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Letter to the Editor

The quarter-power scaling model does not imply size-invariant hydraulic resistance in plants

1. Introduction

West, Brown, and Enquist (1997, 1999) propose an integrated model of the structure and allometry of plant vascular systems, which has come to be known as the 'WBE model' (Enquist, 2002). The WBE model weaves together area-preserving branching (Leonardo da Vinci), elastic similarity (Greenhill, 1881), the constant ratio of foliage mass to sapwood area (Shinozaki et al., 1964), and elements of fractal geometry (Mandelbrot, 1983) into a cohesive quarter-power scaling theory for trees and other plants. This model has become widely cited, but it also has been subjected to both theoretical and empirical criticism. For example, Kozlowski and Konarzewski (2004) argue that the assumption of fixed size of the terminal internode leads to inconsistencies, while the emprical results by Meinzer et al. (2005) are in conflict with the model predictions on conducting cross-sectional area and transpiration rates in trees. From our own analysis, we have noticed an unreported issue that seems to be worthy of comment.

West et al. (1999) concluded that optimal tapering of hydraulic "tubes", i.e. xylem conduits connected longitudinally to each other over the water transport pathway, provides for equal resistance to flow of sap, independent of path length or plant size. This claim conflicts with the hydraulic limitation hypothesis (Yoder et al., 1994; Hubbard et al., 1999), which posits a slow-down in photosynthetic rate per unit leaf mass as trees increase in height, owing to increasing hydraulic resistance. It turns out that hydraulic resistance is not size-invariant, and we provide a proof of this in this comment.

2. Assumptions of the WBE model

The WBE model (West et al., 1997, 1999) is based on the assumption of a fractal-like, volume-filling, vascular branching network, each mother branch ramifying into n daughter branches. The branching units, or internodes, between consecutive points of ramification constitute the full branching network where the basal internode has index 0, and $k = 1, 2, \ldots, N$ indexes higher branching generations (Fig. 1). All internodes in the kth generation have identical size, with radius r_i and length l_i, where $l_i/l_{i+1} = \gamma_i$, $r_i/r_{i+1} = n^{-1/2}$, and $l_i \propto r_i^{2/3}$.

Each internode contains a bundle of conducting tubes, each tube running from the basal internode to a petiole. At each point of ramification, the bundle of tubes of the mother branch is split evenly among the daughter branches, such that the total number of tubes is conserved over the branching generations. Each individual tube radius "tapers", i.e. shrinks from one internode to the next, as $(a_{k+1}/a_k) = n^{(N-i)}$, where $\bar{a}$ is a parameter describing taper strength. Internodes in the Nth generation (i.e. terminal shoots or petioles) have a fixed minimal size, regardless of number of generations in the network, so $r_i/r_N = n^{(N-1)/2}$, and $l_i/l_N = (r_i/r_N)^{2/3}$. West et al. (1997) also indicated that the volume-filling property of the branching network implies $\gamma_i = n^{-1/3}$, independent of k. Internodal mass is $m_i \propto r_i^2 l_i$, so the total mass of the network is $M \propto \sum_{i=0}^{N} n^i r_i^2 l_i$ and the model-tree length (or height) is $H \propto \sum_{i=0}^{N} l_i$.

West et al. (1999) argue that the requirement of hydrodynamic stability yields a constraint for the parameter $\bar{a}$ related to tube tapering, namely that $\bar{a} = 1/6 + \Delta$, where $\Delta > 0$ is infinitesimally small. They claim that if this condition holds, then the hydrodynamic resistance of the tube pathway is independent of total tube length and thus plant size (West et al., 1999, p. 665, Box 2). Below, we show that this is not the case.

3. Proof that resistance is not invariant for $\bar{a} \to 1/6$

The total resistance through a tube (tube i from stem to petiole), Z_i, is calculated by the Poiseuille formula (West et al., 1999, Box 2),

$$Z_i = \sum_{k=0}^{N} Z_k^i = \sum_{k=0}^{N} 8\eta l_k / a_k^4. \tag{1}$$

Because petiole size is assumed fixed, the petiole resistance, $Z_N = 8\eta l_N / a_N^4$, is, by implication, assumed to be an invariant of nature.

Inserting $l_k = l_N n^{(N-k)/3}$, $a_k = a_N n^{(N-k)\bar{a}/2}$ (West et al., 1999, Box 1), we have

$$Z_i = Z_N \sum_{k=0}^{N} n^{(N-k)(1/3 - 2\bar{a})}. \tag{2}$$

This is a geometrical series that sums up to

$$Z_i = Z_N \frac{1 - n^{(N+1)(1/3 - 2\bar{a})}}{1 - n^{(1/3 - 2\bar{a})}}. \tag{3}$$

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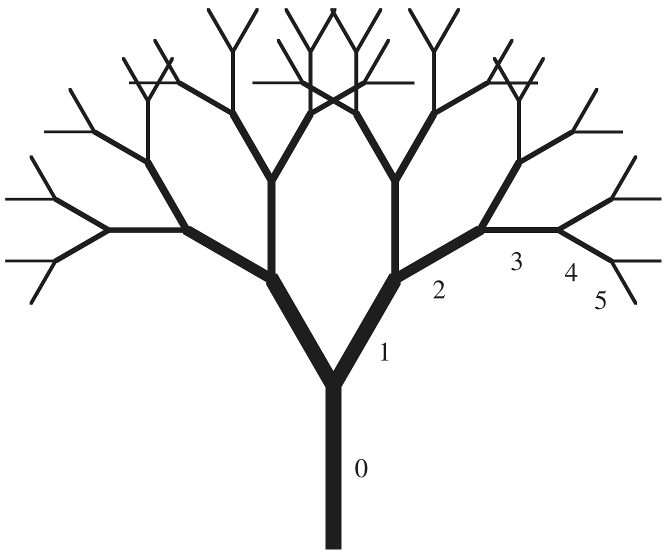

Fig. 1. Schematic presentation of the branching pattern.

