

Cope's Rule and the evolution of long-distance transport in vascular plants: allometric scaling, biomass partitioning and optimization

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ABSTRACT

Recent advances in allometric theory have proposed a novel quantitative framework by which to view the evolution of plant form and function. This general theory has placed strong emphasis on the importance of long-distance transport in shaping the evolution of many attributes of plant form and function. Specifically, it is hypothesized that with the evolutionary increase in plant size natural selection has also resulted in vascular networks that minimize scaling of total hydrodynamic resistance associated with increasing transport distances. Herein the central features of this theory are reviewed and a broad sampling of supporting but yet preliminary empirical data are analysed. In particular, subtle attributes of the scaling of tracheid and vessel anatomy are hypothesized to be crucial for the evolution of increased plant size. Furthermore, the importance of minimizing hydrodynamic resistance associated with increased transport distances is also hypothesized to be reflected in an isometric scaling relationship between stem mass, M_S and root mass, M_R (i.e. $M_S \propto M_R$). Preliminary data from multiple extant and fossil plant taxa provide tantalizing evidence supporting the predicted relationships. Together, these results suggest that selection for the minimization of the scaling of hydrodynamic resistance within plant vascular networks has in turn allowed for the enormous diversification in vascular plant size.

Key-words: Plant size; allometry; biological scaling; macroevolution; hydraulic architecture; xylem evolution.

INTRODUCTION

In 1887 E. D. Cope proposed that over evolutionary time the average size within a clade tends to be marked by a progressive increase in body size (Cope 1887). Cope's 'rule' should now be seen as not a progressive increase in 'average' size within a given clade but an increase in the size range over time (see Jablonski 1996; Alroy 1998; Enquist

et al. 2001). While Cope's observation was originally restricted to animals, the 'rule' also seems to hold across terrestrial plants. For example, each of the major vascular plant clades and grades (e.g. 'Pteridophytes', Gymnosperms and Angiosperms) has been marked by a consistent increase in size range over time (e.g. Niklas 1994; Enquist *et al.* 2001). The first land plants were diminutive, non-vascular organisms occupying marginal habitats at the interface of the terrestrial and aquatic landscapes (see Kenrick & Crane 1997). Since such humble beginnings land plants rapidly diversified in morphological complexity, growth and stature (Stewart & Rothwell 1993; Kenrick & Crane 1997; Niklas 1997). So impressive has been the diversification of size that vascular plants now range well over 12 orders of magnitude in mass (Enquist *et al.* 2001) – a size range larger than that attained by any major animal clade. It is also of note that during ontogenetic development, a single *Sequoia* seedling will span close to the entire 12 orders of magnitude during its lifetime. Yet despite such a large size range vascular plants are still able to procure and transport resources from the environment, maintain homeostasis, grow and reproduce with the same basic anatomical and physiological design.

THE IMPORTANCE OF PLANT SIZE

Plant size is probably the most important axis by which to capture the wide range of plant morphological variation, structural complexity and life history diversity (Enquist *et al.* 2001b). It is important to note that changes in organismal size, however, bring about important structural and resource supply demands. Such biophysical constraints have important implications for potential fitness. Unless these size-determined constraints were reconciled then the evolution of the impressive size ranges attained today would not have been possible.

Several authors have concluded that an increase in the range of plant size over evolutionary time reflects adaptive diversification (e.g. Knoll & Niklas 1985; Vermeij 1987; Enquist *et al.* 2001). These claims have been generally supported by ecological studies showing that under many conditions increases in size reflects selection for one or more

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of the following: (1) the ability to outcompete neighbouring individuals via shading; (2) increased access to limiting resources; (3) increased reproductive output and survivorship; (4) increased probability of dispersing gametes and propagules to distant mates and unoccupied habitats; and (5) the ability to endure increased environmental variability (see Harper 1977). Further, differing abiotic conditions will influence the range of sizes favoured by natural selection (see Niklas & Kerchner 1984; Niklas 1994b). Thus, there are manifold biotic and abiotic routes by which selection may increase the range of plant stature over evolutionary time. However, any changes in organismal form, shape, or size, bring about critical physical limitations, that unless overcome, would preclude any potential increases in size range (e.g. Calder 1984; Raven & Handley 1987; Niklas 1992, 1994).

There are two prominent physical constraints that must have been overcome in order for plants to achieve the current range of sizes observed today. The first constraint is the biomechanical limits associated with supporting a given mass against mechanical buckling and/or wind across differing environments (see Niklas 1992, 2000). For example, the observed allometric scaling of plant dimensions such as height, mass, stem diameter and spread, in addition to changes in the mechanical properties of support tissues (across diverse plant clades), has indicated to several authors that plant evolution has been guided by general biomechanical principles (Barghoorn 1964; King & Louks 1978; Givnish 1986a; Niklas 1992; Niklas 2000). This article argues that the hydrodynamic constraint of long-distance transport has also been a prominent general factor influencing the evolution of plant size. Specifically, I focus on the evolution of long-distance xylem transport in vascular plants.

