A GENERAL MODEL FOR THE STRUCTURE, FUNCTION, AND ALLOMETRY OF PLANT VASCULAR SYSTEMS

Geoffrey B. West*, James H. Brown†, Brian J. Enquist ‡

G. B. West, Theoretical Division, T-8, MS B285, Los Alamos National Laboratory, Los Alamos, NM 87545, USA.

G. B. West, J. H. Brown and B. J. Enquist, The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA.

J. H. Brown and B. J. Enquist, Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

*email: gbw@lanl.gov

†To whom correspondence should be addressed; email: jhbrown@unm.edu

‡email: benquist@unm.edu
Abstract

Vascular plants vary over 12 orders of magnitude in body mass and exhibit complex branching. We provide an integrated explanation for anatomical and physiological scaling relationships by developing a general model for the geometry and hydrodynamics of resource distribution with specific reference to plant vascular network systems. The model predicts: (i) a fractal-like branching architecture with specific scaling exponents; (ii) allometric exponents which are simple multiples of 1/4; and (iii) values of several invariant quantities. It invokes biomechanical constraints to predict the proportion of conducting to non-conducting tissue. It shows how tapering of vascular tubes permits resistance to be independent of tube length, thereby regulating resource distribution within a plant and allowing the evolution of diverse sizes and architectures, but limiting the maximum height for trees.
I. INTRODUCTION

Variation in body size is a major component of biological diversity. Among all organisms, size varies by more than 21 orders of magnitude from $10^{-13}$g microbes to $10^8$g whales. Among vascular plants, the variation is about 12 orders of magnitude, from $10^{-5}$g duckweeds to $10^7$g sequoias, but a single individual sequoia spans nearly this entire range as it grows from a seedling to a mature tree. Size is so fundamental (1,2) to diversity because it influences nearly all structural, functional, and ecological characteristics of organisms, from rates of processes within cells to abundances of species in ecological communities. Most size-related variation can be characterized by allometric scaling laws of the form

$$ Y = Y_0 M^b $$

where $Y$ is the variable of interest, $Y_0$ a normalization constant, $M$ body mass, and $b$ the scaling exponent. A longstanding question in biology has been why $b$ so often takes on values that are simple multiples of 1/4, rather than multiples of 1/3 as expected from purely geometric scaling. Thus, for example, rates of cellular metabolism and heartbeat scale as $M^{-1/4}$, lifespan and blood circulation time as $M^{1/4}$.

Recently we developed a general model to explain the origin of these universal quarter-power scaling laws (3). The model is based on the observation that cellular processes are limited by the rate at which networks of tubes can supply energy and other essential resources. These resource distribution networks are assumed to have three fundamental properties: first, they branch to reach all local parts of the organism; second, the energy required for distribution (or the total resistance of the network) is minimized; and third, the terminal units (e.g. capillaries or petioles) do not vary with body size. The design that satisfies these structural and hydrodynamic constraints is a fractal-like branching network in which the power required to transport materials scales as $M^{D/(D+1)}$, where $D$ is the number of dimensions. So, for a three-dimensional organism, metabolic rate scales as $M^{3/4}$. From this general model many other scaling laws follow including structural and functional allometries of mammalian cardiovascular and respiratory systems.
Further validation of the model will depend on its ability to make similar predictions for other kinds of organisms. Plants provide a critical test. The architecture of both shoots and roots has obvious fractal-like properties (4). Several scaling relationships for anatomical and physiological characteristics of plant vascular systems, both within individual plants and among plants of varying size, have been determined empirically (2). In this paper we show that our general model, supplemented by incorporating essential features of plants, accurately predicts the observed scaling. Two important problems need to be addressed: biomechanical stability of the trunk and branches in response to wind and gravity (5), and equality of resource supply to all leaves, especially those on the most distal branches of the tallest trees. Both of these problems had to be solved in order for the diverse life forms of terrestrial plants to have evolved. The second problem presents an especially subtle challenge, since hydrodynamic resistance of uniform conducting tubes increases linearly with length. If not circumvented, this problem would limit resource supply to apical meristems and forest canopies, severely constraining the evolution of trees and other plant forms.

We model the transport of fluid through xylem vessels and tracheids of an angiosperm tree, from the base of the trunk to the petioles. The model also applies, with only minor modification, to transport through tracheids of gymnosperms, through phloem, and in roots. In addition to the above three general assumptions, we assume that the xylem network is composed of many tubes that run continuously in parallel from trunk to petiole (Figs. 1B and 2). For simplicity, all tubes are taken to be of equal length. Their diameter is taken to be constant within a branch segment but is allowed to vary between segments, thereby incorporating possible tapering from trunk to petiole. This variation will be crucial in circumventing the problem of resistance increasing with tube length. In addition, we allow the ratio of conducting to non-conducting tissue to vary with tree height, thereby avoiding a possible conflict between hydrodynamic and mechanical constraints. Tapering of tubes within branch segments is ignored, as are thickness and structure of tube walls, and connections between tubes, which are thought to be important in circumventing air embolisms (6). Based on these assumptions, we show that the architecture of a tree must
be a self-similar fractal with scaling laws that are supported by the data. We are aware that some of these assumptions are oversimplified abstractions of a more complex anatomy and physiology: below we will consider the consequences of relaxing them. For the moment, however, they provide a zeroth order quantitative model of the entire plant vascular network which makes many testable predictions and which can be used as a point of departure for more detailed investigations. For example, it predicts that metabolic rate scales as $M^{3/4}$ and explains why the maximum height of trees is approximately 100m.

