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Plant physiology in theory and practice: An analysis of the WBE model for vascular plants

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ABSTRACT

The theoretical model of West, Brown and Enquist (hereafter WBE) proposed the fractal geometry of the transport system as the origin of the allometric scaling laws observed in nature. The WBE model has either been criticized for some restrictive and biologically unrealistic constraints or its reliability debated on the evidence of empirical tests. In this work, we revised the structure of the WBE model for vascular plants, highlighting some critical assumptions and simplifications and discuss them with regard to empirical evidence from plant anatomy and physiology. We conclude that the WBE model had the distinct merit of shedding light on some important features such as conduit tapering. Nonetheless, it is over-simplistic and a revised model would be desirable with an ontogenetic perspective that takes some important phenomena into account, such as the transformation of the inner sapwood into heartwood and the effect of hydraulic constraints in limiting the growth in height.

1. Introduction

The fractal-like model of West et al. (1999, hereafter WBE) proposed that the hydraulic transport system (xylem) of all vascular plants is structured in order to maintain a constant flow rate along the entire path length (i.e., the roots-to-leaves distance). Due to the effect of the tapering of xylem conduits (Becker et al., 2000), plants can substantially avoid the effect of the increase in height on the total path-length conductance so that the metabolism of a single leaf becomes size-independent and that of the whole organism scales simply with the geometry of the branching architecture.

While the mathematical and logical propriety of the theoretical structure of the WBE (1997, 1999) model have been challenged by many authors (Dodds et al., 2001; Kozlowski and Konarzewski, 2004; Makarieva et al., 2005; Chaui-Berlinck, 2006; Coomes, 2006; Apol et al., 2008), with the ensuing clarifications by West and colleagues not always appearing entirely convincing (Brown et al., 2005; Savage et al., 2007), the novel ecological perspective that natural selection drove all plants to adopt a universal architecture of the xylem transport system whose efficiency is independent of plant height seems to contrast with the empirical evidence that tree height is limited by increased hydraulic constraints (Koch et al., 2004). Nonetheless, of the universal predictions of the WBE model have been tested and substantially supported by empirical measurements (e.g., Anfodillo et al., 2006; Weitz et al., 2006; Coomes et al., 2007; Petit et al., 2008).

In this paper, we analyse some important features of the WBE model, highlighting their ecological significance and their agreement (or inconsistency) with the ontogenesis and physiology of real plants.

2. WBE model

A brief comparison between the geometry of the WBE (1997) model for cardiovascular systems in animals and that for the stem branching and hydraulic architecture in vascular plants (West et al., 1999) are presented in Fig. 1. The fractal geometry of the transport system in WBE 97 is the same as that of stem branching in WBE 99. Fractality combined with the conservation of flow rate at each k-th level are proposed as the origin of the universal $\frac{3}{4}$ power scaling of metabolism with body mass (cf., Eqs. (3) and (5) in West et al., 1997). Yet the xylem transport system in plants differs substantially from the cardiovascular one in animals. In plants, nutrients are delivered from the roots to the leaves throughout a complex of small conduits that ecologists typically simplify as a set of bundles of tubes running independently and in parallel from roots to leaves (*pipe model theory*: Shinozaki et al., 1964a, b) under a negative pressure gradient (Tyree, 2003). In animals, the blood flows under a positive pressure determined by the pulsatile heart-pump throughout a network in which a single proximal big conduit (aorta) branches continuously into smaller conduits until the terminal units (capillaries). One key simplification

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of the WBE model is that the flow rate, Q (i.e., the metabolic rate, B) of the terminal units is size invariant. In WBE 97, the flow rate is maintained throughout the transport network because, due to the self-similarity, the total volume of the n^k conduits is constant at each k-th level. Instead, in WBE 99, where the conduits are independent of one another, they must taper in order to maintain the flow rate constant at each k-th level. Indeed, since the total flow rate of conduits at the k-th level is $Q_k = n^N q_k \Delta P_k$, where q_k and ΔP_k are the conductance and pressure gradient of the k-th element, respectively, given the constancy of the pressure gradient (ΔP) at each k-th level, the conservation of the flow rate among levels can be expressed as

$$Q = N_k Q_k = n^N q_k \Delta P_k = n^N q_N \Delta P_N \tag{4}$$

Hence, the conductance, or its reverse, the resistance (R_k), of the k-th element must be conserved among levels, so, by using the Hagen–Poiseuille formula for laminar flows in cylindrical tubes (e.g., Tyree and Ewers, 1991), it follows that

