

Effect of height on tree hydraulic conductance incompletely compensated by xylem tapering

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Summary

1. The hydraulic limitation theory proposes that the decline of forest productivity with age is a consequence of the loss of whole-plant and leaf-specific hydraulic conductance with tree height caused by increased friction. Recent theoretical analyses have suggested that tapering (the broadening of xylem vessel diameter from terminal branches to the base of the stem) could compensate completely for the effect of tree height on hydraulic conductance, and thus on tree growth.

2. The data available for testing this hypothesis are limited, but they do not support the implication that whole-tree and leaf-specific hydraulic conductance are generally independent of tree height. Tapering cannot exclude hydraulic limitation as the principle mechanism for the observed decline in growth.

3. Reduction of the leaf-to-sapwood area ratio, decreased leaf water potential, loss of leaf-cell turgor, or osmotic adjustments in taller trees could reduce the effect of increased plant hydraulic resistance on stomatal conductance with height. However, these mechanisms operate with diminishing returns, as they infer increased costs to the tree that will ultimately limit tree growth. To understand the decline in forest growth, the effects of these acclimation mechanisms on carbon uptake and allocation should be considered.

Key-words: hydraulic limitation theory, leaf-specific conductance, pipe-model, plant hydraulic architecture, WBE

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Introduction

The growth rate of trees declines with age. The leading hypothesis to explain this is decreased hydraulic conductance as a consequence of increased tree height (Ryan & Yoder 1997). Assuming a simple pipe model of the plant's hydraulic system (a leaf attached to a unit stem and a unit root pipe: Shinozaki *et al.* 1964b; Shinozaki *et al.* 1964a; Jarvis 1975), the hydraulic path length – and along with it, the resistance of the plant's hydraulic system caused by friction – increases with tree height (Whitehead & Hinckley 1991). Increased stomatal closure to prevent a breakdown of the hydraulic transport system because of cavitation (Ryan & Yoder 1997), or lower leaf water potentials triggering leaf-cell turgor loss or osmotic adjustment, would reduce daily net photosynthesis. Less growth would be the ultimate result, as the other carbon costs (respiration, foliage production and root growth) vary little, or increase slightly with stand age (Ryan & Waring 1992; Mencuccini & Grace 1996b). Increased respiration by itself, as a consequence of the increasing amount of living woody biomass with tree size (Yoda *et al.* 1965),

cannot explain the decline in forest productivity. Maintenance respiration of the sapwood accounts for only 5–12% of the annual C fixation (Ryan *et al.* 1995), and the larger fraction of respiration is associated with growth processes that generally decline as growth declines (Ryan & Waring 1992).

The hydraulic limitation theory has been controversial (Becker, Meinzer & Wullschlegel 2000b; Bond & Ryan 2000; Mencuccini & Magnani 2000). From the formal hydraulic model of Whitehead, Edwards & Jarvis (1984), one might expect acclimation of the ratio between supporting sapwood area and transpiring leaf area. Such an acclimation could result in homeostatic balance between the plant's transport capacity and transpirational demand of the leaves, to either minimize or compensate for the potential hydraulic limitation of stomatal conductance caused by height. Tree height would still affect tree growth, because hydraulic adjustment would increase the relative share of C production that is allocated to sapwood construction and maintenance, thereby diminishing the returns per unit C investment.

Recent theoretical analyses (West, Brown & Enquist 1999; Enquist 2002) have suggested that the observed

tapering of xylem conduits, i.e. the broadening of xylem vessels basipetally (Zimmermann 1978; Pothier, Margolis & Waring 1989), could produce hydraulic homeostasis of the plant. This conclusion is derived from a model of plant branching networks based on the assumption of minimized internal transport resistance while maximizing the plant's surface area. This model describes the plant's architecture and hydraulic system as a self-similar fractal, and in a more detailed way than the pipe model, as it allows for branching and for changes in the xylem anatomy between different branch segments. A basipetal increase in conduit diameter would permit the total resistance of a tube running from trunk to petiole to remain constant, independent of tube length (West *et al.* 1999).

Here, the published evidence relevant to the scaling of hydraulic resistance, as predicted by the model of West *et al.* (1999), is reviewed. I discuss whether the data support the assumptions of the fractal model and the conclusions drawn from it. The aim is to evaluate whether tapering would suffice to discard the hydraulic limitation theory as the most likely explanation for the observed age-related decline in forest productivity.