II. THE MODEL: NOTATION AND GEOMETRIC CONSIDERATIONS

The model can be described as a continuously branching network beginning at the trunk (level 0) and ending with the petioles (level $N$) (Fig. 1C). An arbitrary level will be denoted by $k$. We characterize the architecture of the branching network using three parameters to define the relationship of daughter to parent branches: the ratios of branch radii, $\beta_k \equiv r_{k+1}/r_k \equiv n^{-a/2}$, the ratios of tube radii, $\bar{a}_k \equiv a_{k+1}/a_k \equiv n^{-a/2}$, and the ratios of branch lengths $\gamma_k \equiv l_{k+1}/l_k$. The **branching ratio**, $n$, is the number of daughter branches derived from a parent branch, and is assumed to be independent of $k$. Elsewhere, we have shown (3) that, for the network to be space-filling, $\gamma_k = n^{-1/3}$, independent of $k$. Below, we shall show that, if biomechanical constraints are uniform throughout the tree, then $\beta_k$ and $\bar{a}$ are also independent of $k$, proving that the network is a self-similar fractal (7). If, in addition, we assume that $\bar{a}$ is independent of $k$, so that tapering of tubes is uniform, it then follows that

$$\frac{T_k}{T_N} = n^{(N-k)a/2}, \quad \frac{a_k}{a_N} = n^{(N-k)a/2} = \left( \frac{T_k}{T_N} \right)^{a/a}$$  \hspace{1cm} (2)

$$\frac{l_k}{l_N} = n^{(N-k)/3} = \left( \frac{T_k}{T_N} \right)^{2/3a}$$  \hspace{1cm} (3)

If the total number of tubes is preserved at each branching, then $n_k = nn_{k+1}$, where $n_k$ is the number of tubes in a $k$th level branch. This can be solved to give
\[ n_k = n_N n^{N-k} \]  \hspace{1cm} (4)

where \( N \) is the total number of branching generations from trunk to petiole and \( n_N \) the number of tubes in a petiole (8). With our third assumption, both \( n_N \) and the dimensions of petioles (and leaves) are invariant quantities. Various scaling laws can now be derived. For example, the number of terminal branches distal to the \( k \)th branch is

\[ n_k^T = \frac{n_k}{n_N} = n^{N-k} = \left( \frac{r_k}{r_N} \right)^{2/a} \]  \hspace{1cm} (5)

Similarly, the area of conductive tissue (CT) is given by

\[ A_k^{CT} = n_k \pi a_k^2 = A_N^{CT} \left( \frac{r_k}{r_N} \right)^{2(1+a)/a} \]  \hspace{1cm} (6)

where \( A_N^{CT} = n_N \pi a_N^2 \) is the area of conductive tissue in a petiole. Thus, the proportion of conductive tissue relative to the total cross-sectional area, \( A_k^{TOT} = \pi r_k^2 \), is given by

\[ f_k \equiv \frac{A_k^{CT}}{A_k^{TOT}} = n_N \left( \frac{a_N^2}{r_N^2} \right) \left( \frac{r_k}{r_N} \right)^{2(1+a-a)/a} \]  \hspace{1cm} (7)

Also worth noting is the scaling of the total branch cross-sectional area at level \( k \): clearly, \( nA_k^{TOT}/A_k^{TOT} = n_k^2 = n^{1-a} \). When \( a = 1 \) this reduces to unity and the branching is “area-preserving”, namely \( nA_k^{TOT} = A_k^{TOT} \) (9). Its simplest manifestation is the pipe-model (10), where all tubes have the same constant diameter, are tightly bundled, and there is no non-conducting tissue. In reality, however, tubes are not tightly packed in sapwood and there may be heartwood that provides mechanical stability.

All of the above geometric scaling relations can therefore be parametrized in terms of just two exponents, \( a \) and \( \bar{a} \), which determine how radii of branches and tubes scale within a plant. In the next Section we show how these are determined from dynamics: \( a \) from mechanical considerations, and \( \bar{a} \) from hydrodynamic.
III. DYNAMICAL CONSIDERATIONS

A. Mechanical Constraint

The ability of trunks and branches to resist buckling and bending due to gravitational forces and wind leads to some optimal relationship between length and radius: \( l_k \propto r_k^{\alpha} \). Comparing this with Eq. (3) gives \( a = 2/3\alpha \). If the condition of mechanical stability is the same for all branches, then \( \alpha \) is constant, independent of \( k \). In that case \( a \) and \( \beta_k \) are also constant, giving a branching architecture that is a self-similar fractal (7). Analyses based on scale-invariant solutions to the bending moment equations for beams (elastic similarity) give \( a = 2/3 \) (5). This constraint, which is most important for the trunk and large branches, agrees well with data for these segments (5,11). Assuming this holds for all \( k \) leads to \( a = 1 \), which is precisely the condition for area-preserving branching. In other words, biomechanical stability leads to branches behaving as if they were tightly-packed vascular bundles of constant-diameter tubes. This was the simple model that we originally used to motivate area-preserving branching in plants in ref. (3). Here, however, we relax these assumptions by incorporating non-conducting heartwood, allowing tubes to vary in diameter, and to be loosely packed in the sapwood. Note that the result \( a = 1 \) implies, from Eq. (5), that the leaf area distal to the \( k \)th branch \( A_k = C_L r_k^2 \), where \( C_L \equiv a_L/r_N^2 \) is invariant and \( a_L \) is the area of a leaf. Taking \( r_N \approx 0.5\text{mm} \) and \( a_L \approx 30\text{cm}^2 \) gives \( C_L \approx 1.2 \times 10^4 \). In addition, the number of branches of a given size \( N_k = n^k = n^N (r_N/r_k)^{2/a} \), or \( N_k \propto r_k^{-2} \) if \( a = 1 \). If reproductive structures are supplied by vascular elements in the same way as leaves, the reproductive tissue supplied by a branch should exhibit a similar scaling behaviour. All of these predictions are in good agreement with data (6,10,12,13).