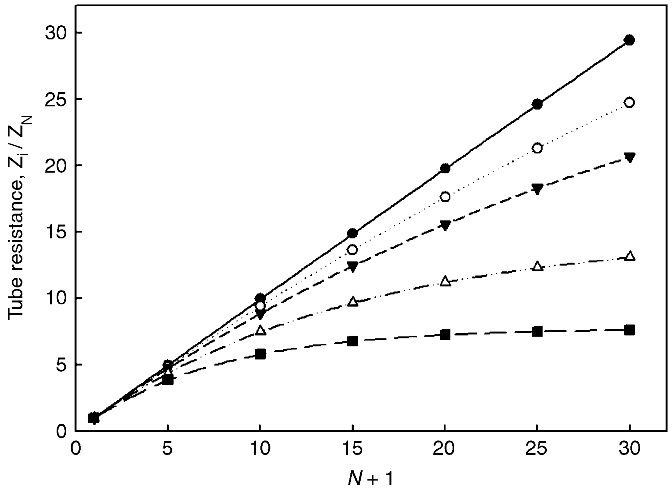

Fig. 2. Tube resistance relative to petiole resistance as a function of number of generations, evaluated from Eq. (2) with $n=2$ and $\bar{a}=1/6+\Delta$: (●) $\Delta=0.001$, (○) $\Delta=0.01$, (▲) $\Delta=0{\cdot}02$, (△) $\Delta=0.05$, and (■) $\Delta=0.1$.

In case $(1/3-2\bar{a})=0$, i.e., $\bar{a}=1/6$, the sum reduces to $Z_i=Z_N\sum_{k=0}^{N}n^0=(N+1)\,Z_N$, i.e. the resistance increases linearly with the number of branching levels. Also, on the basis of L'Hôpital's Rule,

$$\lim_{\bar{a}\to 1/6} Z_i = Z_i|_{\bar{a}=1/6} = (N+1)Z_N. \tag{4}$$

In other words, Z_i is not invariant but depends on N, QED.

West et al. (1999) suggest that $N\approx 18$ would be a reasonable number of generations in the fractal-like model. We evaluated tube resistance relative to petiole resistance, Z_i/Z_N, for a range of values $\bar{a}=1/6+\Delta$ and $(N+1)$ (Fig. 2). If $\Delta=0.001$, the increase in Z_i/Z_N with $(N+1)$ is virtually linear. The invariance of Z_i $(N>18)$ only starts to appear when $\Delta\approx 0.1$, i.e. $\bar{a}\approx 0.27$. This would imply that $a_0/a_N\approx 10$, i.e. tube radius at the base would be ten times as large as tube radius in the petiole, while for $\bar{a}=1/6$, the increase would only be four-fold.

4. Conclusions

The hydraulic resistance to sap flow is not constant in a fractal-like (or fractal) framework of tapering tubes, where $\bar{a}=1/6$. This negates some of the conclusions of West et al. (1999) derived from the assumptions that Z_i is size-invariant and $\bar{a}=1/6$. Importantly, the conclusion that the foliage-specific metabolic rate of plants should be independent of plant size was derived from the assumption that sap flow rate through a single tube, $\dot{Q}_i$, was proportional to Z_i^{-1} and thus size-independent. By contrast, Eq. (4) implies that $\dot{Q}_i$ decreases with increasing number of internodes, N, which implies that $\dot{Q}_i$ decreases with plant size if petiole size is fixed. Secondly, the derivation of a maximum feasible height of plants was based on the assumption that $\bar{a}=1/6$ in an area-preserving, volume-filling branching network. But if the value $\bar{a}=1/6$ has no special significance for tube resistance, then the conclusion by West et al. (1999) that $\bar{a}$ must approach 1/6 for trees to grow tall is called into question.

The increasing resistance with path length or number of internodes is in qualitative agreement with the hydraulic limitation hypothesis (Yoder et al., 1994; Hubbard et al., 1999), and accounting for this might improve the agreement of the model with measurements of water flow (Meinzer et al., 2005). However, it is not clear to what extent water conductance in trees can be described as passage through hollow tubes, regardless of tube taper. The "tubes" consist of separate conduits connected by wall-crossings both longitudinally and radially (Siau, 1983). Especially in gymnosperms, it is not so much the conduit diameter as the number and character of the wall-crossings needed over the entire pathway that determine the hydraulic resistance (Comstock and Sperry, 2000). Resistance is also affected by embolism that may occur in parts of the water-conducting pathway, its severity depending on, e.g. the length and number of the individual conduits and storage capacity affecting the rate of recovery (Comstock and Sperry, 2000; Domec et al., 2005).

However, as total cross-sectional area of the network has no direct connection with tube cross-sectional area, other than the requirement that the bundle of tubes must be contained in the total cross-section at all branching levels, this result does not affect the conclusions of the WBE model regarding the scaling between mass components and total length and basal diameter of the vascular branching network.

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