Can vessel tapering compensate for height growth?

The architecture of the branching network in the general plant model of West, Brown & Enquist (1999) (hereafter WBE) is described by the scaling of branch diameter, branch length, and conduit diameter of adjacent branch segments of the tree according to simple power laws (Appendix, equation A1). Three parameters define the relationships between branch diameter, branch length, and conduit diameter of adjacent branch levels. Conduits are assumed to operate as if they were tightly bundled, not interconnected, and to have a uniform diameter within a branch segment. They form a continuous tube, represented by a linear series of vessels, conserving the total numbers of tubes in each segment. Thus total plant hydraulic resistance depends linearly on the total resistance of a single tube. Total plant resistance can be approximated by the Hagen–Poiseuille formula, which describes capillary flow (Nobel 1983; Becker, Gribben & Lim 2000a). Tapering is included in the model by scaling conduit diameter such that it increases basipetally, thus allowing the ratio of conductive to non-conductive tissue to vary between branch segments.

An intuitive way to see why tapering can compensate for the longer path length of the tree with increasing tree height in the WBE model is to look at total path length L and resistance Z with increasing number of segments. In the WBE model length and conduit diameter, and thus resistance, of the petiole are assumed to be invariant, thus the total path length and resistance of a single tube can be described as simple sums of petiole length l_N and resistance Z_N , respectively, with N the number of branching levels in the network:

$$L = \sum_{k=0}^N l_k = l_N \sum_{k=0}^N m^{N-k} \quad (\text{eqn 1})$$

and

$$Z = \sum_{k=0}^N Z_k = Z_N \sum_{k=0}^N i^{N-k} \quad (\text{eqn 2})$$

The scaling factors m and i linking the two adjacent levels k and $k - 1$ can be derived from the basic equations of WBE (see Appendix for derivations):

$$m = l_{k-1}/l_k = n^{\beta/3} \quad (\text{eqn 3})$$

$$i = Z_{k-1}/Z_k = n^{\beta/3-2\bar{\alpha}} \quad (\text{eqn 4})$$

where n is the number of daughter branches per branch, and $\bar{\alpha}$ and β are the scaling factors for segment conduit diameter and length, respectively. For simplicity, n , $\bar{\alpha}$ and β are assumed to be level-independent, that is, constant for all branch segments (although, as shown below, this is not a requirement). Three conclusions can be drawn from the limiting behaviour of length and resistance for a large number of branching levels.

- (1) For a network without tapering ($\bar{\alpha} = 0$, pipe model), hydraulic resistance grows in proportion to path length ($m = i$), consistent with the hydraulic limitation theory in its original form (Yoder *et al.* 1994, Ryan, Binkley & Fownes 1997).
- (2) Any (level-independent) tapering ($\bar{\alpha} > 0$) will cause hydraulic resistance to grow more slowly than path length, as then m always exceeds i . The extent to which this influences the capacity of trees to compensate for height growth is sensitive to assumptions about the scaling of tapering and branch length (Fig. 1; Becker *et al.* 2000a).

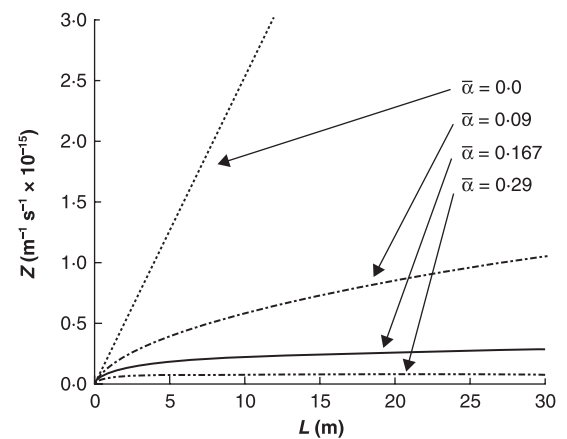


Fig. 1. Total plant hydraulic resistance (Z , in $\text{m}^{-1} \text{s}^{-1} \times 10^{-15}$) as a function of total path length (L , in m), assuming that $l_N = 0.05$ m, $a_N = 10$ μm , and $\beta = 1$ for different tapering coefficients $\bar{\alpha}$. 0 is the pipe-model theory; 0.167 WBE, 0.09 and 0.29 are estimates of the 95% confidence interval of the tapering parameter estimated by Becker *et al.* (2001), assuming $\beta = 1$.

