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1 **Plant physiology in theory and practice: an analysis**
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1 **Abstract**

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

15

16 **Keywords**

17 WBE model; allometry; hydraulic limitations; transport system; xylem
18 architecture

19

20 **Introduction**

21 The fractal-like model of West, Brown and Enquist (1999, hereafter WBE)
22 proposed that the hydraulic transport system (xylem) of all vascular plants is
23 structured in order to maintain a constant flow rate along the entire path length
24 (i.e., the roots-to-leaves distance). Due to the effect of the tapering of xylem

1 conduits (Becker et al., 2000), plants can substantially avoid the effect of the
2 increase in height on the total path length conductance so that the metabolism
3 of a single leaf becomes size-independent and that of the whole organism
4 scales simply with the geometry of the branching architecture.

5 While the mathematical and logical propriety of the theoretical structure of the
6 WBE model (West et al., 1997; West et al., 1999) have been challenged by
7 many authors (Dodds et al., 2001; Kozlowski and Konarzewski, 2004;
8 Makarieva et al., 2005; Chaui-Berlinck, 2006; Coomes, 2006; Apol et al., 2008),
9 with the ensuing clarifications by West and colleagues not always appearing
10 entirely convincing (Brown et al., 2005; Savage et al., 2007), the novel
11 ecological perspective that natural selection drove all plants to adopt a universal
12 architecture of the xylem transport system whose efficiency is independent of
13 plant height seems to contrast with the empirical evidence that tree height is
14 limited by increased hydraulic constraints (Koch et al., 2004). Nonetheless, of
15 the universal predictions of the WBE model have been tested and substantially
16 supported by empirical measurements (e.g., Anfodillo et al., 2006; Weitz et al.,
17 2006; Coomes et al., 2007; Petit et al., 2008).

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

21

22 ***WBE model***

23 A brief comparison between the geometry of the WBE model for cardiovascular
24 systems in animals (West et al., 1997) and that for the stem branching and

1 hydraulic architecture in vascular plants (West et al., 1999) is presented in Fig.
2 1. The fractal geometry of the transport system in WBE 97 is the same as that
3 of stem branching in WBE 99. Fractality combined with the conservation of flow
4 rate at each k -th level are proposed as the origin of the universal $3/4$ power
5 scaling of metabolism with body mass (cf., eq. 3 and eq. 5 in West et al., 1997).
6 Yet the xylem transport system in plants differs substantially from the
7 cardiovascular one in animals. In plants, nutrients are delivered from the roots
8 to the leaves throughout a complex of small conduits that ecologists typically
9 simplify as a set of bundles of tubes running independently and in parallel from
10 roots to leaves (*pipe model theory*: Shinozaki et al., 1964a, 1964b) under a
11 negative pressure gradient (Tyree, 2003). In animals, the blood flows under a
12 positive pressure determined by the pulsatile heart-pump throughout a network
13 in which a single proximal big conduit (aorta) branches continuously into smaller
14 conduits until the terminal units (capillaries). One key simplification of the WBE
15 model is that the flow rate, Q , (i.e., the metabolic rate, B) of the terminal units is
16 size invariant. In WBE 97, the flow rate is maintained throughout the transport
17 network because, due to the self-similarity, the total volume of the n^k conduits is
18 constant at each k -th level. Instead, in WBE 99, where the conduits are
19 independent of one another, they must taper in order to maintain the flow rate
20 constant at each k -th level. Indeed, since the total flow rate of conduits at the k -
21 th level is $Q_k = n^k \cdot q_k \cdot \Delta P_k$, where q_k and ΔP_k are the conductance and
22 pressure gradient of the k -th element respectively, given the constancy of the
23 pressure gradient (ΔP) at each k -th level, the conservation of the flow rate
24 among levels can be expressed as

$$1 \quad Q = N_k Q_k = n^N q_k \Delta P_k = n^N q_N \Delta P_N \quad \text{Eq. 4}$$

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

$$5 \quad \frac{\pi d_k^4}{8\eta l_k} = \frac{\pi d_{k+1}^4}{8\eta l_{k+1}} \quad \text{Eq. 5}$$

6 where η is the fluid viscosity. Combining this equation with equations 1 and 3 in
 7 Fig. 1, it follows that

$$8 \quad \gamma = \bar{\beta}^4 \quad \text{Eq. 6}$$

$$9 \quad n^{-1/3} = n^{-2\bar{a}} \quad \text{Eq. 7}$$

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

$$15 \quad R_{TOT} = \sum_{k=0}^N R_k = \left[\frac{1 - [(n^{1/3} - 1) \cdot L / l_N]^{(1-6\bar{a})}}{1 - n^{(1/3-2\bar{a})}} \right] \cdot R_N \quad \text{Eq. 8}$$

