets. Martínez-Vilalta *et al.* (2002) and McElrone *et al.* (2004) showed that diameters of xylem conduits are wider in roots than in the stem of the same tree, thus allowing (in agreement with WBE) roots to grow in length with no relevant increase in the whole-path resistance.

However, we must be very careful to compare WBE predictions within an ontogenetic perspective (e.g. comparing different trees throughout a chronosequence): in this case the model certainly cannot correctly predict exponents in mature-old plants (as noted by Mencuccini, 2002) because each species has a limited capacity to taper xylem conduits. This knowledge can reconcile most (if not all) measurements on hydraulic limitation carried out on chronosequences, which would widely suggest an increase in plant hydraulic resistance in old trees, with the WBE model.

However, within a general phylogenetic perspective, the WBE model seems correctly to point out the main constraints that have driven the evolution of plant size.

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Appendix

The WBE 'plant'

The WBE model proposes a structure of an 'average idealized plant' that may appear rather far from a real tree. This simplified structure and some important approximations in the relationships have to be considered carefully when testing WBE predictions.

In the WBE plant, water is considered to move through single conduits in parallel from roots to leaves. This simplification might seem particularly inadequate to describe water movement in a highly complex xylem network but, as will be seen, this simplification does not appear substantially to affect the capacity of the model to fit the real network. Branching architecture is believed to be self-similar with a certain degree of bifurcation (typically 2: each branch is split in two). Each branch corresponds to a 'segment' and the total maximum number of segments (N) is predicted to be $c \cdot 20$ in the tallest trees (West *et al.*, 1999a). Regular branching is a mathematical abstraction, suggesting that the WBE segments and the macroscopic structure of a tree, number of branches, regularity of branching pattern or internodal segments in the main stem (Becher *et al.*, 2003) are not matched. This means, for example, that the number of WBE segments (20 in the tallest tree) and internodes cannot be compared because very old

plants should have many hundreds of internodes. Thus, considering the last apical shoot length (Becher *et al.*, 2000) as 'terminal segment' can lead to serious misinterpretations in model validation.

As suggested by Becker *et al.* (2000), the most useful approach for testing the WBE model is to try and express the predicted tapering parameter as a function of tree height, which can easily be measured, instead of as a function of number of WBE segments. For this a cautious reanalysis of the WBE relationships is necessary.

Using the original notations (West *et al.*, 1999a,b), in a given tree, moving from segment k (e.g. stem base) to $k + 1$ (where k is an arbitrary level), branch radius (r) and conduit radius (a) should scale as follows (independently of k):

$$\beta_k = \frac{r_{k+1}}{r_k} = n^{-a/2} \quad \text{Eqn 1}$$

$$\bar{\beta}_k = \frac{a_{k+1}}{a_k} = n^{-\bar{a}/2} \quad \text{Eqn 2}$$

where β_k , $\bar{\beta}_k$ are, respectively, the scaling of the branch and xylem conduits among different k levels; and a , \bar{a} and n are parameters characterizing the plant architecture.

In the 'average idealized plant' proposed by WBE, $a = 1$ (the branching architecture is area-preserving, as suggested by Leonardo da Vinci); $\bar{a} = 1/6$ (hydrodynamic resistance is minimized); and $n = 2$ (plant is bifurcated). In this case $\beta_k = 0.70$ (the daughter segment is 70% the diameter of the parent one) and $\bar{\beta}_k = 0.94$ (the daughter xylem conduit is 94% the diameter of the parent one). It should be noted that the scaling exponent may change if the idealized conditions are not fulfilled, as stressed by West *et al.* (1999a) and Enquist (2002).

Parameter \bar{a} is crucial in the WBE model: it is related to the degree of tapering in xylem conduits. It can be demonstrated that for values of $\bar{a} = 1/6$ (0.167) the conduit resistance does not change significantly with increase in path length (West *et al.*, 1999a; Becker *et al.*, 2000). On the contrary, for $\bar{a} < 1/6$ the resistance increases as trees grow taller ($\bar{a} = 0$ is the condition with the pipe model, precisely cylindrical conduits).

Combining equations 1 and 2, it follows that for each k level:

$$a_k \propto r_k^{\frac{\bar{a}}{a}} \quad \text{Eqn 3}$$

that is, radii of the conduit elements at different levels and those of the branches scale allometrically (branch radius, r_k and branch diameter, D can be used indifferently). Notably, the relationship (which has to be demonstrated) between conduits and branch dimension in different positions along the stem (or branch) would allow us to obtain the value of the exponent \bar{a}/a .

However, in the WBE model the length of segments must also scale properly as:

$$\gamma_k = l_{k+1}/l_k \quad \text{Eqn 4}$$

If the network of conduit elements is designed realistically in order to serve all cells (is volume-filling), then (West *et al.*, 1999a):

$$\gamma_k = l_{k+1}/l_k = n^{-1/3} \quad \text{Eqn 5}$$

Combining equations 1 and 5 again gives for each k level:

$$l_k \propto r_k^{2/3\alpha} \quad \text{Eqn 6}$$

An optimized resource-distribution network should lead to allometric scaling between segment lengths and their diameters.

It has been reported extensively in the forestry literature (Niklas, 1994) that an optimal mechanical relationship between branch (or stem) length and diameter (stem tapering) should also exist. The allometric relationship is:

$$l \propto D^\alpha \quad \text{Eqn 7}$$

where D is the stem diameter (r can be used indifferently) with respect to distance from the tree top (l). An elastic similarity model should lead to $\alpha = 2/3$ and this generally holds for large branches (West *et al.*, 1999a). However, it has been demonstrated that, during ontogenesis, α can vary widely from $\alpha > 1$ in young plants, and/or in trees growing in very dense stands, to $\alpha = 1/2$ in very old trees (Niklas, 1994), because height increments tend to be very small while stem diameter continues to increase. In any case, α can be assessed for each particular tree.

