

Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems

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Summary A general theory of allometric scaling that predicts how the proportions of vascular plants and the characteristics of plant communities change or scale with plant size is outlined. The theory rests, in part, on the assumptions of (1) minimal energy dissipation in the transport of fluid through space-filling, fractal-like, branching vascular networks; and (2) the absence of scaling with plant size in the anatomical and physiological attributes of leaves and xylem. The theory shows how the scaling of metabolism with plant size is central to the scaling of whole-plant form and function. It is shown how allometric constraints influence plant populations and, potentially, processes in plant evolution. Rapidly accumulating evidence in support of the general allometric model is reviewed and new evidence is presented. Current work supports the notion that scaling of how plants utilize space and resources is central to the development of a general synthetic and quantitative theory of plant form, function, ecology and diversity.

Keywords: *diversity, energy dissipation, evolution, fractal networks, metabolism, space-filling.*

Introduction: modeling plant structure and function

A central problem in biology is the identification of general principles governing the evolution of form, function and diversity across different levels of biological organization (Levin 1992). The problem is made more complex because the size of vascular plants spans more than 12 orders of magnitude. A *Sequoia*, for example, spans a large part of this size range as it develops from seedling to adult tree. Yet despite great variation in size, all vascular plants share essentially the same anatomical and physiological design.

Numerous studies have examined the anatomical and physiological implications of size in plants differing in growth form, taxonomic group and environmental setting (e.g., Shinozaki et al. 1964, Yoda et al. 1965, Whittaker and Woodwell 1968, Shidei and Kira 1977, Cannell 1982, Niklas 1994b). Nevertheless, few mechanistic models attempt to link whole-plant architecture, vascular anatomy and the physiology of sap flow and other processes, either among parts of a single plant or among plants differing in size (see Tyree and

Ewers 1991, Niklas 1994b, Dewar et al. 1998). Furthermore, it is still unclear how anatomical structure and physiological processes can be scaled up to predict larger scale ecological and ecosystem patterns (Levin 1992, Ehlerliger and Field 1993).

This paper focuses on the scaling of plant attributes with plant size. It is argued that size provides a mechanistic window by which to interrelate numerous organismal, community and ecosystem properties. The influence of the size of an organism on organismal traits (allometry) has long been of interest (e.g., Huxley 1932, Thompson 1942), but has lacked a firm theoretical foundation (West et al. 1997). Here I review several recent publications outlining how the scaling of metabolic rate determines how many aspects of plant form, function and diversity scale with plant size (West et al. 1997, 1999a, 1999b, Enquist et al. 1999, 2000, Enquist and Niklas 2001, 2002, Niklas and Enquist 2001). The reviewed work shows how allometric scaling provides: (1) a viewpoint that highlights the general “rules” guiding the evolution of plant form and function; and (2) a mechanistic theoretical framework linking physiological and life-history traits of individual plants with higher-level attributes of plant populations and communities across diverse ecosystems. In addition to presenting new material, this paper shows how a focus on allometry, and in particular the scaling of metabolism, integrates many anatomical and physiological features of plants and synthesizes several major themes of botanical and plant functional research.

Traditional whole-plant modeling themes in botany

To study scaling within and across vascular plants, it is necessary to assess the general features that may have guided the evolution of plant form. As set forth below, there appear to be four major research themes that have motivated empirical and theoretical studies of the evolution of whole-plant form and function.

Pipe-model

The first major theme stems from Leonardo da Vinci’s observation on tree construction (see Richter 1970, Zimmermann 1983) that “all the branches of a tree at every stage of its

height, when put together, are equal in thickness to the trunk below them." The assumption that branch architecture directly reflects hydraulic architecture leads to the pipe-model, according to which a unit of leaf area is supplied by a given unit area of conducting tissue (see Huber 1928, Shinozaki et al. 1964). The pipe-model has been used as a basis for understanding the structural and functional design of trees (see Waring et al. 1982, Berninger et al. 1997). Although several authors have highlighted problems with its assumptions and predictions (see Tyree and Ewers 1991), the pipe-model is still the most widely cited model of whole-plant structure and function (Grace 1997).

Hydraulic architecture

A somewhat related theme stems from research integrating the anatomy and physiology of whole-plant vascular systems. Central questions guiding this research are: (1) how plants are able to transport water and nutrients to such impressive heights; and (2) why plants tend to reach similar heights within a local environment (see Zimmermann 1983, Ryan and Yoder 1997). The objective has been to understand the physical and selective processes governing the flow of fluid in the vascular system and how they have influenced the evolution of xylem anatomy (e.g., Huber 1932, Huber and Schmidt 1936, Zimmermann and Brown 1971, Zimmermann 1978*a*, 1978*b*, 1983, Tyree et al. 1983, Tyree 1988, Niklas 1984, 1985, Tyree and Ewers 1991, Sperry et al. 1993, Comstock and Sperry 2000). Some studies have considered functional explanations for differences in anatomy and physiology or the presence of architectures such as those of vines and hemiepiphytes, in plants living in unique environments such as deserts or swamps (e.g., Zimmermann 1983, Carlquist 1988, Patino et al. 1995, Tyree and Ewers 1996).

Resistance-capacitance

A third major research focus has involved detailed modeling of fluid flow along a water potential gradient from the soil through the plant to the atmosphere. These resistance-capacitance models use Ohm's law to show how anatomical, physiological and physical attributes of plants and their environment influence the water potential gradient and the rate of fluid transport throughout the individual (e.g., van de Honert 1948, Jones 1978, Smith et al. 1987, Tyree and Sperry 1988, see also Jones 1992, Schulte and Costa 1996). This approach tends to ignore the complex dynamics of fluid flow through microcapillary vascular tubes and chooses instead to characterize bulk flow by analogies to electrical circuits.

Plant architecture and form

The fourth major theme involves the application of mathematical and biomechanical principles to understand the evolution of plant architecture. For example, although there is an enormous diversity of vascular plants, most can be classified as sharing a limited number of branched architectural forms (Halle et al. 1978). Whole-plant branching patterns can be characterized by mathematical rules reflected in phyllotactic schemes, Fibonacci series and fractal geometry (Honda 1971,

Leopold 1971, Mandelbrot 1977, Aono and Tosiya 1984, see also Rashevsky 1973, Farnsworth and Niklas 1995). Several investigators have highlighted the fractal-like nature of plant architecture (Mandelbrot 1977, Aono and Tosiya 1984, Morse et al. 1985, Farnsworth and Niklas 1995) and measured the fractal dimensions of plant structures (e.g., Morse et al. 1985, Tatsumi et al. 1989, Fitter and Strickland 1992, Bernston and Stoll 1997, Nielsen et al. 1997, Eshel 1998). Other work has focused on whether the architectural design of plants is optimized to intercept sunlight, water or nutrients (Horn 1971, Whitney 1976, Borchert and Slade 1981, Givnish 1982, 1987, Niklas and Kerchner 1984, Ellison and Niklas 1988, Morgan and Cannell 1988, Niklas 1988, 1994*b*, 1997) to resist buckling as a result of wind and gravity (Greenhill 1881, McMahon 1973, King and Loucks 1976, McMahon and Kronauer 1976, Niklas 1994*a*, 1997*b*) or to obey other biomechanical principles (Niklas 1992). However, there have been few attempts to relate the self-similarity of plant anatomy and form at different scales to their function, or to explore the ecological ramifications of these relationships.

Plant allometry

Largely missing from studies of plant structure and function is an explicit consideration of the role plant size plays in the structural and functional characteristics of the vascular system, and in mediating the relationship between biomechanical constraints and resource requirements of individual plants across environments differing in resource availability (see Niklas 1994*a*). Here it is argued that allometry provides a powerful framework for integrating numerous studies of plant form and function—including the four whole-plant modeling themes mentioned above. Since Huxley (1932) defined the allometric equation, many structural and functional variables of organisms (Y) have been shown to scale as power functions of body mass, M (or with other measures of size such as length, l , or diameter, D) (see Appendix 1 for summary of symbols used):

$$Y = Y_0 M^b, \quad (1)$$

where Y_0 is a constant that varies with the type of variable and the kind of organism, and b is the allometric exponent. Zoological research has shown that the value of b often takes the form of a quarter-power (e.g., 1/4, 3/4, 3/8, 1/12) (Peters 1983, Calder 1984, Schmidt-Nielsen 1984). It is unclear whether such canonical allometric relationships also characterize plants.

Although allometry has traditionally been an important component of comparative research in zoology, its application in botanical and plant physiological research has been limited (Reiss 1989). This is unfortunate, because plant size has long been cited as a fundamental feature influencing plant form and function (Sinnott 1921, Murray 1927, Pearsall 1927, Barton-Wright 1932, Turrell 1961). For example, Barton-Wright (1932) states at the beginning of his book, *Recent Advances in Botany*, "Although (the principle) of similarity has been ex-

tensively applied by zoologists, it has received but scant attention at the hands of botanists. Physiological interchange in plants is conducted through limiting surfaces, both external and internal... such interchange will be proportional to the area of surface involved..." Barton-Wright's quote still holds true today. The lack of allometric integration within botany appears to be associated with: (1) a historical lack of allometric investigations such that there is no basis on which to build; (2) the difficulty of measuring total mass or other plant dimensions, especially for large individuals; and (3) the confinement of allometric studies mainly to curve-fitting exercises lacking theoretical explanation. In the absence of a compelling explanation of why so many organismic characters tend to scale with specific allometric relationships, or why one would expect deviations, there has been a strong tendency to treat such relationships as idiosyncratic phenomena (Peters 1983, Niklas 1994b).

Most studies in botany fail to consider that growth, allocation, diversity and scaling between cells, individuals and ecosystems are fundamentally allometric in nature (Reiss 1989, Niklas 1994b, Enquist et al. 2000, Niklas and Enquist 2001). Applications of allometry to plant biology have consisted primarily of the application of biomechanical principles to the scaling of structural and functional features of plants of varying size (McMahon 1973, Niklas 1992, Niklas 1994b, but see Thomas 1996a, 1996b), or of the development of correlative relationships among size-related variables for application to agriculture, forestry and ecosystem ecology (e.g., Shidei and Kira 1977, Cannell 1982, Waring et al. 1982). Few investigators have applied allometry to more mechanistic studies of resource uptake, plant form, evolution and ecology (see Niklas 1994b), or focused on allometry as a means of highlighting general organizing principles in botanical research.