- (3) Total plant hydraulic resistance (equation 2) approaches an asymptotic value with increasing number of segments when $i < 1$. Unlike hydraulic resistance, path length (equation 1) always increases in the WBE model, because $m \geq 1$ for any plausible value of β . Thus total plant hydraulic resistance becomes independent of total path length when the tapering exponent $\bar{\alpha}$ fulfils the inequality $\bar{\alpha} > \beta/6$ (equation 4). Two assumptions are introduced in the WBE model: that biomechanical constraints and tapering are uniform; and that the branching network is volume-filling, leading to the special case of a self-similar fractal model with $\beta = 1$ (West *et al.* 1999). Equation 4 thus implies for the WBE model that $\bar{\alpha}$ would have to be greater than or (in the limiting case of very large trees) equal to $1/6$.

The original version of WBE (West, Brown & Enquist 1997) minimized the energy required to distribute resources without any variation in xylem diameter. Tapering was introduced in a subsequent version of the model, ostensibly because hydraulic constrictions would otherwise preclude the existence of tall trees, and cause leaves high in the canopy to receive less water than leaves deeper in the canopy (West *et al.* 1999). However, WBE describes a fractal-like structure, so that all leaves have equal supply irrespective of their position within the canopy and even with zero tapering, as all tubes have equal path length.

Evidence for even quite small trees (Zimmermann 1978; F. Magnani, unpublished data; cf. Mencuccini 2002) indicates that the degree of tapering diminishes basipetally. Also, James *et al.* (2003) found that conduits tapered within the crown of several tropical tree species, but lumen diameters were virtually constant below the base of the crown. These results raise concerns that the assumption of a uniform tapering might be too strong (Becker & Gribben 2001; Mencuccini 2002). A declining rate of tapering does not necessarily invalidate tapering as a mechanism to avoid the adverse effects of tree height, contrary to the assumption of Becker & Gribben (2001). In the derivation of equation 4, no assumptions were made that require the coefficients to be level-independent (see Appendix). In fact, any combination of n , β and $\bar{\alpha}$ that results in $i < 1$ for a particular segment k will achieve this. It is not necessary to assume fractality to minimize the hydraulic resistance and to decouple total plant hydraulic resistance from plant height, agreeing with the more mathematically exact account of Dodds, Rothman & Weitz (2001).

Recent results from McCulloh *et al.* (2003) suggest for vines and ring-porous trees that the total number of conduits per segment varies between adjacent segments, conflicting with the assumption made in WBE. This would be expected from the application of Murray's law to the hydraulic architecture of plants. If conduits serve transport purposes only (as in ring porous trees), the construction cost of conduits can be assumed to be

proportional to conduit volume (McCulloh *et al.* 2003). Murray's law applied to plant vascular systems suggests that, for such a case, the original pipe model ($\bar{\alpha} = 0$ or no taper) would be optimal for a constant number of conduits. Any degree of taper without variation in total tube number would be less efficient, and would therefore violate the energy minimization principle. If the number of conduits were allowed to vary between segments in the WBE model, as suggested by the data of McCulloh *et al.* (2003), the required taper to decouple hydraulic resistance from path length cannot be calculated by equations 1–4. Whole-plant hydraulic conductance then becomes difficult to predict, limiting the capacity of WBE to predict the whole-plant effect of tapering on hydraulic conductance.

Are the predictions of WBE confirmed by observations?

To judge whether WBE adequately describes the hydraulic architecture of trees, the distribution of hydraulic resistance within the tree needs to be modelled correctly, and the model predictions of the scaling between size parameters (e.g. diameter) and hydraulic resistance should agree with relevant measurements. Unfortunately, although plant hydraulic architecture has long been identified as an important subject (Zimmermann 1978), surprisingly few relevant data are available. Only a few studies have been designed to exclude the effect of differences in environmental factors (e.g. understorey vs canopy trees, unequal access to groundwater resources; Bond & Ryan 2000), and few analyses allow the assessment of whole-plant hydraulic resistance (Mencuccini 2002).