B. Hydrodynamic Constraint

We now address the problem of linear increase of hydrodynamic resistance with length, which would mitigate against the very existence of tall trees, independent of any mechanical
constraint. To appreciate this problem, first consider the resistance, \( Z_k^i \), of a single uniform tube in a branch at level \( k \). That resistance increases linearly with \( l_k \) is explicit in the classic Poiseuille formula (6), \( Z_k^i = 8\eta l_k/a_k^4 \), where \( \eta \) is the fluid viscosity. The total resistance of a tube running from the base of the trunk to a petiole is

\[
Z_i = \sum_{k=0}^{N} Z_k^i = \frac{8\eta}{\pi} \sum_{k=0}^{N} \frac{l_k}{a_k^4}
\]

Using Eqs. (2) and (3) this can be summed to give

\[
Z_i = \left[ \frac{1 - (1/3 - 2\alpha)^{(N+1)}}{1 - (1/3 - 2\alpha)} \right] Z_N = \left[ \frac{1 - \left( (n^{1/3} - 1) l_T/l_N \right)^{(1-6\alpha)}}{1 - n^{(1/3 - 2\alpha)}} \right] Z_N
\]

where \( Z_N = 8\eta l_N/\pi a_N^4 \) is the resistance of a tube in the petiole and \( l_T \) the total path length from trunk to leaf: \( l_T = \sum l_k = l_0/(1 - n^{-1/3}) \). For \( l_T >> l_N \) the behaviour of \( Z_i \) depends critically on the degree of tapering: namely, whether \( \alpha \) is greater than, less than, or equal to \( 1/6 \). First consider \( \alpha < 1/6 \), then Eq. (9) gives \( Z_i \propto (l_T/l_N)^{(1-6\alpha)} \) which is rejected, since it implies that resistance increases with path length. Note that the naive pipe-model (\( \alpha = 0 \)) (10) fits in this class.

Now consider \( \alpha > 1/6 \). Eq. (9) then gives

\[
Z_i = \frac{Z_N}{1 - n^{(1/3 - 2\alpha)}}
\]

which represents its minimum value. This has the remarkable property that the total tube resistance is a constant, independent of both \( N \) and \( l_T \), and therefore the same for all plants. It is exactly what is needed to solve the problem of ensuring that all leaves be supplied with comparable resources independent of total branch length. Since large \( \alpha \) corresponds to steeper tapering, this would eventually lead either to unrealistically large tube radii in the trunk, or unrealistically small ones in the petiole. To avoid such excess tapering, \( \alpha \) should therefore be the minimum possible value consistent with Eq. (10), namely 1/6. As shown below, an extension of this argument leads to an expression for the maximum height of trees.

At the precise value \( \alpha = 1/6 \), representing the transition case in Eq. (9), \( Z_i = NZ_N \approx 3Z_N[ln(l_T/l_N(n^{1/3} - 1))/lnn] \): total tube resistance therefore increases linearly with \( N \) and
logarithmically with $l_T$ rather than being a constant. We will consider this case again below. For the moment it should be viewed as a mathematical artefact in that it is only valid when $\tilde{a}$ is exactly 1/6; it changes to a constant, Eq. (10), as soon as $\tilde{a}$ exceeds 1/6 by an infinitesimal amount, provided $N$ is sufficiently large, namely $N > [2(\tilde{a} - 1/6) \ln n]^{-1}$. In what follows we mainly consider the asymptotic case where $\tilde{a}$ approaches its limiting value of 1/6, which corresponds to large trees. For small trees with low $N$, our analysis suggests $\tilde{a} \approx 1/6 + (2N \ln n)^{-1}$, leading to calculable deviations from some of the results derived below (15). Thus, when setting $\tilde{a} = 1/6$ we actually mean $\tilde{a}$ slightly greater than 1/6.

C. Consequences: Allometric Relations, Metabolic Rate, and Maximum Tree Height

Scaling Relations. Since the conducting area consists of $n_k$ tubes in parallel, the total resistance of a branch segment is $Z_k = Z_k^1/n_k = 8\eta l_k/\pi n_k a_k^4$. Using Eqs. (2), (3), and (4), conductivity, $K_k \equiv l_k/Z_k$, is therefore given by

$$K_k = \frac{\pi n_k a_k^4}{8\eta} = K_N \left(\frac{r_k}{r_N}\right)^{(1+2\tilde{a})/a} \tag{11}$$

where $K_N = \pi n_N a_k^4/8\eta$ is the conductivity of a petiole. Similarly, leaf-specific conductivity (the conductivity per unit leaf area) is given by

$$L_k \equiv \frac{K_k}{n_k a_L} = \frac{\pi n_N a_k^4}{8\eta a_L} = L_N \left(\frac{r_k}{r_N}\right)^{4\tilde{a}/a} \tag{12}$$