A general model for the origin of allometric scaling laws in biology

West, Brown and Enquist have recently presented a general model, hereafter referred to as the WBE model, for the origin of allometric scaling laws in biology (West et al. 1997, 1999b, Brown et al. 2000, Enquist et al. 2000). The WBE model proposes that, in both plants and animals, evolution by natural selection has resulted in optimal fractal-like vascular networks. These networks minimize total hydrodynamic resistance yet maximize whole-organism resource use by maximizing the scaling of surfaces where resources are exchanged with the environment (e.g., root area, leaf area, lung and gut surfaces). The scaling of physiological rates and times must match the ability of vascular networks to obtain and deliver resources. Thus, allometric scaling relationships simply reflect the physical and biological constraints of transporting resources from exchange surface areas through optimal vascular networks to metabolizing tissues. As a result of these general principles, organisms exhibit a common set of quarter-power scaling relationships with body mass. Consequently, the WBE model provides a quantitative basis for a general framework that is capable of predicting how allometric scaling relationships at the

level of the individual influence pattern and process at larger ecological and ecosystem scales (Enquist et al. 1998).

The WBE model indicates that, despite the many idiosyncratic differences observed among different kinds of organisms, most, if not all, living systems appear to obey a common set of design principles. The model is a zeroth-order model—it invokes the minimum possible assumptions necessary to derive the scaling relationships of interest. As such it provides a basis to build more complex modes for biological scaling. It is based on the fact that uptake of essential resources occurs across surface areas in specialized vascular tissues and that these materials are distributed throughout the body by means of a hierarchical vascular network. The WBE model predicts that these vascular systems are hierarchical branching networks that: (1) branch to supply or exploit resources within a three-dimensional volume; (2) minimize the energy required to distribute materials through this network; and (3) have terminal network elements (e.g., the terminal branch or petiole size, terminal vessels in the leaf, capillaries) that do not vary with body size. As a result of these principles of functional design, organisms exhibit a common set of allometric scaling relationships.

Two evolutionary challenges

Application of the WBE model to vascular plants is based on the observation that two evolutionary challenges have influenced the scaling of plant form and function. The earliest vascular plants were small. From such humble beginnings, vascular plants have increased in size by about 12 orders of magnitude (see Enquist et al. 2001). Several studies have documented how certain biotic and abiotic features can select for increased plant size (e.g., Harper 1977). For example, increases in plant size often lead to greater access to limited resources and increases in reproductive output. Selection for an increase in plant size, however, also brings about: (1) an increased probability of mechanical failure as a result of buckling from increased weight and wind throw (Niklas 1992); and (2) an increase in vascular hydrodynamic resistance with increasing transport distance between soil and leaves (see Ryan and Yoder 1997). The functional solutions to these problems will be shown to dictate how branch lengths and radii, and xylem vessel radii scale with changes in plant size and branching level.

Application to vascular plants

A detailed treatment of the WBE model, which has been extended to the specifics of vascular plants, is given in West et al. (1999a) and Enquist et al. (2000). The general plant model predicts that many characteristics of vascular plants will scale with an allometric exponent, b (a quarter-power), if four basic assumptions are upheld: (1) the whole-plant branching architecture is volume-filling; (2) within a species and during ontogenetic development of an individual, the physical dimensions and characteristics of the leaf (i.e., leaf size, photosynthesis transpiration rates per unit leaf mass, number of vascular elements needed to supply an average leaf) are approximately in-

variant with plant size; (3) biomechanical constraints are uniform; and (4) hydrodynamic resistance throughout the vascular network is minimized. The general plant model should also apply, with only minor modification, to the specifics of transport through phloem and roots (see Enquist and Niklas 2002, Niklas and Enquist 2002 for how an extension of the WBE allometric model is applied to patterns of biomass partitioning among roots, shoots and leaves).

In addition, the general plant model assumes that the xylem network system comprises multiple tubular vascular elements (Figure 1). For simplicity, all xylem tubes are aligned in parallel and run continuously from rootlet to leaf. Xylem tubes are assumed to be of equal length. Their diameters are constant within a branch segment but are allowed to vary between segments, thereby allowing for possible tapering of xylem tubes from trunk to petiole. This variation is critical for circumventing the problem of hydrodynamic resistance increasing with tube length. Thickness and structure of tube walls are ignored, as are lateral connections between parallel tubes. Lastly, the general plant model allows the ratio of conducting to non-conducting tissue to vary with tree height, thereby avoiding a possible conflict between hydrodynamic and mechanical constraints. Based on these assumptions, the architecture of a tree is a self-similar fractal with specific scaling exponents. It is important to note that the branching rules outlined below can be manifest in different architectures (strongly apically dominant branching as in conifers versus a less apically dominant branching shown in Figure 1). Nevertheless, the predicted scaling properties do not depend on most details of the system design, including the exact branching pattern, provided it has a fractal-like structure. Together, these assumptions provide a quantitative zeroth-order model of the entire plant network, which makes testable predictions and can be used as a point of departure for more detailed investigations.

The model can be described as a hierarchical branching network running from the trunk (level 0) to the leaf petiole (level N) (see Figure 1). An arbitrary level in the plant branching network is denoted by k . The architecture of the branching network is characterized by three parameters (β , $\bar{\beta}$ and γ) that define the relationship of daughter to parent branches. These

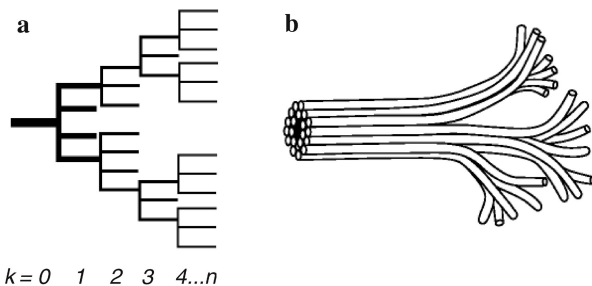


Figure 1. One representation of a hypothetical branching network that satisfies the WBE model. Reproduced from West et al. (1999a). (a) Topology of plant branching network. (b) Symbolic representation of branch vascular structure, showing conducting tubes and non-conducting tissues (black). This is to be contrasted to the tightly bundled vascular system of the pipe-model in which all tissue is conducting.

are determined by the ratios of branch radii (r) at a given branching level ($\beta_k \equiv r_{k+1}/r_k \equiv n^{-a/2}$), the ratios of the xylem tube radii (v) ($\bar{\beta} \equiv a_{k+1}/a_k \equiv n^{-\bar{a}/2}$), and the ratios of branch lengths (l) ($\gamma \equiv l_{k+1}/l_k$). The branching ratio, n , is the number of daughter branches derived from one parent branch, is typically two, and is assumed to be independent of k . Elsewhere, it has been shown that, for the network to be volume-filling (leaves and roots try to fill a three-dimensional space), $\gamma = n^{-1/3}$, independent of k (West et al. 1997, 1999a, 1999b). It is important to note that scaling relationships within the plant are parameterized in terms of just two scaling factors, a and \bar{a} , which determine how the radii of branches and xylem tubes change or scale within a plant. As discussed below, if biomechanical constraints are uniform throughout the tree, then β_k and a are also independent of k , showing that the network is self-similar at different scales (β , $\bar{\beta}$ and γ are independent of k) up to the branching level of the leaf. If, in addition, it is assumed that \bar{a} is independent of k , so that any tapering of xylem tubes is uniform, it can be shown that the scaling of branch radii and xylem vessel radii is:

$$\frac{r_k}{r_N} = n^{(N-k)a/2}; \quad \frac{a_k}{a_N} = \left(\frac{r_k}{r_N}\right)^{\bar{a}/a}, \quad (2)$$

and the scaling of branch lengths together with the volume filling constraint gives:

$$\frac{l_k}{l_N} = \left(\frac{r_k}{r_N}\right)^{2/3a}, \quad (3)$$

where r_N and l_N are petiole radius and length, respectively, and N is total number of branchings. Given that the total number of xylem tubes is preserved at each branching, multiple scaling laws can be derived. For example, the number of terminal branches or leaves is given by $n_k^L = (r_k/r_N)^{2/a}$, the area of conductive tissue by $A_k^{CT} = A_N^{CT} (r_k/r_N)^{2(1+\bar{a})/a}$, and the proportion of conductive tissue by $f_k \equiv A_k^{CT}/A_k^{Tot} = n_N (a_N^2/r_N^2) (r_k/r_N)^{2(1+\bar{a}-a)/a}$ (West et al. 1999a, 1999b, Enquist et al. 2000). Thus, the total cross-sectional area of all daughter branches, nA_{k+1} , at any level k , is given by $nA_{k+1}^{Tot}/A_k^{Tot} = n\beta_k^2 = n^{(1-a)}$. When $a = 1$, this reduces to unity and the branching is area-preserving; i.e., the total cross-sectional area at any given level, $nA_{k+1}^{Tot} = A_k^{Tot}$ (Richter 1970, Horn 2000). The pipe-model, where all tubes have the same constant diameter, are tightly bundled and there is no non-conducting tissue, represents the simple case of $a = 1$. In reality, however, tubes are not tightly packed in the sapwood and there may be heartwood that provides additional mechanical stability. The above scaling relationships can therefore be parameterized in terms of two exponents, a and \bar{a} . As indicated by West et al. (1999a, 1999b), a and \bar{a} are determined from two critical constraints: a from biomechanical stability and \bar{a} from the minimization of hydrodynamic resistance through the vascular network.

Mechanical and volume filling constraint

As plants increase in size they must be able to resist buckling under the forces of gravity and wind. Biomechanical principles indicate that buckling resistance is greatest when the length and radius of branches maintain the relationship: $l_k \propto r_k^\alpha$. Previous studies have shown that if the condition of mechanical stability is the same for all branches, then α is constant and independent of k . In this case a and β_k are constant, giving a branching architecture that is a self-similar at different scales (i.e., fractal). Analyses based on scale-invariant solutions to the bending moment equations for beams (elastic similarity) give $\alpha = 2/3$ (Greenhill 1881, McMahon and Kronauer 1976, King and Louks 1978, Niklas 1992, but see Niklas 1994b, 1997b). This constraint, which is most important for the trunk and large branches, agrees well with data for these segments (McMahon and Kronauer 1976, Bertram 1989, Horn 2000). Assuming that $\alpha = 2/3$ holds for all k , together with the volume filling constraint (see Equations 2 and 3) leads to $a = 1$, which is precisely the condition for area-preserving branching (i.e., Leonardo's original observation).