West *et al.* (1999) claimed that the degree of tapering predicted by their model agrees with the observed distribution of hydraulic resistance in the two *Acer* species analysed by Yang & Tyree (1993). However, no data on the scaling of conduit tapering and branch length are available from Yang & Tyree (1993) to confirm that the observed agreement is a consequence of correct assumptions of the WBE model. In a re-analysis of the data of Zimmermann (1978), Becker *et al.* (2001) found that the parameter estimate for the tapering parameter $\bar{\alpha}$ is sensitive to the assumptions made on the (unknown) scaling of segment length. As only a slight deviation will yield strongly different results in terms of overall hydraulic resistance (Fig. 1), these data cannot indicate if the predicted degree of tapering is sufficient to compensate for height growth.

Becker *et al.* (2001) showed that WBE is potentially useful in interpreting conduit tapering by producing a good fit of the model to the data of Zimmermann (1978), although the estimated value of the tapering parameter $\bar{\alpha}$ was uncertain. A meta-analysis of existing studies on tree hydraulic architecture by Mencuccini (2002) corroborates the capacity of WBE to predict the scaling of hydraulic conductivity of segments to the segment's diameter, illustrating the fact that larger

Table 1. Allometric scaling of hydraulic conductivity of stem-segment hydraulic conductance to stem-segment diameter, and above-ground hydraulic conductance to diameter at breast height and above-ground biomass based on reduced-major-axis regression (cf. Mencuccini 2002)

Species	Segment diameter			Stem diameter			Biomass			Authors
	<i>b</i>	SE	<i>P</i>	<i>b</i>	SE	<i>P</i>	<i>b</i>	SE	<i>P</i>	
<i>Acer rubrum</i>	2.66	0.05	ns	1.72	0.08	***	0.65	0.03	**	Yang & Tyree (1994)
<i>Acer saccharum</i>				1.68	0.12	*	0.65	0.05	ns	Tyree & Sperry (1988), Yang & Tyree (1994)
<i>Pinus sylvestris</i>	2.63	0.08	ns	1.23	0.14	***	0.50	0.05	***	Mencuccini & Grace (1996a)
<i>Pinus banksiana</i>				1.34	0.22	*	0.52	0.09	*	Pothier <i>et al.</i> (1989)
All four species				1.32	0.06	***	0.54	0.02	***	

Analyses using ordinary least-squares regression obtained similar results.

Abbreviations: *b* = regression coefficient; SE = standard error; *P* = significance of *t*-test for difference between regression coefficient and theoretical slopes predicted by the WBE model (2.67 for segment diameter; 2.0 for stem diameter; 0.75 for biomass).

ns = Not significantly different, *P* > 0.05; **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

stems are more permeable (Mencuccini & Grace 1996a; Becker *et al.* 2000b). However, the data do not support the scaling of whole-tree hydraulic resistance to diameter (and total plant biomass): the observed scaling coefficients are smaller than predicted (Table 1), and whole-plant hydraulic conductance declines with increasing size, contradicting the WBE model.

Smaller scaling coefficients than predicted by WBE do not necessarily suggest that the water supply to leaves (leaf-specific hydraulic conductance) is reduced with height, as data also support the hypothesis that leaf-to-sapwood area ratio declines with tree height (Whitehead *et al.* 1984; Mencuccini & Magnani 2000; McDowell *et al.* 2002). Yet there is a significant reduction of leaf-specific hydraulic conductance with height in three out of the four studies summarized in Table 1; in the fourth, the sample size was too limited to draw any significant conclusion (Mencuccini *et al.* 2000). Similar results were obtained for *Pinus ponderosa* (Ryan *et al.* 2000) and *Fagus sylvatica* (Schäfer, Oren & Tenhunen 2000). Saliendra, Sperry & Comstock (1995) found no evidence for acclimation of either specific sapwood conductance or leaf area with increasing path length in *Betula occidentalis*, however, there was a more than twofold decline in whole-plant leaf specific conductance between juvenile and adult individuals. Apparently, the acclimation of leaf area with height is not sufficient to prevent leaf-specific hydraulic conductance from declining with height; it merely mitigates the reduction in leaf-specific hydraulic conductance (McDowell *et al.* 2002).