16 where L is the total path length (i.e., tree height) and l_N and R_N are the length
 17 and hydraulic resistance of the terminal elements respectively. When $L \gg l_N$, the
 18 behaviour of R critically depends on the degree of conduit tapering, that is
 19 whether \bar{a} is less than, more than, or equal to $1/6$. In order to stabilize R with the
 20 increased path length (L), West and colleagues stated that \bar{a} must be $\geq 1/6$.
 21 According to Becker et al. (2000), the effect of \bar{a} in making the resistance
 22 independent of path length is even more evident for fixed conduit lengths, but

1 this seems quite reasonable as the conduit radii would increase exponentially
 2 (rather than with a power function) from the terminal to the basal level. Despite
 3 Mäkelä and Valentine (2006) correctly showing that the WBE model considers
 4 the total hydraulic resistance as a succession of equal resistances connected in
 5 series and hence it increases isometrically with the number of levels ($k+1$), the
 6 rate of this increase in resistance for a unit length (ΔRr) becomes irrelevant
 7 after a short distance (Fig. 2). Theoretically, this implies that either the
 8 metabolism of leaves becomes slightly reduced or that the pressure gradient
 9 (ΔP) between the basal and terminal elements slightly increases during the very
 10 start of the longitudinal growth. However, this effect would become negligible
 11 after a couple of metres (Fig. 2).

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

$$14 \quad A_{CT,k} \propto A_{TOT,k}^{7/6} \quad \text{Eq. 14}$$

15 where $A_{CT,k}$ and $A_{TOT,k}$ are the area of conductive tissues and total area of the k -
 16 *th* level respectively. This means that there must be some non-conductive
 17 tissue compensating for the decrease in conduction areas with the increasing
 18 levels ($k+1$). As stated by McCulloh and Sperry (2005), this condition would
 19 suggest an unrealistic top-heavy structure. Also, it seems to hamper the
 20 essential WBE assumption that the density of wood must be uniform within the
 21 plant. The authors overcame both problems by simply stating that the “*tubes are*
 22 *loosely packed in sapwood and there may be non-conducting heartwood*
 23 *providing additional mechanical stability*”. In this way, they assumed that
 24 heartwood is a heavier tissue than sapwood and, since its formation is an age-

1 related phenomenon so that its proportion increases with the stem diameter
 2 (e.g., Sellin, 1994), it can compensate for the reduction in non-conductive tissue
 3 with the stem diameter and so guarantee the constancy of the wood density.
 4 The amount of non-conducting tissues was also proposed as the key factor
 5 limiting tree growth. Indeed, given the total cross-section area of a k -th level
 6 ($A_{TOT,k} = \pi r_k^2$), the sum of the areas of all the cell lumina, i.e., the conduction
 7 area (A_{CT}), is

$$8 \quad A_{CT,k} = n_k \pi d_k^2 = A_{CT,N} \left(\frac{r_k}{r_N} \right)^{\frac{2(1+\bar{a})}{a}} \quad \text{Eq. 15}$$

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

$$11 \quad f = \frac{A_{CT,k}}{A_{TOT,k}} = n_N \left(\frac{d_N}{r_N} \right)^2 \left(\frac{r_k}{r_N} \right)^{\frac{2(1+\bar{a}-a)}{a}} \quad \text{Eq. 16}$$

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

$$15 \quad L_{MAX} = \frac{l_N}{1 - n^{1/3}} \left(\frac{r_N^2}{d_N^2 n_N} \right)^{\frac{1}{3(1+\bar{a}-a)}} \quad \text{Eq. 17}$$

$$16 \quad r_{0,MAX} = r_N \left(\frac{r_N^2}{d_N^2 n_N} \right)^{\frac{a}{2(1+\bar{a}-a)}} \quad \text{Eq. 18}$$