Note that the result $a = 1$ implies that the leaf area distal to the k th branch $A_k^L = C_L r_k^2$, where $C_L \equiv A_L / r_N^2$ is a constant and A_L is the area of a leaf. In addition, the number of branches of a given size at a given k level is $N_k = n^N (r_N / r_k)^{2/a}$, or $N_k \propto r_k^{-2}$. If reproductive tissues are supplied by vascular elements in the same way as leaves, they should exhibit similar scaling behavior (see Shinozaki et al. 1964, Stevens 1987, Niklas 1993, 1994, Thomas 1996b).

Hydrodynamic constraint

As plants increase in size, the distance over which resources must be transported increases. The hydrodynamic resistance of a given xylem tube, Z_k^i , is theoretically given by the classic Poiseuille formula that governs flow through pipes, $Z_k^i = 8\eta l_k / \pi a_k^4$, where η is fluid viscosity (Zimmermann 1983). Note that any slight change in xylem tube diameter leads to a disproportionate change in total tube resistance because of the fourth power dependence on a_k . If xylem tube diameter does not change, then hydrodynamic resistance increases linearly with transport distance, l_k , independently of any mechanical constraint. Furthermore, because path lengths from the soil to the leaves and branch meristems differ, resources tend to be delivered at higher rates over shorter paths, limiting resource supply to terminal shoots. This linear increase in resistance would seemingly have limited plant size diversification (see also Raven and Handley 1987, Raven 1993, Ryan and Yoder 1997).

The total resistance of a single xylem tube running from the trunk to the petiole can be summed to give:

$$Z_i = \frac{1 - n^{(-1/3 + 2\bar{a})(N+1)}}{1 - n^{(-1/3 + 2\bar{a})}} Z_N \tag{4}$$

$$= \frac{1 - ((n^{1/3} - 1)l_T / l_N)^{(1 - 6\bar{a})}}{1 - n^{(1/3 - 2\bar{a})}} Z_N ,$$

where Z_N is the resistance of the petiole (West et al. 1999a). Here we see how Z_i changes with increasing total path length, l_T , through the plant from the base of the branch to the leaf, where $l_T = \sum_{k=0}^N l_k = l_0(1 - n^{-1/3})$. Thus, as l_T changes, the behavior of the resistance of the total system Z_i depends critically on the exponent that dictates xylem vessel tapering with branching level: namely, whether \bar{a} is greater than, less than or equal to 1/6. If \bar{a} is less than 1/6, the total resistance of the network increases as the path length from soil to petiole increases with size. However, if $\bar{a} > 1/6$, this equation indicates that the total tube resistance is constant and independent of both the number of branchings, N , and the total xylem tube length, l_T . Therefore, the model makes a novel prediction that, for a plant with at least several branching generations, Z_i is invariant with increases in plant size. Such tapering of xylem elements is exactly what is needed to ensure that all leaves have comparable rates of resource supply independent of total branch length. Because large \bar{a} 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 extreme tapering, \bar{a} may be as close as possible to the minimum value (1/6) consistent with Equation 7.

General plant model: allometric predictions

Together the values of a and \bar{a} dictate the scaling of several plant allometric relationships. The assumptions and optimization principles stated above lead to quantitative predictions of how numerous aspects of plant geometry, physiology and anatomy scale within a plant of a given size and also for some interspecific exponents. Detailed derivations for numerous allometric predictions for the plant vascular network are given in West et al. (1999a) and Enquist et al. (2000). Table 1 summarizes some of these allometric predictions. Allometric relationships can be expressed in terms of plant mass by assuming that the total volume, V , occupied by plants is filled with a tissue density that is approximately constant across sizes (see West et al. 1999a). Specifically, in terms of scaling of mass with the basal stem length, l_0 , and diameter, r_0 , so that $l_0 \propto M^{1/(a+3)} \propto M^{1/4}$ and $r_0 \propto M^{2a/(2(a+3))} \propto M^{3/8}$.

The predictions of WBE mainly focus on the derivation of scaling exponents. However, the WBE model also quantitatively predicts their normalizations (the scaling intercept Y_0), which includes many subtle aspects of leaf-level anatomy and physiology. Here I focus on the full derivation of two allometric relationships (leaf mass and conductivity). These examples show how the WBE model quantitatively predicts not only the allometric exponent but also the value for the allometric intercept, and shows how subtle taxonomic and environmental variations may influence variation in allometric relationships.

Leaf mass

The WBE model predicts that the total number of leaves, n_k^L , should scale with the total number of branches, N , and with branch radius, r_k , as $n_k^L = n_k / n_N = n^{N-k} = (r_k / r_N)^{2/a}$. Here one can see the influence of biomechanical considerations as shown by

Table 1. Predicted within-plant scaling exponents as functions of plant mass and branch radius. Symbols are represented in terms of scaling relationships for the main stem or trunk (Level 0), in terms of a branch or stem in the k th level of the branching hierarchy, or in terms of the whole-plant (no subscript). Adapted from West et al. (1999a). Abbreviation: nd = no data available.

Variable	Plant mass (M)		Branch radius (r)		
	Exponent predicted	Symbol	Symbol	Exponent predicted	Exponent observed
No. leaves	3/4	n_0^L	n_k^L	2 (2.00)	2.01 ¹
No. branches	3/4	N_0	N_k	-2 (-2.00)	-2.00 ²
No. tubes	3/4	n_0	n_k	2 (2.00)	nd
Branch length	1/4	l_0	l_k	2/3 (0.67)	0.65 ²
Branch radius	3/8	r_0			
Area of conducting tissue	7/8	A_0^{CT}	A_k^{CT}	7/3 (2.33)	2.13 ³
Tube radius	> 1/6	a_0	a_k	1/6 (0.167)	nd
Conductivity	1	K_0	K_k	8/3 (2.67)	2.63 ¹
Leaf-specific conductivity	1/4	L_0	L_k	2/3 (0.67)	0.73 ⁴
Fluid flow rate	3/4	Q_0	Q_k	2 (2.00)	nd
Metabolic rate	3/4	B			
Pressure gradient	-1/4	$\Delta P_0/l_0$	$\Delta P_k/l_k$	-2/3 (-0.67)	nd
Fluid velocity	-1/8	u_0	u_k	-1/3 (-0.33)	nd
Branch resistance	-3/4	Z_0	Z_k	-1/3 (-0.33)	nd
Tree height	1/4	h			
Reproductive biomass	3/4				
Fluid volume	25/24				

¹ *Acer saccharum*, Yang and Tyree (1993); ² Shinozaki et al. (1964); ³ *Ficus spp.*, Patino et al. (1995); ⁴ *Thuja occidentalis*, Tyree et al. (1983).

a , and by the dimensions of the leaf as given by the radius of the petiole, r_N , and the number of petioles, n_N . Given that leaf area and petiole size remain approximately invariant (assumption 2), $n_k^L \propto A_k^L$ where $A_k^L = C_L r_k^2$ and $C_L \equiv A_L / r_N^{2/a}$ where A_L is mean area of a leaf and r_N is the average petiole radius. So, with $a = 1$, total leaf area, A_k^L , or number of leaves, n_k^L , should scale with stem diameter as $n_k^L \propto A_k^L = C_L r_k^2$ or $n_k^L \propto r_k^2 \propto M^{3/4}$. Taking typical values of petiole radius, $r_N = 0.5$ mm and leaf area, $A_L = 30$ cm², gives $C_L = 1.2 \times 10^4$, which is well supported by empirical data (see West et al. 1999a). Note that differences in r_N or A_L , or in variation in the biomechanical or volume-filling assumptions reflected in the value of a within or between species will lead to calculable differences in values of C_L and the scaling exponent of leaf area.

Conductivity

Another key example is given by the scaling of conductivity. Conductivity is a measure of resistance across a branch of a given length. Specifically, the hydrodynamic resistance of a branch segment is given by $Z_k = Z_k^i / n_k = 8\eta l_k / \pi n_k a_k^4$, and conductivity is given by $K_k \equiv l_k / Z_k = K_N (r_k / r_N)^{2(1+2\bar{a})/a}$, where η is fluid viscosity, K_N is conductivity of the petiole, l_k is branch length at level k and v_k is radius of a xylem vessel within a given k th branch. Here $K_N = \pi n_N a_N^4 / 8\eta$, where n_N and a_N are the mean number of vascular strands per petiole and the mean cross-sectional area of a xylem vessel, respectively. The predicted values of $\bar{a} > 1/6$ and $a = 1$ give $K_k \propto r_k^{8/3} \propto M^{3/4}$. Therefore, by measuring η , and anatomical values of n_N , a_N , r_N and the radius of the branch, r_k , the model quantitatively predicts a specific value for the normalization of conductivity for a given branch size. Further, potential variation in these parameters between species or environments will lead to predictable devi-

ations. A series of additional hydrodynamic allometric predictions, such as fluid velocity, total plant resistance, leaf specific conductivity, branch fluid content and branch resistance are listed in Table 1 (see West et al. 1999a and Enquist et al. 2000 for additional details).

Whole-plant resource use

The rate of whole-plant resource use will be equal to the total number of leaves multiplied by the average rate of resource use per leaf. The WBE model predicts that the total number of leaves, n_L , and the total leaf area, A_L^{Tot} scale as $A_L^{\text{Tot}}, n_L^2 \propto M^{3/4}$. If all leaves require approximately the same amount of resource, then, for example, the rate or whole plant transpiration or fluid flow rate, Q_0 , is directly proportional to the total number of leaves. Thus, $Q_0 \propto n_L \propto A_L^{\text{Tot}} \propto r_0^2 \propto M^{3/4}$.

Allometric exponents for a series of additional physiological and anatomical attributes of vascular plants are predicted to be quarter-powers when plotted in terms of plant mass, M , which can be converted to allometric predictions based on stem diameter, D , or stem radius r_k (Table 1). One important prediction for whole-plant allometry is that the total volume of fluid within the plant should increase, although slightly, with plant size (Table 1) indicating an increased role of water storage in the largest trees. This prediction appears to match recent empirical measures of water content in trees (N. Phillips, personal communication). Empirical support is given for several of the predicted exponents; however, several relationships have yet to be tested.

Comparison with the pipe-model

The WBE model appears to accurately predict many attributes of vascular plants and provides a more realistic characteriza-

tion of plant structure and function than previous formulations such as the pipe-model (see Table 2). A comparison of allometric predictions by the WBE model and the pipe-model (Shinozaki et al. 1964) reveals several important differences (Table 2). For example, the WBE model predicts that total hydrodynamic resistance is approximately constant with plant size, whereas the pipe-model predicts a directly proportional increase with size (see also Ryan and Yoder 1997). The pipe-model does not explicitly include biomechanical constraints, or allow for the presence of nonconducting tissue. More critically, it does not account for the increase in total hydrodynamic resistance with increasing path length from root to leaf. Thus, it cannot account for the observed scaling exponents for the tapering of xylem vessels and tracheids and the resulting change in conductivity and leaf-specific conductivity, observed sapwood/heartwood ratios, and how total vascular resistances in branch segments should change as terminal branches are experimentally removed.