With $\tilde{a} = 1/6$ and $a = 1$, this predicts $K_k \propto r_k^{8/3}$, $L_k \propto r_k^{2/3}$, and $a_k/a_N = (r_k/r_N)^{1/6}$. Taking $a_N = 10\mu m$ and $n_N = 200$ gives for the normalization, $K_N \approx 7 \times 10^{-10} m^4 sec^{-1} MPa^{-1}$. These relations can also be expressed as a function of the conducting tissue area: $K_k \propto (A_k^{CT})^{(1+2\tilde{a})/(1+\alpha)} \propto (A_k^{CT})^{8/7}$ and $L_k \propto (A_k^{CT})^{(2\tilde{a})/(1+\alpha)} \propto (A_k^{CT})^{2/7}$. Notice that these exponents do not depend explicitly on $\alpha$. All of these predictions are in good agreement with data (12,14,16). For comparison, the naive pipe model, where $a = 1$ and $\tilde{a} = 0$, gives $K_k \propto r_k^2$ and $L_k \propto r_k^0$. Note also that, since $n_N$ and $a_L$ are invariants, Eq.(9) implies that $L_k \propto a_k^4$, independent of $a$ and $\tilde{a}$. 
Allometric Relations. These can be derived by noting that the total plant volume (the total volume of all branches) is

\[ V_B = \frac{M}{\rho} = \sum_{k=0}^{N} \pi n^k r_k^2 l_k = \frac{(\gamma \beta^2)^{-N}}{1 - n \gamma \beta^2} V_N \]  

(13)

where \( \gamma = n^{-1/3} \), \( \beta = n^{-a/2} \), \( V_N \) is the volume of a petiole, and \( \rho \) the tissue density. This leads to \( n^N \propto M^{3/(1+3a)} \propto M^{3/4} \) when \( a = 1 \). Consequently, the number of branching generations grows only logarithmically with mass, \( N \propto \ln M \). In addition, the total number of terminal branches, or leaves, is predicted from Eq. (5) to scale as \( n_0^* \propto r_0^2 \propto M^{3/4} \). Eqs. (2), (3), and (13), can now be combined to give \( l_k \propto M^{(1-k/N)/(a+3)} \propto M^{(1-k/N)/4} \), and \( r_k \propto M^{(1-k/N)3a/2(a+3)} \propto M^{3(1-k/N)/8} \). Notice that the length and radius of a \( k \)th level branch scales more slowly with \( M \) than does the trunk: \( l_0 \propto M^{1/4} \) and \( r_0 \propto M^{3/8} \). Since the total height of a tree, \( h \), is equivalent to the length of a tube from trunk to leaf: \( h = l_T \approx l_0/(1 - \gamma) \), this gives \( h \propto M^{1/4} \). The number of branching generations, \( N \), can be estimated from \( N = 2 \ln(r_0/r_N)/\ln n = 3 \ln(l_0/l_N)/\ln n \). For a tree with trunk diameter 50cm, a petiole radius of 0.5mm, and \( n = 2 \), this gives \( N \approx 18 \) in agreement with our observations. The tube radius scales as \( a_k/a_N = (r_k/r_N)^{1/6} \propto M^{3a(1-k/N)/2(a+3)} \propto M^{(1-k/N)/16} \), so that \( a_0/a_N = n^{N/12} \propto M^{1/16} \). Taking \( N = 18 \), and \( n = 2 \) this gives \( a_0/a_N \approx 2.8 \), so that, if \( a_N \approx 10 \mu m \), then \( a_0 \approx 30 \mu m \). Furthermore, even over 12 orders of magnitude variation in mass, \( a_0 \) is predicted to change by only about 60%. So the small variation in tube radius (6,17) predicted by the model not only overcomes the problem of resistance increasing with tube length but also is the basis for many of the observed scaling relationships.

Metabolic Rate. Driven by a pressure difference, \( \Delta P \), which is independent of plant size, the volume rate of fluid flow through a single tube is \( \dot{Q}_i = \Delta P/Z_i \). In Eq. (10) we have shown that, when \( a > 1/6 \), \( Z_i \) is also independent of plant size, scaling as \( M^0 \). Thus, \( \dot{Q}_i \propto M^0 \) so that the volume flow rate through a single vascular tube from trunk to petiole is predicted to be the same for all plants. The total volume flow rate through all vascular tubes is \( \dot{Q}_0 = n_0 \dot{Q}_i = n^N n_N \dot{Q}_i \propto M^{3/(1+3a)} = M^{3/4} \) when \( a = 1 \). Elsewhere (18) we show that the total rate of xylem flow must equal the metabolic rate, or the rate of respiration
or gross photosynthesis when the plant is in steady state. The model therefore predicts that whole plant metabolic rate scales as $M^{3/4}$. For comparison note from Eq. (9) that, in the naive pipe-model where $\bar{a} = 0$ and $a = 1$, then $Z_i \propto n^{N/3} \propto M^{1/4}$, which would give $\dot{Q}_0 \propto M^{1/2}$.

**Pressure Gradient.** The pressure drop across a $k$th level branch is $\Delta P_k = \dot{Q}_i Z_k^i$, so the ratio of pressure gradients between adjacent branch levels is $(\Delta P_{k+1}/l_{k+1})/(\Delta P_k/l_k) = (a_k/a_{k+1})^4 = (l_k/l_{k+1})^{6\bar{a}} = l_k/l_{k+1}$, when $\bar{a} = 1/6$. The pressure gradient is therefore steeper in smaller branches than in larger ones; in particular, the ratio between trunk and petiole is predicted to be $(\Delta P_0/l_0)/(\Delta P_N/l_N) = l_N/l_0 \propto M^{-1/4}$. So, for a tree with trunk length 4m and petiole length 4cm, this ratio is $\sim 1/100$. This also predicts that the ratio of pressure gradients should be smaller in larger trees and that the pressure drop, $\Delta P_k$, should be the same for all branch segments, independent of level. These predictions are in good agreement with data (6). In contrast, the naive pipe model predicts that the pressure gradient rather than the pressure difference is size-independent.