$$\frac{\pi d_k^4}{8\eta l_k} = \frac{\pi d_{k+1}^4}{8\eta l_{k+1}} \tag{5}$$

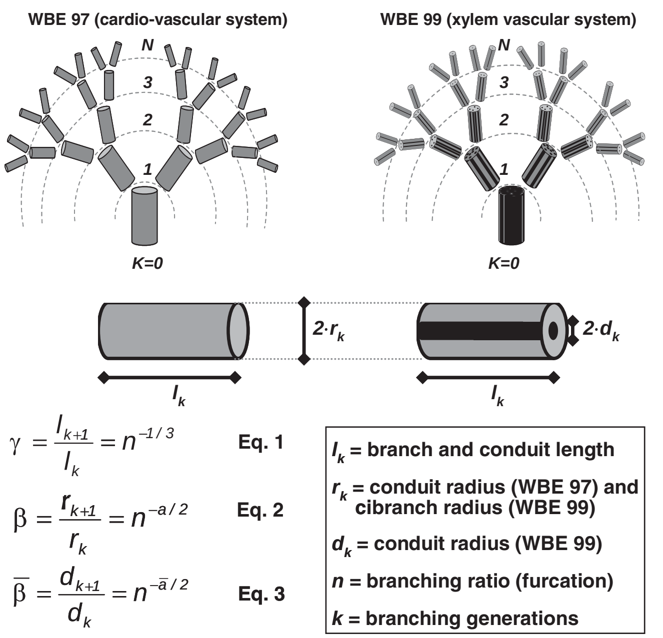

Fig. 1. Schematic geometry and fundamental relationships of WBE 97 for the cardiovascular system of animals (left) and WBE 99 for the xylem structure of vascular plants (right). A list of variables is added in the inbox.

where η is the fluid viscosity. Combining this equation with Eqs. (1) and (3) in Fig. 1, it follows that

$$\gamma = \bar{\beta}^4 \tag{6}$$

$$n^{-1/3} = n^{-2\bar{a}} \tag{7}$$

which gives $\bar{a} = \frac{1}{6}$, that represents the precise degree of conduit tapering at which the flow rate is conserved at each k-th level. This is an important feature of the whole transport system, because it strongly affects the behaviour of the whole-path resistance from the basal to the terminal level (R_{TOT}), which is given by

$$R_{TOT} = \sum_{k=0}^{N} R_k = \left[\frac{1-[(n^{1/3}-1)L/l_N]^{(1-6\bar{a})}}{1-n^{(1/3-2\bar{a})}}\right] R_N \tag{8}$$

where L is the total path length (i.e., tree height) and l_N and R_N are the length and hydraulic resistance of the terminal elements, respectively. When $L \gg l_N$, the behaviour of R critically depends on the degree of conduit tapering, that is whether $\bar{a}$ is less than, more than, or equal to $\frac{1}{6}$. in order to stabilize R with the increased path length (L), West and colleagues stated that $\bar{a}$ must be $\geqslant \frac{1}{6}$. According to Becker et al. (2000), the effect of $\bar{a}$ in making the resistance independent of path length is even more evident for fixed conduit lengths, but this seems quite reasonable as the conduit radii would increase exponentially (rather than with a power function) from the terminal to the basal level. Despite Mäkelä and Valentine (2006) correctly showing that the WBE model considers the total hydraulic resistance as a succession of equal resistances connected in series and hence it increases isometrically with the number of levels (k+1), the rate of this increase in resistance for a unit length (ΔRr) becomes irrelevant after a short distance (Fig. 2). Theoretically, this implies that either the metabolism of leaves becomes slightly reduced or that the pressure gradient (ΔP) between the basal and terminal elements slightly increases during the very start of the longitudinal growth. However, this effect would become negligible after a couple of metres (Fig. 2).

Given the area preserving branching constraint (i.e., $a = 1$ in Eq. (2) of Fig. 1) and the tapered shape of conduits (i.e., $\bar{a} = \frac{1}{6}$ in Eq. (3) of Fig. 1), it follows that

$$A_{CT,k} \propto A_{TOT,k}^{7/6} \tag{9}$$

where $A_{CT,k}$ and $A_{TOT,k}$ are the area of conductive tissues and total area of the k-th level, respectively. This means that there must be some non-conductive tissue compensating for the decrease in conduction areas with the increasing levels (k+1). As stated by McCulloh and Sperry (2005), this condition would suggest an unrealistic top-heavy structure. Also, it seems to hamper the

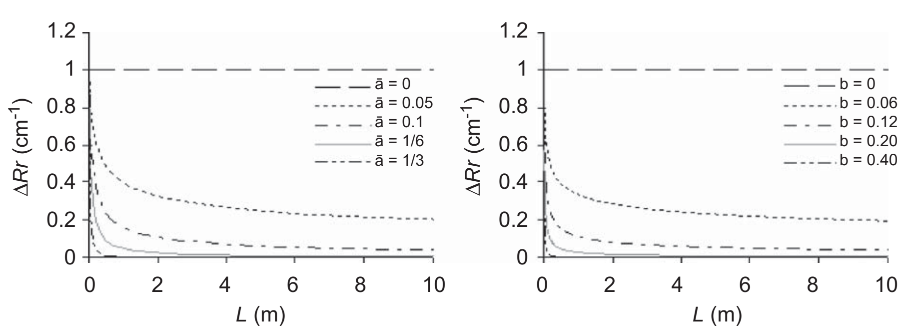

Fig. 2. The relative variation in total hydraulic resistance (ΔR) for a unit distance (ΔL, in cm) plotted against the distance from the stem apex (i.e., tree height, L). Left: the geometry of the single root-to-leaf pipe follows the WBE prediction (length and diameter of the k-th conduit given, respectively, by Eqs. (1) and (3) of Fig. 1, with $n = 2$), with the terminal unit of 10 mm in length. Right: the length of the k-th conduit is kept constant at 10 mm and the diameter scales with the distance from the apex as $Dh = aL^b$, where b can be approximated as ($\bar{a}$/0.84) (see Anfodillo et al., 2006). The red lines represent the value of conduit tapering predicted by the WBE model.