Comparing equation 6 (which considers hydrodynamic constraints) and equation 7 (which considers mechanical constraints, and can be written as $l \propto r^\alpha$) gives:

$$\alpha = 2/3a \quad \text{Eqn 8}$$

Therefore the value of a in each specific tree, which can be quite far from the area preserving 'rule' (Horn, 2000), can be calculated after having estimated α using equation 7.

Moreover, combining equations 3 and 7 where $r \propto l^{1/\alpha}$:

$$a_k \propto l_k^{\frac{\bar{a}}{\alpha a}} \quad \text{Eqn 9}$$

where conduit diameter (a_k) is expressed as a function of length of segment k (l_k): this equation appeared to depend on conduits tapering parameter (\bar{a}) and on the product αa (which, assuming a volume-filling network, can be considered constant at $2/3$). Overall, the exponent of equation 9, given the WBE model conditions, should be equal to 0.25 ($a_k \propto l_k^{0.25}$), but higher values are considered in agreement with WBE.

The relationship between total distance from the tree top (l , tree height) and l_k must now be defined. Importantly, tree height (l) was estimated by WBE with an approximate relationship (West *et al.*, 1999a) as:

$$l_{\text{app}} \approx l_0/(1 - n^{-1/3}) \quad \text{Eqn 10}$$

where l_{app} represents the total plant height calculated approximately, and l_0 is the length of the first (basal) segment. This means that $l_{\text{app}} \propto l_0$, so l_{app} can be used in equation 9 instead of l_k . This approximation must be considered carefully because it has a relevant impact on estimated exponents defining conduit tapering (\bar{a}), and also on other allometric exponents.

Indeed, without approximation (Becker *et al.*, 2000), l should be calculated as the sum of the different k segments ($l_0 + l_1 \dots l_N$) that is a geometric progression at rate $n^{-1/3}$ so that:

$$l = l_0[(1 - n^{-N/3})/(1 - n^{-1/3})] \quad \text{Eqn 11}$$

where N = number of segments. For elevated N (e.g. $N > 10$), $l_{\text{app}} \rightarrow l$, but for small plants the difference is significant, therefore the error of estimation of l is dependent on N which, as mentioned, cannot be assessed on a real tree. Using the WBE parameters ($\gamma = 2^{-1/3} = 0.794$), and assuming a given length of terminal segment (0.25 m), we calculated both l_{app} and l using equations 10 and 11 at different N , from 1 to 20. That is, given the supposed conditions, comparing trees from 0.25 to approx. 96 m in height. Comparing l_{app} vs l (Fig. 5), it is possible to quantify the difference in tree height between the two calculation methods, and the exponent of the fitting curve (0.794) could be used as correction factor which compensates for the approximation proposed by the WBE model when calculating total plant height. This correction factor is larger for a small plant (correction is dependent on N), however, a constant one may be considered simpler for our aims and, importantly, more conservative because we can

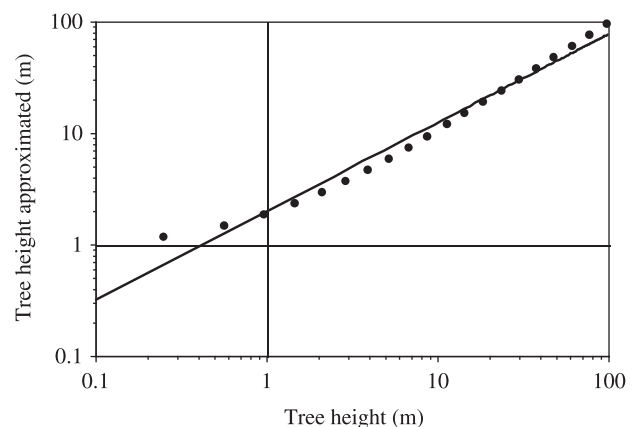


Fig. 5 Relationship between total plant height calculated using the WBE approximation (tree height approximated) and the sum of the length of all segments, which represents the real tree height ($Y = 2.023x^{0.794}$, $r^2 = 0.978$, $P < 0.001$). This relationship permits a simple correction factor to be estimated in order to compare WBE model predictions with empirical measurements.

be sure that the calculated parameters (\bar{a} in particular) might be slightly underestimated, but never overestimated.

Correction of l must be taken into account when comparing empirical measurements with theoretical WBE exponents, otherwise a systematic and relevant underestimation of the tapering parameter (\bar{a}) occurs. Equation 9 thus becomes:

$$a_k \propto l^{0.794 \frac{\bar{a}}{\alpha a}} \quad \text{Eqn 9b}$$

Similarly equation 7 becomes:

$$l \propto D^{0.794\alpha} \quad \text{Eqn 7b}$$

The above relationships and correction factor allow us to estimate, from empirical measurements, the main parameters related to xylem tapering of the WBE model in two ways that give the same results: (1) \bar{a} can be calculated using equation 3 after having estimated α from equation 7b and a from equation 8; (2) directly using equation 9b multiplying the estimated exponent for 0.84 [(2/3)/0.794] thus again obtaining \bar{a} . This parameter can, in the same conditions, be compared with that predicted by WBE, which should be ≥ 0.167 (1/6).



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