**Removing Branch Segments.** A particularly sensitive test of the model is its quantitative prediction of how total plant resistance changes as progressively larger branch segments are removed. Suppose that only branches up to the $k$th level remain, then the total number of tubes in the trunk is still $n_0$; however, they now terminate at the $k$th level rather than the $N$th. The total resistance of the remaining branch network is

$$Z_k^{TOT} = \frac{1}{n_0} \sum_{k'=0}^{k} Z_k^{i}_{k'} = \left[ \frac{r(2a-1/3)(k+1)}{r(2a-1/3) - 1} \right] Z_0$$

where $Z_0$ is the trunk resistance. The total resistance of the whole uncut tree, $Z_N^{TOT} = Z_N^{TOT}$. Using Eq. (2), the ratio $R_k \equiv Z_k^{TOT}/Z_k^{TOT}$ can be expressed as

$$R_k = \frac{(r_{k+1}/r_0)^p - 1}{(r_{N+1}/r_0)^p - 1}$$

where $p \equiv 2(1 - 6\bar{a})/3a$ and $r_{N+1} \equiv r_N^{-a/2}$. Note that $R_N = 1$ and $R_{-1} = 0$, the latter corresponding to the limit where all conducting tissue has been removed. For $p > 0$ (so $\bar{a} < 1/6$), then $R_k \approx 1 - (r_{k+1}/r_0)^p$. The pipe model ($p = 2/3$) is a special case of this. For $p < 0$ (so $\bar{a} > 1/6$), then $R_k \approx (r_N/r_k)^{|p|}$. For the case of interest here, $p \approx 0$ (so $\bar{a} \approx 1/6$),
As shown in Fig. 3 this agrees very well with data (13); also shown for illustrative comparison are $\bar{a} = 0$, the classic pipe model, and $\bar{a} = 1/3$.

**Fluid Velocity.** Since tubes taper, fluid velocity, $u_k$, must increase in smaller branches. The volume rate of fluid flow through a single tube is $Q_i = \pi d_k^2 u_k$; so, when $a = 1$ and $\bar{a} = 1/6$, then $u_k \propto a_k^{-2} \propto r_k^{-2\bar{a}/a} \propto r_k^{-1/3}$. This predicts that the ratio of petiole to trunk velocities is $u_N/u_0 = (r_0/r_N)^{1/3}$. Taking $r_N \approx 0.5\text{mm}$ and $r_0 \approx 50\text{cm}$, gives $u_N/u_0 \approx 4.6$. Allometrically, $u_k$ scales as $M^{-(1-k/N)a/2(a+3)} \propto M^{-(1-k/N)/8}$ when $a = 1$. For the trunk this gives $u_0 \propto M^{-1/8}$. So, over a range of 8 orders of magnitude in mass, corresponding roughly to a 50cm sapling relative to a 50m tree, the fluid velocity in the trunk is predicted to decrease by a factor of $\sim 10$. The above predictions are supported by the data (6).

**Conducting Tissue and the Maximum Height of Trees.** From Eq. (6), the area of conducting tissue in a branch at the $k$th level scales as $A_k^{CT} \propto r_k^{2(1+\bar{a})/a} \propto A_k^{TOT}r_k^{7/6}$, where $A_k^{TOT}$ is the total cross-sectional area of a branch. Alternatively, Eqs. (5) and (6) can be combined to give $A_k^{CT} \propto (n_k^{L_k})^{(1+\bar{a})} \propto (n_k^{L_k})^{7/6}$, which depends only on $\bar{a}$. The proportion of conductive tissue relative to total branch cross-sectional area is given in Eq. (7): $f_k = (n_A a_k^2 / r_N^2) (r_k/r_N)^{2(1+\bar{a}-a)/a} \propto r_k^{1/3}$. All of these results are well supported by the data (12,19,20). Since $f_k \leq 1$, this last formula leads to a limitation on the maximum height and radius of a tree. From Eqs. (7) and (3) the maximum radius and length of the trunk are

$$r_0^{MAX} = r_N \left( \frac{r_N^2}{a_N^2 n_N} \right)^{a/2(1+\bar{a}-a)}$$
$$l_0^{MAX} = l_N \left( \frac{r_N^2}{a_N^2 n_N} \right)^{1/3(1+\bar{a}-a)}$$

Since maximum height is equivalent to the total tube length, $h^{MAX} = l_0^{MAX} / (1 - n^{-1/3})$.