Does acclimation to increased hydraulic resistance affect forest growth?

A recent study on a moist-tropical *Eucalyptus saligna* plantation suggested that a decline in growth occurred, even though an acclimation of leaf area with height compensated for the hydraulic effect of height (Barnard & Ryan 2003). Direct and indirect evidence suggests that maintenance and growth respiration costs of the

stem are not greater in taller trees (Ryan *et al.* 1992; Mencuccini & Grace 1996b), so increasing respiration cannot be invoked as an explanation. Instead, the hydraulic limitation theory might need to be extended. Even in the absence of any hydraulic limitation related to path length, tree height might affect leaf water potential through gravity (Woodruff, Bond & Meinzer 2004). Osmotic adjustments as a response to loss of turgor (Woodruff *et al.* 2004), or increased leaf construction costs to maintain lower minimum leaf water potentials (Barnard & Ryan 2003; Koch *et al.* 2004) in taller trees, could only partly offset reductions in growth, as these adaptations would divert resource allocation from photosynthesis. Similarly, increased below-ground C allocation and decreased leaf-to-sapwood area ratios to minimize the increase of total plant hydraulic resistance with height (Magnani, Mencuccini & Grace 2000) could mitigate the effect of tree height on stomatal conductance, but only at increased costs per unit foliage, thereby ultimately limiting tree growth.

Concluding remarks

The WBE model shows that tapering could theoretically compensate for the effect of tree height on hydraulic resistance, and therefore limit the hydraulic effect of tree height on tree growth. The predicted scaling of hydraulic conductance matches observed scaling on a segment scale, but not at more aggregated levels. Thus, either the WBE model lacks an important process, or one or more of its assumptions (e.g. conservation of total tube number; uniformity of tapering; or the volume-filling and area-preserving branching network) are invalid. However, the data available are insufficient to evaluate all the assumptions underlying the WBE model, even though they indicate that the assumption of constant tube numbers is too strong. Nevertheless, the data do not support the prediction of the WBE model that whole-tree hydraulic conductance is generally independent of height. Tapering cannot exclude that the hydraulic limitation hypothesis describes

the principal mechanism for the observed decline in stand productivity with age. Instead, the hydraulic limitation theory should be extended to account for hydraulic acclimation and the associated consequences for gross primary production and C allocation. For the mechanistic modelling of forest development with age, it is essential to understand tree hydraulic architecture and its implications for tree growth.

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Appendix

The initial equations from the West *et al.* (1999) model (WBE) describe a fractal network for the adjacent levels of branches k and $k + 1$:

$$\frac{r_{k+1}}{r_k} = n_k^{-\alpha_k/2} \quad \frac{a_{k+1}}{a_k} = n_k^{-\bar{\alpha}_k/2} \quad \frac{l_{k+1}}{l_k} = n_k^{-\beta_k/3} \quad (\text{eqn A1})$$

where n is the number of daughter branches, and α , $\bar{\alpha}$ and β are the scaling coefficients for branch diameter r , tube radius a and segment length l , respectively. As the WBE assumes invariant petiole conduit diameter and length, it is more convenient to invert the equations in equation A1. The hydraulic resistance Z of a single

Zimmermann, M.H. (1978) Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Forest Research* **56**, 2286–2295.

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tube j within a branch segment k can be approximated by the Hagen–Poiseuille formula, which describes capillary flow. This formula neglects the substantial contribution of pit membrane resistance to total resistance, but this does not affect relative comparisons of resistance (Nobel 1983; Becker *et al.* 2000a).

$$Z_k^j = [(8\eta l_k)/(\pi a_k^4)] \quad (\text{eqn A2})$$

where η is viscosity. Assuming that the number of total tubes is preserved, the ratio of resistances i between adjacent levels is given by:

$$i = \frac{Z_{k-1}}{Z_k} \propto \frac{l_{k-1}}{a_{k-1}^4} \cdot \frac{a_k^4}{l_k} \rightarrow \frac{n_{k-1}^{-4\bar{\alpha}_{k-1}/2}}{n_{k-1}^{-\beta_{k-1}/3}} = n_{k-1}^{\beta_{k-1}/3 - 2\bar{\alpha}_{k-1}} \quad (\text{eqn A3})$$