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; Chau–Berlinc, 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 3 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
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 $Q_k = n^k q_k \Delta P_k$, where $q_k$ and $\Delta P_k$ are the conductance and pressure gradient of the $k$-th element, respectively, given the constancy of the pressure gradient ($\Delta P$) at each $k$-th level, the conservation of the flow rate among levels can be expressed as

$$Q = N_k Q_k = n^k q_k \Delta P_k = n^k q_n \Delta P_N \quad \text{(4)}$$

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

$$\frac{\pi d_k^4}{8\eta} = \frac{\pi d_{k+1}^4}{8\eta} \quad \text{(5)}$$

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

$$\gamma = \frac{R_{k+1}}{R_k} = n^{-1/3} \quad \text{Eq. 1}$$

$$\frac{r_k}{L} = n^{-a/2} \quad \text{Eq. 2}$$

$$\frac{d_k}{L} = n^{-2} \quad \text{Eq. 3}$$

$$\beta = \frac{r_k}{L} = n^{-a/2} \quad \text{Eq. 2}$$

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where $a = 0.8$ in Eq. (2) of Fig. 1 and the tapered shape of conduits (i.e., $a = b$) in Eq. (3) of Fig. 1, it follows that

$$A_{T,Z,R} \propto L^{7/6} \quad \text{(9)}$$

where $A_{T,Z,R}$ and $A_{T,Z,TOT}$ 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. 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.

Fig. 2. The relative variation in total hydraulic resistance ($\Delta R$) for a unit distance ($\Delta L$ 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 10mm 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 $D_h = \text{al}^2$, where $b$ can be approximated as $(d/0.84)$ (see Anfodillo et al., 2006). The red lines represent the value of conduit tapering predicted by the WBE model.
essential WBE assumption that the density of wood must be uniform within the plant. The authors overcome both problems by simply stating that the “tubes are loosely packed in sapwood and there may be non-conducting heartwood providing additional mechanical stability”. In this way, they assumed that heartwood is a heavier tissue than sapwood and, since its formation is an age-related phenomenon so that its proportion increases with the stem diameter (e.g., Sellin, 1994), it can compensate for the reduction in non-conductive tissue with the stem diameter and so guarantee the constancy of the wood density.

the amount of non-conducting tissues was also proposed as the key factor limiting tree growth. Indeed, given the total cross-section area of a k-th level ($A_{KT,k} = \pi r_k^2$), the sum of the areas of all the cell lumina, i.e., the conduit area ($A_{CT}$), is

$$A_{CT,k} = n_k \pi r_k^2 = A_{CT,N} \left( \frac{r_k}{r_N} \right)^{2(1+\delta)/\alpha}$$  \hspace{1cm} (10)

where $A_{CT,N} = n_N \pi r_N^2$ is the conduit area of the terminal element. The proportion of conducting tissue relative to the total cross-section area is

$$f = \frac{A_{CT,k}}{A_{KT,k}} = n_k \left( \frac{dr_k}{dr_N} \right)^2 \left( \frac{r_k}{r_N} \right)^{2(1+\delta-\alpha)/\alpha}$$  \hspace{1cm} (11)

This ratio must be $\leq 1$ and the three-dimensional plant growth is limited by the absence of non-conducting tissue at the basal level, i.e., $f = 0$. It follows that the maximum height ($h_{MAX}$) and maximum basal radius ($r_{0,MAX}$) are given by

$$h_{MAX} = \frac{r_0}{1 - n^{\alpha/3} \left( \frac{r_0^2}{r_N^2} \right)^{1/(1+\delta-\alpha)}}$$  \hspace{1cm} (12)

$$r_{0,MAX} = r_N \left( \frac{r_0^2}{r_N^2} \right)^{1/(2(1+\delta-\alpha))}$$  \hspace{1cm} (13)