With $a = 1$ and $\bar{a} = 1/6$, these give $r_0^{MAX} = r_N^7 / a_N^6 n_N^3$ and $l_0^{MAX} = l_N r_N^4 / a_N^4 n_N^2$. The maximum size is therefore extremely sensitive to the parameters of the petiole. As an example, take $r_N = 0.5\text{mm}$, $a_N = 10\mu\text{m}$, and $n_N = 200$, then these give $r_0^{MAX} \approx 1\text{m}$ and $h^{MAX} \approx 40\text{m}$; if instead, $a_N = 8\mu\text{m}$, then $r_0^{MAX} \approx 4\text{m}$ and $h^{MAX} \approx 100\text{m}$. Thus, these formulae cannot be used to accurately calculate maximum size. On the other hand,
the argument does show why $h^{MAX}$ is of the order of 100m rather than 1m or 1000m. Furthermore, it provides an explanation from fundamental principles why the size of trees is limited and how that size is related to basic parameters which depend on both mechanical and hydrodynamic constraints. Finally, note that if $\bar{a}$ were increased so that tapering is much steeper, then the maximum height of a tree would be substantially reduced. For instance, taking $\bar{a} = 1/3$ rather than $1/6$ gives $h^{MAX} \approx 1\text{cm}$! Thus, if trees are to grow tall under competition for light, for example, then $\bar{a}$ must approach its minimum value, $1/6$, consistent with total tube resistance being a constant.

Constrictions. In addition to the Poiseuille resistance there may also be resistance due to constrictions within or between vessels and tracheids. If these constrictions had roughly the same resistance and were uniformly distributed along the length of the tube, the total tube resistance would increase linearly with length. This would only be a problem if their total resistance were comparable to the conventional Poiseuille resistance. In any case, we conjecture that the effect of constrictions is similar to that of tapering so that total resistance does not vary with tube length. In some plants there are constrictions at petioles and perhaps at other branch junctions (6,21). If these are of approximately the same size, $z$, say, at all branch juctions, they would contribute $Nz$ to the total tube resistance. The resulting consequence is almost identical to the special case $\bar{a} = 1/6$, leading to an additional resistance which grows logarithmically with length. If too large, it would cause a problem, but leads to the same scaling laws as derived above, except for some logarithmic modulations. Thus, we conclude that constrictions may change normalizations but not scaling exponents.

IV. DISCUSSION

The above treatment should viewed as a zeroth order model. It represents a variant of the general model for linear branching resource networks which incorporates salient features of plants. It makes several simplifying assumptions, and incorporates only those essentials of plant anatomy and physiology necessary to derive an integrated formalized characterization.
of the architecture, biomechanics, and hydrodynamics of vascular plants. It can serve as a starting point for more elaborate models that incorporate special features of particular kinds of plants growing in different environments. Nevertheless, several of our assumptions warrant further comment:

i) *No horizontal flow between parallel tubes.* Openings in vessel and tracheid walls allow for some exchange between tubes, so that flow through the network can bypass air embolisms or damaged vessel elements (6). Our conclusions are not sensitive to such transport as long as the resistance between tubes is greater than resistance to flow through tubes.

ii) *Terminal vascular tubes have the same radius.* The model accounts for the observed tapering of tubes from trunk to petiole, but not for the variation of radii among xylem elements within a petiole or among petioles of different plants growing in different environments. We implicitly assume some average radius for such tubes. Our results are not sensitive to observed variations in size around this average value (22), which may serve an adaptive function in regulating flow in specific environments or protecting against embolisms.

iii) *Vascular tubes are the same length.* The distance from trunk to leaves varies somewhat. In the model, however, the tapering of tubes regulates xylem flow by compensating for variation of resistance with tube length. Path length therefore plays almost no role, so the assumption of equal tube length can be relaxed (23).

iv) *All branches are subject to the same biomechanical constraint.* We assume that biomechanical constraints lead to \( l_k \propto r_k^\alpha \) with \( \alpha \) independent of \( k \). Resistance to elastic buckling, which gives \( \alpha = 2/3 \) and area-preserving branching, may not apply throughout the plant, especially in the "butt-swell" at the base of the trunk and in the smallest branches. This can be easily incorporated into the model as a variation in \( \alpha \) for either small or large \( k \), leading to calculable corrections to corresponding scaling laws. The model also assumes that biomechanical properties of branches are due to "non-conducting tissue" but does not explicitly distinguish between heartwood and sapwood. Different kinds of plants vary widely in the structural and functional composition of their branches. These complications do not
v) The branching pattern is fractal. Rather than an assumption, this is a prediction which follows from ratio-preserving branching of a volume-filling network. However, like real plants, the model is not a true "mathematical" fractal in that the network contains a minimum branch size. In an idealized mathematical fractal, there is no fundamental scale and branching continues ad infinitum. To the extent that the volume-filling assumption is violated, whole plant structure and function can be expected to deviate somewhat from the detailed predictions of our model. While some plants have obvious volume-filling fractal-like architectures (4), others, such as palms, vines, grasses, and even saplings of small trees have simpler branching patterns. It would be instructive to explore the structural and functional consequences of such alternative architectures (24).

The model is able to account for many features of plant structure and function. First, it predicts many scaling relationships, which compare favorably with empirical values (see Table I). The close correspondence between predicted and observed scaling exponents demonstrates the power of this single model to provide a quantitative integrated explanation for many features of vascular anatomy, physiology, and whole-plant architecture. Because it also predicts several scaling relationships that have not yet been measured, the model is subject to rigorous tests. Second, the model predicts the magnitudes of certain variables, including: conductivity of different branch segments; surface area of leaf supplied by each tube, \( \sim 0.1 \text{mm}^2 \); pressure gradient differential between leaf and trunk, \( \sim 10^{-2} \) for a tree 3m tall; the ratio of conducting to non-conducting tissue; and maximum radius, \( \sim 5\text{m} \), and maximum height, \( \sim 100\text{m} \), of a tree. These predictions correspond well with observed values, and illustrate how the design of resource distribution networks constrains anatomy and physiology; they follow from an interplay between geometrical, hydrodynamical, and biomechanical principles.