17

1 ***Implications for plant anatomy and physiology***

2 The ideal plant described by the WBE model is very simplistic. Not only the
3 geometry and morphology differ from those of real plants, but also some
4 assumptions and simplifications made in order to derive its universal scaling
5 predictions can be disproved by evidence from plant anatomy and physiology.
6 Firstly, the branching geometry proposed by the WBE model is quite unlikely to
7 be found in real plants, where branches can easily be of different length and
8 diameter even when generated at the same internode. Internodes are also
9 unlikely to be likened to the WBE branching ranks (or levels), not only because
10 the internode lengths do not seem to scale as the conduit/branch lengths in the
11 WBE model, but also because conduits continue to taper along the internodes
12 (cf., Anfodillo et al. 2006; Petit et al. 2008). Secondly,
13 The WBE model substantially lacks an ontogenetic perspective. The presence
14 of heartwood, for instance, is tacitly proposed to be functional to the
15 maintenance of an overall constancy of the wood density, so that it must be
16 present throughout the plant regardless of the plant size. Instead, the formation
17 of heartwood, or, better, the loss of conductivity of the internal sapwood, is an
18 important, but yet not very well-known, process during ontogenesis and may
19 have a considerable impact on the whole tree hydraulic efficiency (e.g.,
20 McDowell et al., 2002), and hence on its metabolism. The sapwood is described
21 as a set of conduits contained within a matrix, presumably constituted of cell
22 walls, fibres and parenchymatic rays. Given equation 14, it follows that in the
23 WBE model the “sapwood” (as commonly considered by ecologists) scales
24 isometrically with the basal area and must not be confused with what is called

1 conductive tissue, i.e., the total surface of cell lumina. This means that what is
2 usually considered and measured as sapwood does not actually correspond to
3 the conductive tissues in the WBE model, so any empirical measurement aimed
4 to test whether the actual sapwood area scales with the stem diameter raised to
5 2.33 (rather than 2) would be a simple misinterpretation of the model.

6 A key trait of the WBE model is a precise degree of conduit diameter. Conduit
7 diameters were found to increase from the apices downwards rather than from
8 the stem base towards the periphery (Anfodillo et al., 2006; Weitz et al., 2006;
9 Coomes et al., 2007; Petit et al., 2008), with a degree of tapering similar to that
10 predicted by the WBE model. This apical control of conduit size (see Aloni
11 1987) also determines a “radial” conduit tapering from the pith to the last annual
12 ring. This feature of the xylem must be carefully taken into account when
13 measuring the sapwood permeability, which is actually an averaged measure of
14 the different portions along the sapwood thickness. Theoretically, given two
15 trees with equal radial profile of conduit diameter, but different sapwood widths,
16 a higher sapwood permeability can paradoxically be measured in that with the
17 thinner sapwood.

18 The WBE model proposes the tapering of xylem conduits as the most effective
19 mechanism to minimize the effect of increased plant height on the root-to-leaf
20 hydraulic resistance, and empirical measurements seemed to support this
21 theory (Petit et al., 2008). However, as a plant gets taller, the stabilizing effect of
22 conduit tapering appears to be critically dependent on the possibility of
23 enlarging the basal conduits. It has been proposed that growing in height
24 without enlarging the basal elements and without another effective mechanism

1 of compensation is likely hampered by the faster increase in hydraulic
2 resistance (Anfodillo et al. 2006; Petit et al. 2008). A departure from the WBE
3 prediction for conduit tapering and the consequent outcome of a progressive
4 hydraulically related decrease in metabolism were observed in trees and
5 proposed as the cause of the limit to tree height. However, despite it is
6 commonly accepted that the maximum height is set by the increase in hydraulic
7 constraints (Koch et al., 2004), if we allowed the conduit tapering to vary in the
8 WBE model, we would obtain the paradox that it predicts taller heights and
9 larger basal diameters for plants hydraulically less efficient, i.e., with lower
10 values of \bar{a} for a fixed diameter of apical conduits or with narrower apical
11 conduits for a given \bar{a} (Fig. 3).

12

13 **Conclusions**

14 The WBE model had the distinct merit of introducing a novel perspective in the
15 study of tree physiology: that is the natural selection drove all living organisms
16 towards self similarity of the transport system in order to minimize the
17 hydrodynamic resistance of nutrient transport and to maximize the exchange
18 surfaces with the environment. Recent findings highlighted that the tapering of
19 xylem conduits more or less follows the WBE trajectory in plants of different size
20 and species (Anfodillo et al., 2006; Weitz et al., 2006; Coomes et al., 2007; Petit
21 et al., 2008) and that it is likely the most efficient strategy to reduce the effect of
22 height on the total path-length resistance (Petit et al., 2008). Despite the
23 important contribution of these researches to the progress of knowledge, it
24 would be desirable that such analyses on scaling relationships were also

1 integrated with quali-quantitative measurements of other important physiological
2 processes, such as the loss of conductivity of the inner sapwood (i.e., the
3 heartwood formation) and the ontogenetic variation of the proportion of
4 conductive and non-conductive tissues.

5 To conclude, we have highlighted the important role played by the very
6 simplistic model of West et al. (1999) in shedding light on an important feature
7 of plant anatomy and physiology. Nonetheless, the theoretical structure of an
8 ideal WBE tree is over-simplistic and does not account for important
9 modifications to the transport system that occur during ontogenesis, such as
10 heartwood formation.