Empirical support for general plant model and quarter-power scaling in vascular plants

Allometric tapering of xylem dimensions

Although it is difficult to measure xylem dimensions, there is indirect evidence to support the predicted degree of xylem tube tapering with increasing plant size. Many have noted that, within a plant, xylem dimensions tend to increase with branch size (e.g., Zimmermann 1983). Intraspecific data for *Tsuga canadensis* L. (Ewers and Zimmermann 1984) provide support for the prediction that the dimensions of the xylem scale with an exponent greater than or equal to 1/6. Figure 2 shows that tracheid diameter scales as a power-law of branch diameter. The observed exponent in Figure 2 is within the 95% confidence intervals of the predicted values of the general plant model. Further, intraspecific data for *Acer* (West et al. 1999a; reproduced in Figure 3) and for four *Rhododendron* spp. presented by Noshiro and Suzuki (2001) as analyzed by B.J. Enquist (unpublished data), and recent analyses by Becker et al. (2000) for several tree species also indicate that vascular element diameters scale within the predicted bounds of the

model, supporting the prediction that total hydrodynamic resistance is invariant with plant size. Further, an analysis of fossil tracheid and branch radii during the initial diversification of tracheophytes shows that evolutionary increases in plant size are also marked by an increase in xylem dimensions as predicted by the WBE model (Enquist 2003). Although it is often technically difficult to measure whole-plant resistance, the fact that numerous anatomical and physiological attributes scale according to exponents predicted by the WBE model strongly suggests that there has been selection to minimize whole-plant hydrodynamic resistance, independent of plant size.

Common scaling laws

A striking prediction of the WBE model is that plants and animals share many allometric scaling relationships. This is supported by various data compilations. For example, the relationship for a given network $r_0 \propto M^{3/8}$ has been confirmed in the scaling of aorta radius (r_0) with whole-animal mass (see Peters 1983). The allometric relationships between basal diameter ($D_0 = 2(r_0)$) and aboveground dry mass, M , has a mean interspecific exponent (b) across 73 species of temperate trees of 2.611 (95% = ± 0.105), which is indistinguishable from the predicted exponent of 8/3 or 2.667, which is also indistinguishable from the predicted $r_0 \propto M^{3/8}$ (Smith and Brand 1983). Similarly, compilation of the interspecific relationship between D_0 and M for tropical trees (Figure 4) provides additional support for the model. Again, the observed exponent $r_0 \propto D_0 \propto M^{0.38}$ is indistinguishable from the predicted exponent of 0.375. As trees begin to senesce and drop branches, deviation below the theoretical exponent is expected and is empirically observed. Additional compilation of data from the literature, including Smith and Brand (1983) and references listed in Enquist et al. (1998, 1999) shows that, across both angiosperms ($n = 55$) and gymnosperms ($n = 30$), total leaf area, A_L , scales with an average exponent that is statistically indistinguishable from the predicted value of 2 (i.e., $A^L \propto r^2 \propto M^{3/4}$). Further, a global compilation of leaf mass and total plant mass, for both angiosperms and gymnosperms, shows that leaf mass scales as the 3/4 power of total plant mass (Enquist and Niklas 2002, Niklas and Enquist 2001, 2002).

Table 2. Comparison of within-plant allometric predictions made by the WBE allometric plant model and the pipe-model (Shinozaki et al. 1964) for several physiological and anatomical variables. Notice that because the pipe-model does not include biomechanics or hydrodynamics, it makes a series of faulty predictions (noted by asterisks), especially of dynamics associated with the vascular network.

Variable	Exponent predicted Allometric WBE model	Exponent predicted Pipe-model
Leaf area	$A_k^L \propto r_k^2$	$A_k^L \propto r_k^2$
Reproductive biomass	$M_{\text{Rep}} \propto r_k^2$	$M_{\text{Rep}} \propto r_k^2$
Number of branches	$N_k \propto r^{-2}$	$N_k \propto r^{-2}$
Fluid velocity*	$u_0 \propto M^{-1/8}$	$u_0 \propto M^0$
Proportion of conducting tissue*	$f_k \propto r_k^{1/3}$	$f_k \propto r_k^1$
Pressure gradient*	$(\Delta P_0/l_0)/(\Delta P_N/l_N) \propto M^{-1/4}$	$(\Delta P_0/l_0)/(\Delta P_N/l_N) \propto M^0$
Total fluid flow/metabolic rate*	$Q_0 \propto M^{3/4}$	$Q_0 \propto M^{1/2}$
Conductivity*	$L_k \propto r_k^{8/3}$	$L_k \propto r_k^0$
Leaf-specific conductivity*	$L_k \propto r_k^{2/3}$	$L_k \propto r_k^0$

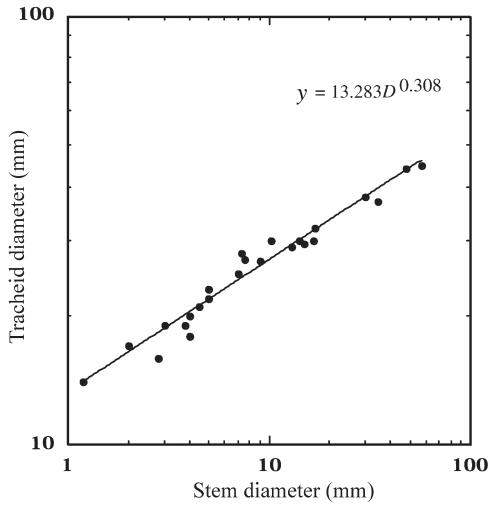


Figure 2. Scaling of tracheid diameter with branch diameter ($2r_k$) in *Tsuga canadensis*. The relationship is best described by a power-law, showing that tracheid diameter increases with branch diameter according to a characteristic allometric scaling relationship. The 95% confidence intervals for the exponent include the value predicted in Table 1. The observed exponent is within the range predicted for optimal networks where the total hydrodynamic resistance is independent of plant size. Data are assembled from Ewers and Zimmermann (1984).

Stem sap flux

The WBE model predicts that xylem flux should scale as basal stem diameter raised to power of 2. Several studies report the total rate of fluid transport in the xylem (Q_0) as a function of

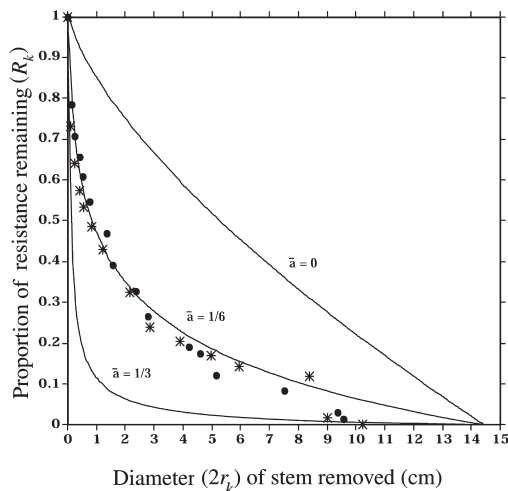


Figure 3. Effect of removing branch segments: the proportion of total resistance remaining, R_k , as a function of the diameter of the removed stem, $2r_k$ (West et al. 1999a). The data points, taken from Yang and Tyree (1994), represent two different *Acer saccharum* Marsh. trees. The solid lines are derived from the WBE model. With $\bar{a} = 1/6$, as predicted from our model, the agreement is excellent. By contrast, with $\bar{a} = 0$, which corresponds to no tapering of xylem elements as in the pipe-model, the agreement is poor.

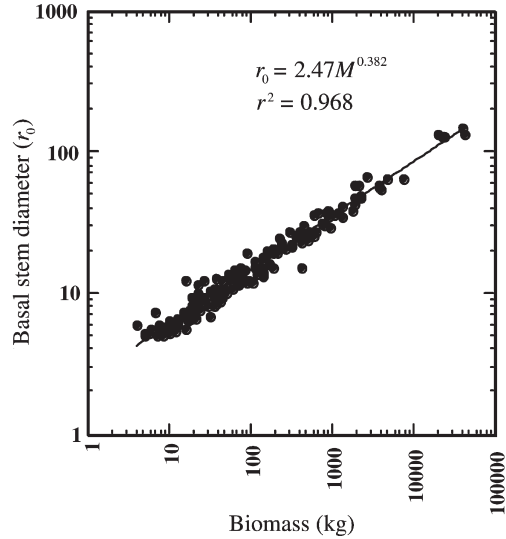


Figure 4. Interspecific allometric scaling of aboveground biomass for numerous neotropical trees. Data assembled from Brown (1997). Allometric theory predicts $r_0 \propto M^{3/8}$ (0.375), and the 95% confidence intervals for the fitted regression are indistinguishable from this value.

stem diameter D , (e.g., Huber 1932, Sakurantani 1981, Schulze et al. 1985). However, it is technically difficult to measure sap flow. For example, measurements of sap flow in the outer few cm of sapwood of large trees are often scaled up to a whole-tree basis without knowledge of the variation in sap flow with radial depth. There is evidence that radial variation is substantial and somewhat unpredictable (James et al. 2002). Further, differences in local conditions (e.g., high humidity, resource limitation) lead to wide variation in sap flux for a given plant size. Therefore, caution must be exercised when analyzing sap flux data. On the basis that use of maximum reported flux likely minimizes these problems, Enquist et al. (1998) tested the WBE prediction by assembling maximum rates of stem flux as a function of stem diameter from small herbaceous plants to large trees. They showed that, interspecifically, sap flux scales allometrically with a characteristic exponent, $Q_0 \propto D^{1.87}$ (the 95% confidence interval for the exponent ranges from 2.01 to 1.736), which is statistically indistinguishable from that predicted by the general allometric model. Further, recent data collected by James et al. (2002) show that the scaling exponent is about 2.3 among four individuals over a diameter range of 34–98 cm with 95% confidence intervals that approximate the predicted value of 2. In addition, Meinzer et al. (2001) showed that sap flux for several species of tropical trees also scales according to prediction of the WBE model. A scaling exponent that approximates 2 also indicates that rates of xylem flux scale as plant mass raised to the 3/4 power. Model II (Reduced Major Axis Regression, RMA) should be used to analyze this data set, as there are likely errors in basal stem diameter measurements because the protocol used to measure diameter differed between studies. Nevertheless, because of such high r^2 values, conclusions based on either Model I or Model II regressions are similar.