Perhaps the most novel feature of the model is that it shows how plants can overcome the potentially devastating effect of resistance increasing with tube length so as to maintain
comparable xylem flow to all leaves. Such regulation can be accomplished in two ways: by moderate tapering of the tubes over the generations of branching, or by placing constrictions in the tubes. Real plants appear to use both mechanisms. There is evidence that vessel radii taper from trunk to leaf, and the magnitude of this variation is consistent with our model (17). In addition, some plants have constrictions in vessels at the junction of petioles and perhaps also at branch nodes (6,21). Often interpreted as limiting damage to the vascular system due to branch breakage and embolisms, these constrictions may also play a role in regulating xylem flow.

On the one hand, therefore, the model explains how it is possible for small herbs, tiny seedlings, and tall trees to grow in the same environment, and all have sufficient delivery of water and nutrients to their leaves to maintain roughly comparable photosynthetic and respiratory rates. The model predicts that in a given environment with a certain pressure differential between air and soil, all xylem tubes of all plants conduct water and nutrients at approximately the same rate (18). This surprising result is confirmed by compilation of data from field measurements from plants spanning 12 orders of magnitude in mass (Fig. 4). As plants vary in size, modest tapering of conducting elements and associated changes in resistance and velocity maintain relatively constant flow through the xylem vessels. Of course, rates of flow are not precisely identical; they vary somewhat among different species, functional groups, and developmental stages of plants as well as among tissues within individual plants. Small variations in radii of tubes are sufficient to accommodate this variation, such as the higher flow to rapidly growing apical meristems than to metabolically less active tissues.

On the other hand, the model implies that constraints on vascular structure and function may limit the maximum height of trees. This limit is quite sensitive to the number and minimum size of vascular tubes in the petiole. If radii of tubes in the petiole are in the range 5 – 10\(\mu\)m and their number in the range of a few hundred, then our model predicts that tree height cannot exceed approximately 100m. Competition for light has apparently led to a maximum height and a corresponding architectural and hydrodynamic design of trees.
that minimizes tapering of vascular tubes subject to the constraint that total \( R \) resistance remains independent of path length.

The model shows that quarter-power scaling laws, well known in animals, also apply to many characteristics of plants. Traditionally, allometry has not been a major theme in plant anatomy, physiology, and ecology, but it has played a seminal role in animal studies. Our model for plant and mammalian vascular networks shows many parallels: whole-organism metabolic rate should scale as \( M^{3/4} \), radius of trunk and aorta as \( M^{3/8} \), and size of, and fluid velocity flow in terminal vessels as \( M^0 \). In all organisms, the quarter-power scaling of life history and ecological variables (such as development time, lifespan, and population density) presumably has its roots in fundamental constraints on the structure and function of individual organisms, and specifically in their fractal-like resource distribution networks. It appears that quarter-power scaling laws are nearly universal in biology, and that they have their origins in common geometric and hydrodynamic principles that govern the transport of essential materials to support cellular metabolism.

Remarks and comments from participants at the Symposium on Scaling in Biology held at the Santa Fe Institute in October, 1997 are gratefully acknowledged. We especially thank Karl Niklas and Melvyn Tyree for their interest and constructive criticisms. JHB was supported by NSF Grant DEB-9318096, BJE by NSF Grant GER-9553623 and a Fulbright Fellowship, and GBW by the Department of Energy. We also acknowledge the generous support of the Thaw Foundation.
REFERENCES


(7) Strictly speaking, the network is not a mathematical fractal in that self-similarity does not continue *ad infinitum* since there is a finite cut-off scale at the petiole.

(8) Since leaves are effectively two-dimensional and therefore obey different scaling relationships, the terminal units of the network are taken to be petioles; see M. J. Canney, *Phil. Trans. R. Soc. Lond.* **B341**, 87 (1993).


(15) For a typical tree with $r_0 = 25$ cm, $N \approx 20$, so the correction to $\bar{a}$ is only $\approx 1/30$. For a small tree, however, with $N \approx 5$ the correction is $\approx 1/7$, an almost 100% change. Roughly speaking, a small tree corresponds to one whose height, $h \ll e^{(6\bar{a} - 1)} l_N/(n^{1/3} - 1) \approx$ a few meters.


(22) To estimate the effects of variation in petiole radii, $a_N$, a gaussian distribution was assumed with a standard deviation comparable to its mean.
(23) Based on computer simulations of networks generated by diffusion limited aggregation, it has recently been shown that scaling exponents derived in our general model are not sensitive to variation of total path length; see D. L. Turcotte, J. D. Pelletier, and W. I. Newman, Networks with Side Branching in Biology, to be published in J. Math. Biol.

(24) For example, in saplings and small shrubs, where there are relatively few branches, the presumption of a volume-filling network is suspect. A more likely geometry is that of an area-filling umbrella architecture, in which case \( \gamma \equiv \frac{l_{k+1}}{l_k} = n^{-1/2} \) rather than \( n^{-1/3} \). If branches are predominantly conducting tissue so that area-preserving branching is maintained and \( a = 1 \), then this leads to \( l_k \propto r_k \) in agreement with observation (11).
FIGURES

FIG. 1. (A) Macroscopic architecture of part of a plant branching network; (B) Pipe-model representation of the microscopic architecture of such a network illustrating a tightly-bundled plant vascular system comprised of diverging vessel elements; (C) Topological representation of such a network, where $k$ specifies the order of the level, beginning with the trunk, or main stem, ($k = 0$) and ending with the petiole ($k = N$); (D) Parameters of a typical branch at the $k$th level.