3. Implications for plant anatomy and physiology

The ideal plant described by the WBE model is very simplistic. Not only the geometry and morphology differ from those of real plants, but also some assumptions and simplifications made in order to derive its universal scaling predictions can be disproved by evidence from plant anatomy and physiology. Firstly, the branching geometry proposed by the WBE model is quite unlikely to be found in real plants, where branches can easily be of different length and diameter even when generated at the same internode. Internodes are also unlikely to be likened to the WBE branching ranks (or levels), not only because the internode lengths do not seem to scale as the conduit/branch lengths in the WBE model, but also because conduits continue to taper along the internodes (cf., Anfodillo et al. 2006; Petit et al. 2008). Secondly, the WBE model substantially lacks an ontogenetic perspective. The presence of heartwood, for instance, is tacitly proposed to be functional to the maintenance of an overall constancy of the wood density, so that it must be present throughout the plant regardless of the plant size. Instead, the formation of heartwood, or, better, the loss of conductivity of the internal sapwood, is an important, but yet not very well-known, process during ontogenesis and may have a considerable impact on the whole tree hydraulic efficiency (e.g., McDowell et al., 2002), and hence on its metabolism. The sapwood is described as a set of conduits contained within a matrix, presumably constituted of cell walls, fibres and parenchymatic rays. Given Eq. (9), it follows that in the WBE model the “sapwood” (as commonly considered by ecologists) scales isometrically with the basal area and must not be confused with what is called conductive tissue, i.e., the total surface of cell lumina. This means that what is usually considered and measured as sapwood does not actually correspond to the conductive tissues in the WBE model, so any empirical measurement aimed to test whether the actual sapwood area scales with the stem diameter raised to 2.33 (rather than 2) would be a simple misinterpretation of the model.

A key trait of the WBE model is a precise degree of conduit diameter. Conduit diameters were found to increase from the apices downwards rather than from the stem base towards the periphery (Anfodillo et al., 2006; Weitz et al., 2006; Coomes et al., 2007; Petit et al., 2008), with a degree of tapering similar to that predicted by the WBE model. This apical control of conduit size (see Aloni, 1987) also determines a “radial” conduit tapering from the pith to the last annual ring. This feature of the xylem must be carefully taken into account when measuring the sapwood permeability, which is actually an averaged measure of the different portions along the sapwood thickness. Theoretically, given two trees with equal radial profile of conduit diameter, but different sapwood widths, a higher sapwood permeability can paradoxically be measured in that with the thinner sapwood.

The WBE model proposes the tapering of xylem conduits as the most effective mechanism to minimize the effect of increased plant height on the root-to-leaf hydraulic resistance, and empirical measurements seemed to support this theory (Petit et al., 2008). However, as a plant gets taller, the stabilizing effect of conduit tapering appears to be critically dependant on the possibility of enabling the basal conduits. It has been proposed that growing in height without enlarging the basal elements and without another effective mechanism of compensation is likely hampered by the faster increase in hydraulic resistance (Anfodillo et al., 2006; Petit et al., 2008). A departure from the WBE prediction for conduit tapering and the consequent outcome of a progressive hydraulically related decrease in metabolism were observed in trees and proposed as the cause of the limit to tree height. However, despite it is commonly accepted that the maximum height is set by the increase in hydraulic constraints (Koch et al., 2004), if we allowed the conduit tapering to vary in the WBE model, we would obtain the paradox that it predicts taller heights and larger basal diameters for plants hydraulically less efficient, i.e., with lower values of $\alpha$ for a fixed diameter of apical conduits or with narrower apical conduits for a given $\alpha$ (Fig. 3).

4. Conclusions

The WBE model had the distinct merit of introducing a novel perspective in the study of tree physiology: that is the natural selection drove all living organisms towards self-similarity of the transport system in order to minimize the hydrodynamic resistance of nutrient transport and to maximize the exchange surfaces with the environment. Recent findings highlighted that the tapering of xylem conduits more or less follows the WBE trajectory in plants of different size and species (Anfodillo et al., 2006; Weitz et al., 2006; Coomes et al., 2007; Petit et al., 2008) and that it is likely the most efficient strategy to reduce the effect of height on the total path-length resistance (Petit et al., 2008). Despite the important contribution of these researches to the progress of knowledge, it would be desirable that such analyses on scaling relationships were also integrated with qualitative measurements of other important physiological processes, such as the loss of conductivity of the inner sapwood (i.e., the heartwood formation) and the ontogenetic variation of the proportion of conductive and non-conductive tissues.
To conclude, we have highlighted the important role played by the very simplistic model of West et al. (1999) in shedding light on an important feature of plant anatomy and physiology. Nonetheless, the theoretical structure of an ideal WBE tree is over-simplistic and does not account for important modifications to the transport system that occur during ontogenesis, such as heartwood formation.

A necessary step forward in modeling plants would be to include an ontogenetic perspective, which might be important in the analyses and interpretations of some important phenomena, such as the variation of the scaling parameters during the different ontogenetic phases (Pilli et al., 2006); the reduction of longitudinal growth in very tall plants and maximum tree height (Ryan and Yoder, 1997; Koch et al., 2004).

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Fig. 3. WBE model predictions for the maximum height (LMAX left) and basal diameter (DMAX right) as functions of conduit tapering (q) for various conduit radii (dq) and given length (Lq) and radius (rq) of the terminal elements. The black circles are the prediction for the specific value of dqmax = q. In the example Lq = 0.05 m; rq = 0.5 mm, n = 2 and Nq = 200, as in West et al. (1999).