Whole-plant xylem transport provides a measure not only of nutrient and water use, but also of gross photosynthesis, and therefore of metabolic rate. Because of stoichiometric and physiological constraints, the allometric scaling exponents for water, nutrient and photosynthate fluxes are approximately equivalent. Although differences in water-use efficiency must be taken into account, rates of transpiration or xylem transport are appropriate, although generally overlooked, indices of whole-plant metabolism.

Rates of biomass production

Based on short-term rates of biomass production, G , as a surrogate for rates of metabolism, Niklas and Enquist (2001) found robust support for the 3/4 scaling exponent. Annualized rates of biomass production, G , scale with a 3/4 exponent of whole-plant body mass, M , for the species representing individual higher taxa or evolutionary grades (e.g., angiosperms, gymnosperms and even unicellular algae). Specifically, among all metaphyte species, the slope of the RMA exponent is essentially indistinguishable from the predicted value of 3/4 ($\alpha_{\text{RMA}} = 0.749 \pm 0.007$, y-intercept = 0.214 ± 0.016 , whereas across tree species, $\alpha_{\text{RMA}} = 0.791 \pm 0.03$ and y-intercept = 0.301 ± 0.16). Similarly, for unicellular algae, G is scaled as the 3/4-power of cell (body) mass ($\alpha_{\text{RMA}} = 0.749 \pm 0.008$, y-intercept = 0.119 ± 0.107). Finally, when data for G and M were pooled and regressed for all plant species, a single allometric scaling (regression) formula with a 3/4 exponent was found to span the 20 orders of magnitude of body size represented in the data set ($\alpha_{\text{RMA}} = 0.763 \pm 0.003$ and y-intercept = 0.208 ± 0.016). Plotting these data with allometric rates of biomass production in animals (Damuth 2001) shows that growth rates in both plants and animals scale with exponents indistinguishable from 3/4. Surprisingly, for a given size, rates of biomass production for both plants and animals are similar (Damuth 2001).

Both the theoretical model and the empirical evidence indicate that whole-plant metabolic rate scales as $M^{3/4}$. Because whole-plant mass scales as M^1 , mass-specific rates scale as $M^{-1/4}$. This agrees with the qualitative observation that size-specific growth rates are generally highest in annuals and small herbs and lowest in large trees (Grime and Hunt 1975, Tilman 1988). See results in Whittaker and Woodwell (1968) for additional empirical values of G that bracket the predicted value of $M^{3/4}$.

Extensions of allometric theory: deviations from predicted scaling exponents

Variations in any of the model assumptions (space filling, minimization of resistance, uniform biomechanical constraints) or in limiting aspects of ecological environments will lead to calculable deviations from the predicted exponents. It is assumed that biomechanical constraints lead to $l_k \propto r_k^\alpha$ with α independent of k . Resistance to elastic buckling, however, which gives $\alpha = 2/3$, leading to $\alpha = 1$ 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 (e.g., Bertram 1989). This can be easily incorporated into the model as a variation in α for either small or large k , and will lead to calculable corrections to corresponding scaling laws. Furthermore, grasses, palms, saplings and small shrubs, with relatively few branches, may not have an area-filling architecture. A more likely geometry is $\gamma = 1/2$ rather than $1/3$ (West et al. 1999a). Because their branches are predominantly conducting tissue, they maintain area-preserving branching, where $a = 1$, and therefore branch length should be directly related to stem radius, $l_k \propto r_k$, which is in agreement with observation (Niklas 1997b). Thus, throughout ontogeny, a most likely varies, leading to calculable deviations in other allometric relationships. Similarly, variation in the tapering of xylem vessel or tracheid cross-sectional areas, as indexed by \bar{a} (see Figure 2), will lead to concomitant variation in several scaling exponents.

Additional slight variation in plant allometric relations may stem from subtle violations of the models central assumptions. As such, it is important to fully test the central assumptions of the WBE model. For example, the model assumes that leaf size, A_k^L (and other anatomical and physiological attributes of leaves) is approximately constant during plant ontogeny. However, it is possible that leaf anatomical and physiological traits may differ, especially in some old trees (Apple et al. 2002). Furthermore, the largest trees may also deviate from predicted "optimal" allometric scaling relations due to the shedding of terminal branches associated with senescence (Chambers 2001). Therefore, it is critical that future research assessing the WBE model understand that possible violation of assumptions will likely add subtle detail to the model's predictions. As an example, a hypothetical 2-fold increase in A_L during ontogeny will lead to a predictable, but slight, deviation in the scaling of A_k^L . Using the equation from Box 3 in West et al. (1999a), $L_k^{\text{con}} \equiv K_k/n_k^L a_L = L_N^{\text{con}} (r_k/r_N)^{4\bar{a}/a}$, it is straightforward to substitute $2a_L$ while keeping other parameters constant. Using values of $r_N = 0.5$ mm and r_0 (basal stem radius) of 5 mm, 5 cm, or 50 cm leads to a predictable change in the value of \bar{a} of 0.243, 0.205 and 0.193, respectively. Such variation will thus yield, extremely slight, but yet calculable changes in the expected scaling exponent. Nevertheless, the results are still consistent with the model prediction that $\bar{a} \geq 0.167$.

It is important to note, that even a 2-fold variation in A_k^L is very small compared to the 10,000 to even 100,000-fold variation in plant size experienced by a single individual during ontogeny. As such, any focus on applicability of the WBE model must assess the predictions in terms of relative importance in magnitude. More importantly, these examples show how the WBE model is a zeroth-order model providing a basis for the development of even more rigorous and detailed models for understanding how the scaling of various anatomical and physiological traits are fundamentally linked. Variation in the fundamental principles or assumptions will lead to predictable deviations from the optimal expectations as outlined by West et al. (1997, 1999a).

Extensions of allometric theory: life history variation—the importance of tissue density

The general allometric model has so far assumed that tissue density within and between species is constant. For a given animal tissue type, tissue density, $\rho = (M/V)$, does not vary significantly. Plants, on the other hand, often show large differences in tissue specific density. For example, in trees, wood density values range from less than 0.1 to well over 1 (Niklas 1992). Extensions of the general allometric model indicate that such variation reflects a unique way by which plants differ in many life history traits such as growth rate, time until reproduction and death (Enquist et al. 1999). Variation in wood density and leaf tissue density are associated with many anatomical, physiological and ecological differences among species. For example, wood density is correlated with numerous other traits including: leaf phenology (deciduousness), stem water storage, probability of embolism, water transport capacity, resistance to seasonal drought, resistance to pathogenic decay and patterns of phenology, and these, in turn, limit local ecological distributions (see literature cited in Enquist et al. 1999 and Hacke et al. 2001, Hacke and Sperry 2001). Enquist et al. (1999), however, showed that variation in allometric rates of stem growth (dD/dt) is influenced by variation in ρ among species. Specifically, Enquist et al. (1999) assumed that, for a given plant, the rate at which plant mass, M , increases over time (dM/dt) is directly proportional to its metabolic rate, B (the rate of gross photosynthesis). Thus, at any time t , $dM/dt = C_G B$, where C_G is a proportionality constant that can be time-dependent. Note, from the WBE model $B \propto M^{3/4}$. Data presented in Enquist et al. (1998) in addition to Niklas and Enquist (2001) suggest surprisingly little variation in the scaling of $C_G B$ across plant taxa. The WBE model also predicts that metabolism is proportional to total plant volume, $B \propto V^{3/4}$ and stem diameter, $D \propto V^{3/8}$. If $\rho = M/V$ is the tissue specific density, then, at any time t , these relationships can be expressed as:

$$B = C_B \left(\frac{M}{\rho} \right)^{3/4} \quad D = C_D \left(\frac{M}{\rho} \right)^{3/8}, \quad (5)$$

where C_B and C_D are corresponding proportionality constants. Implicit in these results is the assumption that the ratio E/ρ , where E is Young's modulus of elasticity, is constant for all plants (Niklas 1994b). Note that the predictions in Table 1 are modified accordingly by the inclusion of variation in ρ . Here ρ is modeled as an average species-specific value for wood tissue density. As shown below, variation in ρ leads to important differences in allometric growth intercepts. As such, incorporation of ρ into botanical studies will likely explain a significant degree of residual allometric variation. From above, we have $dD/dt = (3C/2\rho)D^{1/3}$ where $C \equiv 1/4C_G C_B C_D^{2/3}$. Note here, C reflects many biological attributes of a plant, which may or may not differ between species. Hence, the model provides the basis for the integration of many functional attributes of plants. This formula can be integrated to give:

$$\rho(D(t)^{2/3} - D(t_0)^{2/3}) = \int_{t_0}^t C(t) dt, \quad (6)$$

where the time dependence of all variables has been made explicit and the integration has been carried out from some initial time t_0 up to some arbitrary time t . Assuming that the proportionality constants, exponents and density are constant over time, a plot of $D(t)^{2/3}$ versus $D(t_0)^{2/3}$ for fixed times t and t_0 for any species should yield a straight line with a universal slope of unity, but with an intercept that depends on the time interval and the species. If, however, ρ of a given plant is taken to be independent of time, but is allowed to vary across species, the intercept of the production relationship should be inversely proportional to ρ . If C_G , C_B and C_D are independent of time, then the intercept, namely the right-hand side of Equation 6, is given by $C(t - t_0)$. Furthermore, if C does not vary among species and the time interval is the same for all species, then weighting $D(t)^{2/3}$ and $D(t_0)^{2/3}$ by ρ and replotting all species together should yield a universal line of unit slope so that $\rho(D(t)^{2/3} - D(t_0)^{2/3}) = C(t - t_0)dt$. Thus, the weighted allometric growth intercept should no longer depend on the species but only on the time interval and C (but see below for the reproductive period).

This framework allows one to recast the mass-production law as a function of basal stem diameter, D , where $dM/dt = (C_G C_B / C_D^2) D^2$. This gives the novel prediction that across species, dM/dt , for trees of fixed diameter is explicitly independent of wood density ρ . Enquist et al. (1999) tested these allometric growth predictions in 45 species of tropical trees, differing dramatically in their rates of stem diameter growth. Specifically, they compiled long-term growth rates in basal stem diameter with species differing in ρ . Plotting $D(t)^{2/3}$ versus $D(t_0)^{2/3}$ for each species provides robust support for the prediction that the slope of the relationship between $D(t)^{2/3}$ and $D(t_0)^{2/3}$ is 1. Despite species-specific differences, a slope of 1 indicates that the average production of new mass across all species scales as $M^{3/4}$. However, species differ in their growth intercepts because of differences in dD/dt , reflecting life-history variation from fast-growing disturbance specialists with short life spans to slower growing emergent trees of mature forest with relatively longer life spans. As predicted by the model, plotting the growth intercept C against ρ yields a negative relationship where $C \propto \rho^{-1}$. In other words, despite allocation differences among species, all species appear to be producing biomass at the same rate (cf. Niklas and Enquist 2001). Enquist et al. (1999) further utilize this general form of the growth equation and prior life history theory (Charnov 1993) to predict how the timing of life history events (e.g., time until reproduction, mean life span) must be related to variation in allocation as indexed by wood tissue density.