FIG. 2. Symbolic representation of the vascular structure of a “realistic” branch, showing the division between conducting and non-conducting tissue; this is to be contrasted to the tightly-bundled vascular system of the pipe-model, shown in Fig. 1(A), in which all tissue is conducting.

FIG. 3. Effect of removing branch segments: the proportion of total resistance remaining, $R_k$, as a function of the diameter of the removed stem, $2r_k$. The data points, taken from ref. (13), represent two different trees. The solid lines are derived from Eq. (15). With $\tilde{a} = 1/6$, as predicted from our model, the agreement is excellent. By contrast, with $\tilde{a} = 0$, corresponding to no tapering of tubes as in the pipe-model, and with $\tilde{a} = 1/3$, the agreement is poor. Note that the curves terminate when only the trunk remains. If extrapolated all would converge at the trunk diameter, $\sim 14.5$cm, where $2r_k = 2r_0$ and no conducting tissue remains so that $R_k = R_1 = 0$.

FIG. 4. Relationship between total xylem flux and average mass of the dominant plants in diverse ecosystems, taken from ref. (18). Note that over 12 orders of magnitude variation in plant mass there is some variation in xylem flux reflecting differences in primary production, but this variation is independent of plant size, as predicted by the model.
TABLE I. Predicted values of scaling exponents of some physiological and anatomical variables of plant vascular systems as a function of total plant mass, $M$, and branch radius, $r_k$. For the latter case predictions are compared with measured values in the last column, with corresponding references; ND indicates no data yet available. Since there is very little data on allometric scaling with mass, no measured values for these exponents are quoted.

<table>
<thead>
<tr>
<th>PLANT MASS</th>
<th>VARIABLE</th>
<th>EXPONENT</th>
<th>SYMBOL</th>
<th>BRANCH RADIUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\frac{3}{4} = 0.75$</td>
<td>Number of Leaves</td>
<td>$n_0^L$</td>
<td>$\frac{3}{4} = 0.75$</td>
<td>$n_k^L$</td>
</tr>
<tr>
<td>$\frac{3}{4} = 0.75$</td>
<td>Number of Branches</td>
<td>$N_0$</td>
<td>$\frac{3}{4} = 0.75$</td>
<td>$N_k$</td>
</tr>
<tr>
<td>$\frac{3}{4} = 0.75$</td>
<td>Number of Tubes</td>
<td>$n_0$</td>
<td>$\frac{1}{4} = 0.25$</td>
<td>$n_k$</td>
</tr>
<tr>
<td>$\frac{1}{4} = 0.25$</td>
<td>Branch Length</td>
<td>$l_0$</td>
<td>$\frac{3}{8} = 0.375$</td>
<td>$l_k$</td>
</tr>
<tr>
<td>$\frac{7}{8} = 0.875$</td>
<td>Area of Conductive Tissue</td>
<td>$A_0^{CT}$</td>
<td>$\frac{1}{16} = 0.0625$</td>
<td>$A_k^{CT}$</td>
</tr>
<tr>
<td>$\frac{1}{16} = 0.0625$</td>
<td>Tube Radius</td>
<td>$a_0$</td>
<td>$1 = 1.00$</td>
<td>$a_k$</td>
</tr>
<tr>
<td>$1 = 1.00$</td>
<td>Conductivity</td>
<td>$K_0$</td>
<td>$\frac{1}{4} = 0.25$</td>
<td>$K_k$</td>
</tr>
<tr>
<td>$\frac{1}{4} = 0.25$</td>
<td>LSC</td>
<td>$L_0$</td>
<td>$\frac{1}{4} = 0.25$</td>
<td>$L_k$</td>
</tr>
<tr>
<td>$\frac{3}{4} = 0.75$</td>
<td>Fluid Flow Rate</td>
<td>$\dot{Q}_0$</td>
<td>$\frac{3}{4} = 0.75$</td>
<td>$\dot{Q}_k$</td>
</tr>
<tr>
<td>$\frac{3}{4} = 0.75$</td>
<td>Metabolic Rate</td>
<td>$\dot{Q}_0$</td>
<td>$\frac{3}{4} = 0.75$</td>
<td>$\dot{Q}_k$</td>
</tr>
<tr>
<td>$\frac{1}{4} = -0.25$</td>
<td>Pressure Gradient</td>
<td>$\Delta P_0/l_0$</td>
<td>$\frac{1}{4} = -0.25$</td>
<td>$\Delta P_k/l_k$</td>
</tr>
<tr>
<td>$\frac{1}{8} = -0.125$</td>
<td>Fluid Velocity</td>
<td>$u_0$</td>
<td>$\frac{1}{8} = -0.125$</td>
<td>$u_k$</td>
</tr>
<tr>
<td>$\frac{3}{4} = -0.75$</td>
<td>Branch Resistance</td>
<td>$Z_0$</td>
<td>$\frac{3}{4} = -0.75$</td>
<td>$Z_k$</td>
</tr>
<tr>
<td>$\frac{1}{4} = 0.25$</td>
<td>Tree Height</td>
<td>$h$</td>
<td>$\frac{3}{4} = 0.75$</td>
<td></td>
</tr>
<tr>
<td>$\frac{25}{24} = 1.0415$</td>
<td>Reproductive Biomass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\frac{25}{24} = 1.0415$</td>
<td>Total Fluid Volume</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>