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

17

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21

22

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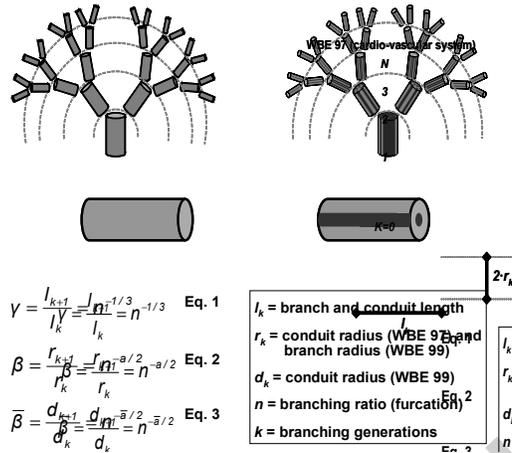
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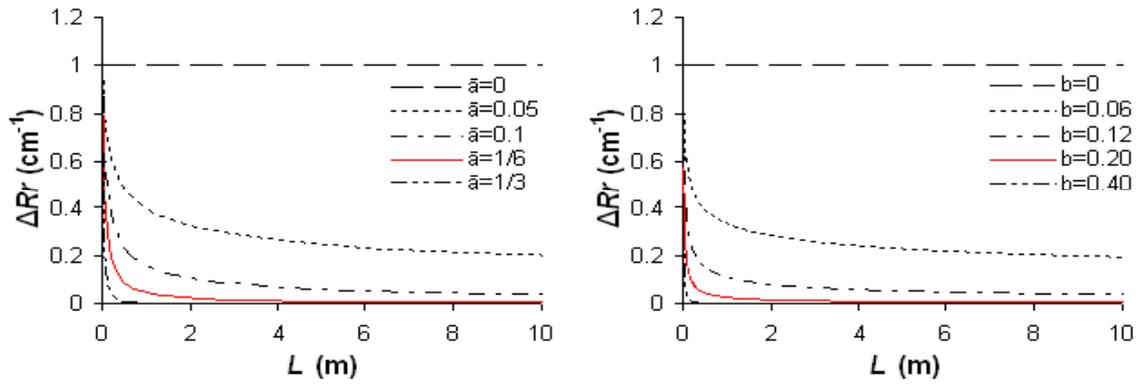


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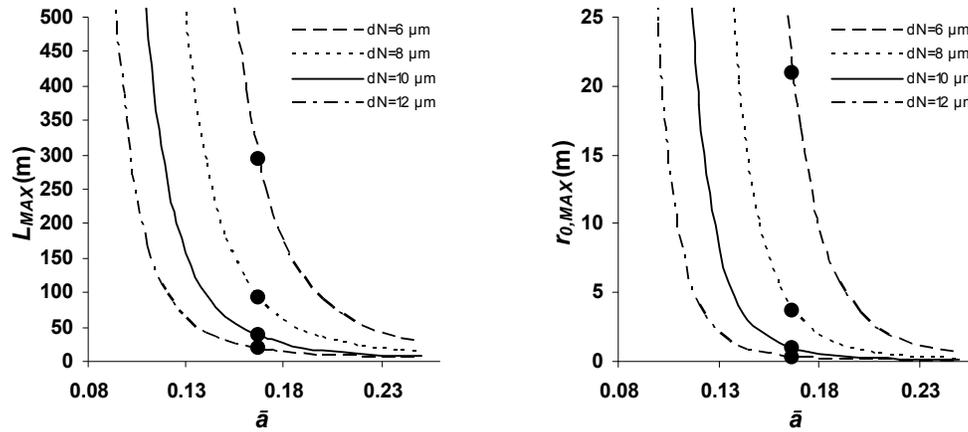
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1 Fig. 2 The relative variation in total hydraulic resistance (ΔR) for a unit distance
 2 (ΔL , in cm) plotted against the distance from the stem apex (i.e., tree height, L).
 3 Left: the geometry of the single root-to-leaf pipe follows the WBE prediction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



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- 1 Fig. 3 WBE model predictions for the maximum height (L_{MAX} , left) and basal
 2 diameter ($r_{0,MAX}$, right) as functions of conduit tapering (\bar{a}) for various conduit
 3 radii (d_N) and given length (l_N) and radius (r_N) of the terminal elements. The
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 5 $l_N=0.05$ m ; $r_N=0.5$ mm, $n=2$ and $N_N=200$, as in West et al. (1999).



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