A full treatment of ontogenetic growth is complex. Nevertheless, the growth model outlined here is a first step in predicting how variation in allocation (as reflected in ρ) influences plant allometry and plant growth. A more detailed treatment of how allometry influences ontogenetic growth is given in West et al. (2001). Further, the derivation thus far has assumed that the plant is not reproducing, so that all produc-

tion is given to growth. Growth, however, must slow with the onset of reproduction, as some fraction of production, $\lambda dM/dt$, is then devoted to reproduction and not individual growth $(1 - \lambda)dM/dt$. Life history theory (Stearns 1992, Charnov 1993) predicts the age (size) course of reproductive allocation (λ). Thus, reproduction will cause growth allometries to deviate from the simple power-function.

Summary of model

The above treatment should be viewed as a zeroth-order model for plant allometry. It represents a variant of the WBE model (West et al. 1997) 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 (i.e., variation in ρ , A_L , etc.).

The model can account for many features of plant structure and function. First, it predicts several anatomical and physiological scaling relationships, which compare closely with empirical values (see Table 1). 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 and physiology as well as whole-plant architecture. Because it also predicts several scaling relationships that have yet to be 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; pressure gradient differential between leaf and trunk (the pressure difference between the base of the trunk and leaf); the ratio of conducting to nonconducting tissue; and maximum radius and height 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 important prediction of the model is that of quarter-power scaling, which has been widely commented on in animals, predicted theoretically and demonstrated empirically in vascular plants. Quarter power scaling emerges from selection to maximize the scaling of surface areas while minimizing the scaling of internal transport distance (West et al. 1999b).

Importantly, the model shows how plants can overcome the potentially devastating effect of increasing resistance with tube length, so as to insure comparable xylem flow to all leaves of the plant. Measurements of changes in vessel radius and branch resistance support this prediction (Zimmermann 1983, Ewers and Zimmermann 1984). Furthermore, there is evidence for increasing range in xylem tube size with increasing plant size in the fossil record—supporting the prediction that xylem tube diameter taper increases with increasing

branch diameter (Niklas 1984).

In 1983, Martin Zimmermann proposed the hydraulic segmentation hypothesis of plant architecture and postulated that strong selection for restricting embolisms to peripheral branches has led to observed patterns of vascular resistance (Zimmermann 1983). During times of extreme negative water potentials, xylem conduits are prone to cavitation. Zimmermann (1983) hypothesized that constriction of xylem tubes at branching junctions served to isolate these damaging embolisms and was responsible for observed patterns of hydraulic architecture. Xylem elements in expendable peripheral branches and petioles were therefore more subject to catastrophic failure, thus, protecting the main trunk and secondary branches from hydraulic failure.

There is evidence for such branch constrictions in several species of vascular plants (Zimmermann 1983, Lev-Yadun and Aloni 1990, Ellison et al. 1993, Aloni et al. 1997, others). If these constrictions are of approximately the same size, z , at all branch junctions, they would contribute Nz to the total tube resistance. The resulting consequence is almost identical to the result with tapering tubes, i.e., $\bar{a} = 1/6$, leading to an additional resistance that increases logarithmically with length. Nevertheless, recent studies have indicated that these constrictions appear to play a minor role in the total hydrodynamic resistance of the xylem network (Tyree and Alexander 1993, Yang and Tyree 1994). Although our work proposes a different mechanism for whole-plant hydrodynamic resistance than that proposed by Zimmermann, our model shows how several anatomical, physiological and architectural characteristics of vascular plants can be functionally linked by the biological demands of resource transport through fractal-like branching networks. Furthermore, selection for isolation of embolisms to peripheral branches may occur in the framework of our model as long as (1) the number of constrictions are proportional to the number of branchings; and (2) the overall hydrodynamic resistance, due to constrictions, does not scale with plant size.

Ecological consequences of allometric scaling

The last section of this paper shows how a common allometric model for the origin of anatomical and physiological scaling relationships is critical for understanding the origin of scaling relationships observed at the population, community and ecosystem levels. The scaling of metabolism at the level of the individual ramifies to influence numerous scaling relationships at multiple levels of organization in biology. Thus, several disparate patterns are hypothesized to have a common mechanistic basis. More importantly, a general model of metabolic scaling in biology provides a quantitative framework for scaling from cells to ecosystems.

Scaling of plant population density

Perhaps the most powerful attribute of a general allometric model is that it provides the basis on which to build quantitative ecological models. Because the WBE model offers a mechanistic hypothesis for many observed anatomical and physiological allometries at the level of the individual, it also

offers a basis from which to construct mechanistic connections between these organismal processes and their ecological consequences (Enquist et al. 1998, 1999, Enquist and Niklas 2001, Niklas and Enquist 2001). The biological and physical principles imposed on vascular networks powerfully determine the space over which plants utilize resources and the rates of whole-plant resource use. These principles, in turn, constrain biological organization in populations, ecological communities and ecosystems. One example is the relationship between population density and body size in ecological communities (Damuth 1981, Enquist et al. 1998).

When the dry mass of the average plant (\bar{M}) in mature populations is plotted against maximum plant density (N_{\max}) there is a distinct upper boundary that has traditionally been characterized by a power law with an exponent $\approx -3/2$ (Yoda et al. 1963, Harper 1967, Gorham 1979, White 1985). This pattern, known as the “ $-3/2$ thinning-law,” has been proposed to hold for plants in both single and mixed species stands and over a size range spanning 12 orders of magnitude from unicellular algae to the tallest trees (Gorham 1979, White 1985, see also Agusti et al. 1987). As plants grow, they fill a three-dimensional volume (a linear distance, l^3) and cover an exclusive area (a linear distance, l^2), suggesting a simple geometric explanation for the $-3/2$ density/mass relationship (see Yoda et al. 1963, Miyanishi et al. 1979, White 1981, Norberg 1988, see also Harper 1967). The constraint of packing geometric shapes into a finite area leads to a geometric limit between density and mass, hence $N_{\max} \propto M^{3/2}$.

Recently, however, the theoretical and empirical bases for the density mass boundary have been questioned (see Hutchings 1983, Weller 1987, 1989, 1990, 1991, Zeide 1987, 1991, Norberg 1988, Osawa and Suigita 1989, Lonsdale 1990, Dewar 1993, Petraitis 1995, see also White 1985, Ellison 1987). The $-3/2$ exponent, derived from purely geometrical considerations, is difficult to reconcile with known mechanisms of plant growth, resource uptake and competition. Furthermore, increasingly precise data suggest that the interspecific boundary is closer to $-4/3$ (Weller 1989, see also Lonsdale 1990), indicating that population density scales as $M^{-3/4}$, which is the same exponent reported in animals (Damuth 1981, 1987, McMahon and Bonner 1983, Brown 1995). Because metabolic rates of animals scale as $M^{3/4}$, similar relationships in plants suggest that both share a common scaling law, which reflects how resource requirements of individual organisms affect competition and spacing among individuals within ecological communities.

Enquist et al. (1998) developed a simple extension of the WBE model by following the ecological ramifications of allometry in ecological communities. They assumed that: (1) sessile plants compete for spatially limiting resources; (2) their rate of resource use scales as $M^{3/4}$, and (3) plants grow until they are limited by resources, R (where R has units of energy per unit area), so that the rate of resource use by plants approximates resource supply. The maximum number of individuals, N_{\max} , that can be supported per unit area is related to the average rate of resource use per individual, Q , and the total rate of resource use of all individuals, by $Q_{\text{Tot}} \approx R \approx N_{\max}Q \approx$

$N_{\max}C_B M^{-3/4}$, where C_B is an allometric constant reflecting tissue-specific metabolic demand, Q , in units of watts. At equilibrium, when rates of resource use approximates rates of resource supply, R is constant, Equation 7 yields:

$$N_{\max} = \frac{R}{C_B} \bar{M}^{-3/4} \quad (7)$$

This ecological extension of the WBE model, based on resource use by individual plants, therefore predicts a mass-density-scaling exponent of $-4/3$, rather than $-3/2$ as predicted by the geometric model (Yoda et al. 1963). Further, residual variation is predicted to be primarily due to physiological and environmental differences as indexed by variation in possible C_B and R . Data presented in Enquist et al. (1999) and Niklas and Enquist (2001) indicate little variation in C_B between forest trees and even across major plant taxa. Nevertheless, future studies are needed to assess the degree to which C_B varies across taxa. If correct, most residual variation in the scaling of plant density will be a result of variation in R . Thus, environments where rates of limiting resource supply are higher will be characterized by more dense populations for a given plant size.

Enquist et al. (1998) analyzed data from the literature relating \bar{M} and N_{\max} (Figure 5) and found an exponent, -1.341 , which has statistical confidence intervals that include $-4/3$ but not $-3/2$. Recent studies also suggest that the thinning exponent is close to $-4/3$ (see Weller 1987, Lonsdale 1990). Other sources in the literature express total aboveground plant biomass per unit area (M_{Tot}) as a function of maximum population

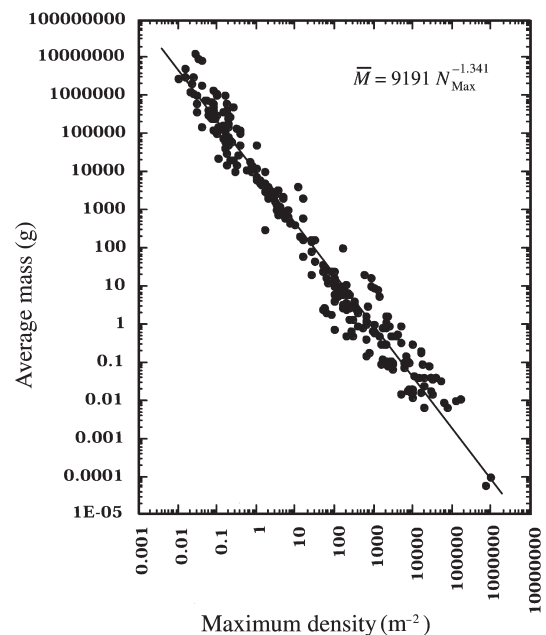


Figure 5. Relationship between maximum population density observed across plants and their maximum average mass. The fitted exponent indicates that population density, $N \propto M^{-3/4}$ as $M \propto N^{-4/3}$. Data from Enquist et al. (1998).

density (see Weller 1987, 1989, Lonsdale 1990, Petraitis 1995). Further, the general allometric model predicts the scaling of total plant mass, $M_{\text{Tot}} = N_{\text{max}} \bar{M} \propto N_{\text{max}} N_{\text{max}}^{-4/3} \propto N_{\text{max}}^{-1/3}$. The observed scaling relationship between M_{Tot} and N_{max} show an exponent indistinguishable from $N_{\text{max}}^{-1/3}$.

Invariance of energy use in ecosystems

Because the total rate of resource use per unit area, Q_{Tot} , is the product of population density and the mean rate of resource use per individual, Q , from above, we have $Q_{\text{Tot}} \approx N_{\text{max}} Q \approx (R/C_B) \bar{M}^{-3/4} C_B \bar{M}^{3/4} = R \bar{M}^0$, where \bar{M} is the average mass of an individual and C_B is an allometric constant. Therefore, a general allometric model gives the nonintuitive prediction that the total energy use, Q_{Tot} , or productivity of plants in ecosystems is invariant with respect to body size, but directly proportional to rates of limiting resource supply R . Enquist et al. (1998) tested this prediction by calculating Q_{Tot} from the data used to compile Figures 4 and 5. As shown in Enquist et al. (1998), the rate of resource use per surface area scales as $M^{0.0135}$. This empirical value does not differ statistically from the size invariance M^0 predicted by the model. The relationship holds across 12 orders of magnitude variation in plant size. Energetic equivalence indicates that, within a given environment, an approximate amount of limiting resource is divided among either many small individuals or a few large individuals. The variation around the regression line is predicted to reflect variation in resource supply and therefore in productivity (reflected by variation in R) among ecosystems ranging from grasslands and tundra to temperate and tropical forests (e.g., Rosenzweig 1968). The allometric estimation of maximum xylem surface flux in terrestrial ecosystems (mean of 10.45 l m⁻² day⁻¹) is well within the previously reported range for terrestrial ecosystem flux rates (data summarized in Jones 1992). Thus, more productive environments (high values of R) have more dense populations for their mass than less productive environments (low values of R).

The Enquist et al. (1998) model does not predict thinning trajectories as plants approach the limit where $Q \approx R$. It does, however, predict that the rate of resource use per unit area varies among plant communities with differences in resource supply but not with plant size. Thus, ecosystems composed of plants of contrasting sizes and life forms, such as certain forests, grasslands and agricultural fields, can have identical productivities (see Rosenzweig 1968, Harper 1977, Schulze et al. 1994, K. Gross, Michigan State University, personal communication, see also Dewar et al. 1998).

Implications of organismal allometry for the structuring of plant communities

One of the most prominent allometric patterns observed in both plant and animal communities is the inverse relationship between body mass and abundance (e.g., De Liocourt 1898, Morse et al. 1985). Because an inverse community relationship between size and abundance reflects how biomass and productivity are partitioned among individuals, it offers con-

siderable insight into the mechanisms structuring ecological communities across varying environments. However, relatively little is known about how size distributions vary across differing environments or how they vary among species.

Enquist and Niklas (2001) showed how community size distributions originate from the common allometric constraints across plant species. In particular, extensions of allometric theory predict that total standing community biomass will be invariant with respect to species composition and thus latitude. Furthermore, the intrinsic capacity to produce biomass on an annual basis will vary little across communities. As outlined above, allometric theory predicts that the total number of individuals per unit area, N , in any size class m , equals $C_m M^{-3/4}$, where C_m is the number of individuals per unit area normalized to a given size class m , and M is the body mass of size class m . The general allometric model for plant vascular systems also predict that M is proportional to the 8/3-power of stem diameter D of any size class (i.e., $M \propto D^{8/3}$), such that N will scale as $N \propto M^{-3/4} \propto D^{-2}$. If these scaling laws hold for entire communities, organismal traits can be used to link to larger scale properties of communities across different ecosystems. Enquist and Niklas (2001) show how the total standing community biomass, M_{Tot} , is given by the formula:

$$M_{\text{Tot}} = C_m \int_{\text{min}}^{\text{max}} M^{-3/4} dM = 4C_m (M_{\text{max}}^{1/4} - M_{\text{min}}^{1/4}), \quad (8)$$

where the subscripts min and max denote the minimum and maximum body masses within a given community, respectively. Since both the minimum and maximum body sizes are largely insensitive to species composition or latitude (see Enquist and Niklas 2001, and results below), any variation in M_{Tot} will be determined by variation in C_m . However, for closed canopy forest, both theory and observation suggest that C_m varies little, such that M_{Tot} is expected to vary little across communities. Specifically, for any given size class, the rate of resource use per size class, $R_m \approx Q_m \approx C_m B_m$, where the average metabolic rate of a class size $B_m = C_B A_m$. Here, A_m is leaf or root area, and C_B is the rate of resource use per unit area, which can vary across species. Because allometric theory and empirical data show that $A_m = C_A (M/\rho)^{3/4}$, where ρ is bulk tissue density and C_A is a constant of proportionality reflecting the species-specific amount of leaves or roots per individual per unit area, the following formula was derived:

$$C_m \approx \frac{R_m}{C_A C_B (M_m/\rho)^{3/4}}, \quad (9)$$

which shows quantitatively how numerous biological and abiotic factors can influence plant population density per size class. Nonetheless, biometric and physiological data indicate no differences in the mean values of C_B , C_A and ρ across tropical and temperate tree species or with variation in species richness (Whittaker and Woodwell 1968, Brown 1997, Enquist et al. 1998, 1999). This invariance indicates that total community biomass is likely to be insensitive to species diversity, even though C_m can vary in response to a variety of environ-

mental factors (e.g., temperature, precipitation) known to influence R_m . As the total rate of community resource use $R_{Tot} \approx \Sigma N_m B_m \propto G_{Tot}$, where G_{Tot} is the net primary production of a given community and N_m is the number of individuals in a given m th size class, it follows that $G_{Tot} \approx QN \approx C_B M^{3/4} C_m M^{-3/4} = C_B C_m M^0$, where C_B and C_m are allometric constants. Thus, within a community, there is energetic equivalence between size classes, with the small size classes utilizing the same amount of energy per unit time as a large size class. Furthermore, if C_m , and the maximum and minimum sizes within a given community, M_{max} and M_{min} , do not vary across communities, then it also follows that variation in rates of plant community total biomass production, G_{Tot} , are more influenced by ecological factors that reduce the capacity of metabolic production (e.g., abiotic and biotic features of ecosystems that influence the extent to which plants can maximally transpire water and assimilate CO_2) than by species-specific physiological capacities or variation in species diversity.

Enquist and Niklas (2001) tested these predictions based on macroecological data sets that span taxonomically and physiognomically diverse plant communities. They primarily draw on a large data set assembled by Gentry (1988, 1993), which spans near-monospecific stands to some of the most biodiverse forested communities on Earth. Specifically, the Gentry data set represents a 22-year accumulation from 227 sites across six continents of tropical and temperate closed canopy forest communities ranging between 60.4° N and 40.43° S and between 20 and 3,050 m in elevation. The complete data set contains a total of 83,121 individual plants. Based on the aforementioned protocol, the maximum number of species per 0.1 ha increases toward the equator. Yet, total tree standing biomass per 0.1 ha is invariant with respect to species number, latitude, or elevation even though tree density increases from northern to southern latitudes (see Enquist and Niklas 2001). Finally, as predicted by theory, the number of individuals per sample area scales as the -2 power of stem diameter or as the $-3/4$ power of plant mass, both within and across communities (Figures 6 and 7).

The -2 scaling rule also appears to hold with increasing geographic sampling areas, including continental and global samples (Enquist and Niklas 2001). Latitude and species number do not contribute greatly to the variance observed in local size distribution exponents, indicating that similar allometric constraints across species similarly influence community size distributions across major biomes (Figure 7). Furthermore, neither the size frequency distribution exponent nor the number of individuals is correlated with annual precipitation. The principal exceptions to these findings are the size distributions for communities at high latitudes ($\geq 40^\circ$ N or S). For these communities, the size distribution exponent tends to be less negative than D^{-2} , indicating lower densities of smaller individuals. Yet, even for these communities, total standing biomass is, on average, indistinguishable from that of communities at lower latitudes or elevations. Furthermore, as shown in Enquist and Niklas (2001), with increased geographic sampling area, even the high latitude North American forests ap-

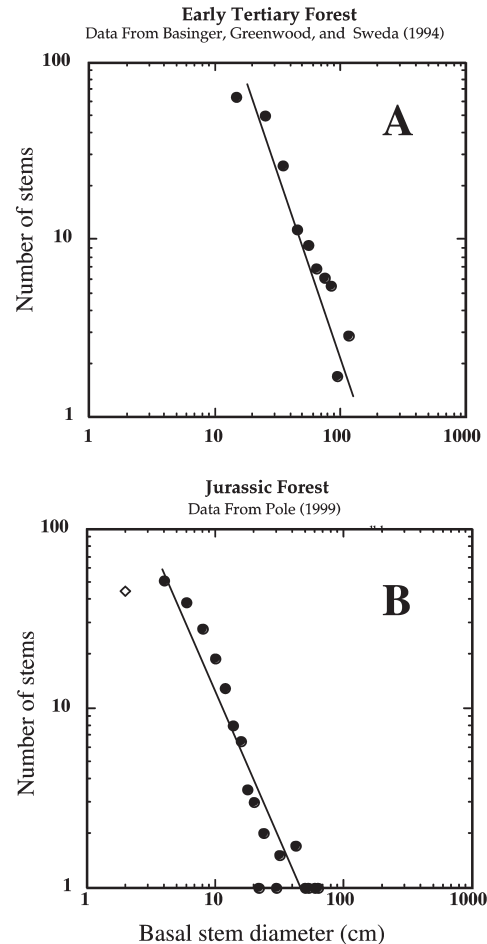


Figure 6. Diameter distributions for in situ fossil forests for an Early Tertiary (A) and a Jurassic (B) forest. For each fossil community the sizes and spatial positions of stumps have been preserved so as to preserve the size distribution. Note, the Jurassic forest has a smaller sample size and there appears to be a paucity of the smallest stems (\diamond omitted from statistical analysis). Fitted scaling exponents show that fossil forests scale with exponents indistinguishable from modern forests indicating that $N \propto D^{-2} \propto M^{-3/4}$ (A: $\alpha_{RMA} -2.195$, 95% CI -1.79 to -2.60 , $F = 129.75$, $n = 14$, $r^2 = 0.92$; B: $\alpha_{RMA} -1.737$, 95% CI -1.43 to -2.04 , $F = 131.47$, $n = 18$, $r^2 = 0.89$).

proximate the -2 power law.

Recent analyses by Enquist (2002) provides preliminary evidence suggesting that the -2 scaling rule for forests has apparently not changed over hundreds of millions of years of plant evolution. Assembling diameter distributions for in situ fossil forests for an Early Tertiary forest (dominated by species within the Taxodiaceae, Cupressaceae, Pinaceae, Ginkgoaceae, Fagaceae, Juglandaceae, Menispermaceae and Ulmaceae (see Basinger et al. 1994)), and a middle Jurassic forest (dominated by conifers of extinct taxa likely related to Arucariaceae and Podocarpaceae (see Pole 1999)), provides a unique window by which to assess allometric scaling across ancient communities containing extinct taxa (Figure 6). Within each fossil community the sizes and spatial positions of stumps have been preserved so as to preserve the size distribu-

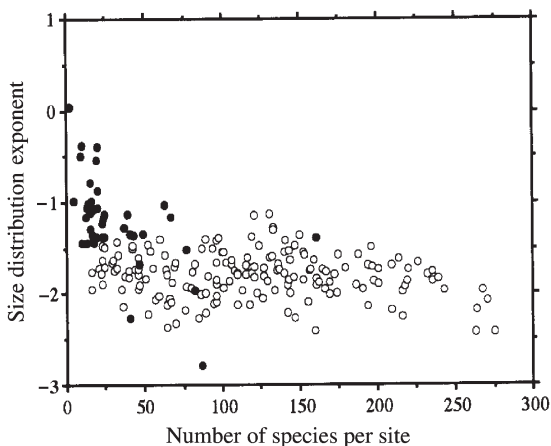


Figure 7. Exponents of size-frequency distribution of individual forest communities from across the globe plotted against species number in each community (filled circles denote data from communities in high latitudes or elevations). Except for the highest latitude forests, the size distribution is remarkably steady around the predicted value of -2 .

tion of a once living community. Fitted scaling exponents show that both fossil forests scale with exponents indistinguishable from modern forests and from predictions from the general allometric model, indicating that $N \propto D^{-2} \propto M^{-3/4}$ (Early Tertiary forest: $\alpha_{\text{RMA}} -2.195$, 95% CI -1.79 to -2.60 , $F = 129.75$, $n = 14$, $r^2 = 0.92$; Jurassic Forest: $\alpha_{\text{RMA}} -1.737$, 95% CI -1.43 to -2.04 , $F = 131.47$, $n = 18$, $r^2 = 0.89$). Because of the likely increase in error associated with measuring basal stem diameter in fossil forests, Model II RMA regression was used. Note, the Jurassic forest data set has a smaller sample size and appears to have a paucity of the smallest stems (open diamond symbol, Figure 6, which was omitted from statistical analysis). The apparent invariance of the size distribution exponent across fossil forests and extant forests suggests that the underlying allometric constraints and the fashion by which plants compete for limiting resources within ecological communities have not changed appreciably over millions of years of plant evolution.

Conclusions

A general theory of allometry appears to offer a theoretical framework from which to draw mechanistic connections between several major areas of botanical research. Quarter-power allometric scaling laws, well known in animals, also apply to many plant characteristics. There are many allometric parallels, including: metabolic rate $M^{3/4}$, radius of trunk or aorta $M^{3/8}$, size of, and fluid velocity, in terminal vessels M^0 , population density and community abundance $M^{-3/4}$, and energy use per unit area M^0 . Furthermore, because both animals and plants are predicted to have many identical allometric exponents, a common influence of body size in nearly all aspects of biological structure, function and diversity is suggested. This framework, however, also shows how some fundamental differences between species can be viewed as differences in

patterns of allocation and the timing of life-history events.

Perhaps the most intriguing attribute of a developing theory for biological allometry is the assertion that allometric relationships observed at multiple levels of biological organization have a common mechanistic basis. Furthermore, despite wide variation in taxonomic diversity and differences between local abiotic conditions, plants and plant communities can be shown to exhibit approximately invariant scaling exponents. For example, despite wide variation in species diversity, abundance and biomass, tree-dominated communities are characterized by nearly identical size-frequency distributions reflecting nearly equivalent standing biomass. Thus, the number of individuals within a given community sample scales as D^{-2} and thus $M^{-3/4}$. These observations are consistent with allometric theory but contrast in many important ways with speculations, geometric models of plant species packing and recent niche-based theoretical predictions. A general allometric theory suggests that variation in plant species composition is instead associated with concomitant changes in the degree of partitioning of a limited amount of resources rather than increases (or decreases) in community biomass and, potentially, depending on the local environment, productivity (Tilman et al. 1997). Such partitioning is most likely reflected in life-history tradeoffs in the allocation of metabolic production, such as in tissue density, ρ , or between leaf, stem, root and reproductive biomass (Enquist et al. 1999, Enquist and Niklas 2002, Niklas and Enquist 2002).

Extensions of a general allometric framework reveal how several prominent organismal-, community- and ecosystem-level properties emerge from relatively few allometric and biomechanical rules. The constraints of resource transport through fractal-like vascular networks ultimately dictate how individuals fill space, use resources, and produce and allocate biomass. Such constraints are reflected in allometric scaling relationships, which are evident at multiple levels in biology. A central challenge to environmental scientists is to predict how ecosystems will respond to future variation in biotic and abiotic attributes. This mandate requires the development of a rigorous and predictive science, which by definition requires a central focus on scaling. The work presented here points to the importance of physiological rates and times in influencing many patterns in biology. Allometric rules dictate how metabolic production and biomass are partitioned among different plant parts at the level of the individual. Furthermore, these rules provide a quantitative basis for drawing mechanistic connections between numerous features of organismal biology, ecology, ecosystem studies and evolutionary biology. Thus, a common body of allometric theory promises to provide a general framework for predicting how variation in many attributes of plant form, function and diversity are fundamentally interrelated.

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Appendix 1

Table A1. Summary of symbols and mathematical notation used.

Symbol	Definition	Additional definitions
A_L	Total leaf area	
A_m	Mean leaf area of a given m th size class	
A_k^{CT}	Cross-sectional area of conducting tissue for a given k th branch	
A_k^{Tot}	Total cross-sectional area of a given k th branch	
a	Scaling factor describing potential tapering of branch radii	See definition of β , $\frac{r_k}{r_N} = n^{(N-k)a/2}$
\bar{a}	Scaling factor describing potential tapering of xylem vessel or tracheid radius across branching levels	See definition of β , $\frac{a_k}{a_N} = \left(\frac{r_k}{r_N}\right)^{\bar{a}/a}$
a_k	Average cross-sectional area of a given xylem tube (vessel or tracheid) in a branch in the k th branching level	
a_N	Average cross-sectional area of a xylem tube (vessel or tracheid) in the petiole	
α	Exponent relating stem diameter and stem height	$r_k \propto l_k^\alpha$
α_{LS}	Slope of Model I regression	
α_{RMA}	Slope of Model II regression	
B	Rate of total plant	
B_m	Average metabolic rate of a given size class	
b	Allometric exponent	
β	Ratio of branch radii	$\beta_k \equiv r_{k+1}/r_k \equiv n^{-a/2}$

Continued on overleaf.

Table A1 cont'd. Summary of symbols and mathematical notation used.

Symbol	Definition	Additional definitions
$\bar{\beta}$	Ratio of xylem tube radii	$\bar{\beta} \equiv a_{k+1}/a_k \equiv n^{-\bar{a}/2}$
C_A	Proportionality constant	$A_m = C_A \left(\frac{M}{\rho}\right)^{3/4}$
C_B	Proportionality constant	$B = C_B \left(\frac{M}{\rho}\right)^{3/4}$
C_D	Proportionality constant	$D = C_D \left(\frac{M}{\rho}\right)^{3/8}$
C_G	Proportionality constant	$\frac{dM}{dt} = C_G B$
C_m	Proportionality constant, reflecting the number of individuals within a given m th size class. See Equation 9	
D_0	Basal stem diameter	$D_0 = 2(r_0)$
E	Young's modulus of elasticity	
G	Whole-plant biomass production per year	
G_{Tot}	Total biomass production per unit area per year	
γ	Ratio of branch lengths	$l_{k+1}/l_k; \gamma = n^{-1/3}$
H	Pigment content per algal cell; foliage biomass, M_L per metaphyte	
K_k	Conductivity of the k th branch	$K_k \equiv l_k/Z_k = K_N(r_k/r_N)^{2(1+2\bar{a})/a}$
K_N	Conductivity of petiole	$K_N = \pi n_N a_N^4/8\eta$
k	Branching level within a hierarchical branching plant network ranging from the basal branch, where $k = 0$, to the leaf, where $k = N$	
η	Fluid viscosity	
L	Total plant length	
L_k^{con}	Leaf conductivity (the conductivity per unit leaf area)	$L_k^{\text{con}} \equiv K_k/n_k^L a_L$
l_k	Length of a given k th branch	
l_N	Length of leaf petiole	
l_T	Total path length from basal branch to leaf	$l_T = \sum_{k=0}^N l_k = l_0(1 - n^{-1/3})$
λ	Fraction of annual metabolic production allocated to reproduction	
M	Body mass	
M_{max}	Maximum body mass	
M_{min}	Minimum body mass	
M_{Tot}	Total standing biomass per unit area	
m	Size class	
N	Total number of branching levels or generations, within a given plant, from trunk (or basal stem) to petiole	
N_{max}	Maximum number of individuals	
N_{Tot}	Total number of plants per unit area	
n	Branching ratio; number of daughter branches derived from a parent branch	$n = n_{k+1}/n_k$
n_k	Total number of branches within a given k th branching level	$n_k = n_N n^{N-k}$
n_k^L	The total number of branches or leaves distal to the k th branch	$n_k^L = n_k/n_N$
n_N	Mean number of xylem tubes (vessels and or tracheids) per petiole	
Q	Rate of resource use per individual per unit time	
Q_0	Rate of fluid flow through the basal stem of a plant	
R	Rate of supply of limiting resource per unit area, in units of watts	
r_k	Radius of a given k th branch	
r_N	Radius of leaf petiole	
ρ	Tissue density	$\rho = M/V$
t	Time	
V	Volume	
Z_i	Total resistance of plant xylem	