Herein a new and general hypothesis for the evolution of long-distance transport through xylem networks and allometric allocation metabolic production is utilized (Enquist, Brown & West 1998; West, Brown & Enquist 1999a; Enquist & Niklas 2002; Niklas & Enquist 2002a, b). This work focuses on how attributes of organisms (e.g. anatomical, physiological, and life-history) change with their size (allometry). The central hypothesis is that evolution by natural selection has acted to minimize the scaling of the total hydrodynamic resistance through vascular networks (West *et al.* 1997) but yet maximize the surface areas (i.e. leaves) where resources are exchanged and supplied by the vascular network. The result has been the evolution of vascular networks and the partitioning of plant biomass between stems, roots and leaves, which are governed by characteristic allometric scaling exponents. For the purposes of this article, an important insight is that adaptive innovations in the scaling of xylem dimensions and allocation between stem and root biomass have allowed for the evolution of a vascular network capable of transporting fluid from the soil to increasingly greater distances from the soil (i.e. increased plant size) with minimal hydrodynamic resistance. While additional studies are needed, several examples from numerous extant species in addition to pre-

liminary data from extinct fossil lineages provide robust support for the model.

THE PROBLEM OF INCREASING HYDRODYNAMIC COSTS OF RESOURCE TRANSPORT AND SUPPLY

The problem of how plants transport resources to impressive heights has long been of interest in plant physiology and has been the subject of much research (see Zimmermann 1983; Meinzer, Clearwater & Goldstein 2001). There is broad consensus that the driving force for fluid transport is generated by transpirational water loss and the corresponding tension through continuous water columns linking leaf evaporative surfaces to the roots (e.g. Scholander *et al.* 1965; Zimmermann 1983; Meinzer *et al.* 2001). Thus, according to the cohesion–tension theory (Dixon & Joly 1894) terrestrial plants utilize the water potential gradient between the soil and the atmosphere to drive the transport of nutrients and water through the xylem. However, as is shown below, with increasing transport distances (transport path lengths) there is an increase in hydrodynamic resistance (see Ryan & Yoder 1997). Indeed, several studies have called attention to the importance of variation in path length and the associated problem of increasing hydrodynamic cost of transport of fluid through vascular networks (Maggs 1964; Ryan & Yoder 1997; West, Brown & Enquist 1999a; Enquist, West & Brown 2000; Becker, Gribben & Lim 2000; Becker, Meinzer & Wullschlegel 2000).

Long-distance transport of fluid through xylem conduits presents several problems for plants (Maggs 1964). While much focus has been placed on the mechanism by which fluid is transported vertically (i.e. the cohesion–tension theory) there has not been an appreciation of the hydrodynamic costs associated with the transport of fluids with increasing distance (Niklas 1984; Raven & Handley 1987; see also Bower 1908; Raven 1977, 1984; Roth & Mosbrugger 1996; Roth, Mosbrugger & Wunderlin 1998). In particular, there are two central problems stemming from the hydrodynamic cost of resistance with increasing plant size. First, with increasing height (i.e. plant size) comes increasing transport distance (and the associated hydrodynamic resistance) between soil and leaves (Ryan & Yoder 1997; see also Maggs 1964; Friend 1993). Second, with increasing plant size there is a problem of allocation between the main plant organs (stems, leaves and roots) that also have important implications for whole plant transport and hydrodynamic resistance (see also Bower 1908, 1930; Niklas 1984; Givnish 1986a and references within). For example, an increase in leaf mass demands an increase in roots and stems (xylem conduits) in order to supply an increase in transpiration and nutrient demand.

Hydrodynamic cost of transport – path length

The volume of fluid flowing per unit time per unit area, J_V , through a given xylem conduit (vessel, tracheid), will be

influenced by its length and radius. Here it is assumed that fluid flow through a given xylem conduit can be modelled as fluid flow through a 'pipe' or 'tube'. Flow rates can be straightforwardly modelled by utilizing the Hagen–Poiseuille equation,

$$J_v = \frac{\pi a_k^4 \partial P}{8\eta \partial l_k} \quad (1)$$

where $\partial P/\partial l_k$ is the pressure gradient (the change in pressure along a vessel or tracheid of length l_k), η is the fluid viscosity which is also dependent on temperature, solute concentration, etc., a_k is the cross-sectional area of a given conduit or 'tube' at a given k th branching level and l_k is the length of the tube in a given k th branching level (see Zimmermann 1983). Assuming a constant pressure gradient, the total resistance of fluid transport through a given xylem 'tube' is given by the following equation,

$$Z_i = \frac{8\eta l_k}{\pi a_k^4} \quad (2)$$

Note, for a given 'tube', the total hydrodynamic resistance is directly proportional to its length, l_k , independent of any biomechanical constraint. This is an important prediction of Eqn 2 as the total resistance or cost of transport increases in direct proportion to the transport distance. For example, because path lengths from the soil to the leaves and branch meristems differ, resources would tend to be delivered at higher rates over the shorter paths (because those paths have reduced resistance). Such inequality of path lengths would then limit resource supply to the terminal shoots and favour branches with shorter path lengths. However, Eqn 2 also shows that if the radius of a given xylem 'tube' is allowed to vary then any slight change in the tube diameter will lead to an *enormous* change in total resistance because of the fourth-power dependency on a_k .

Hydrodynamic cost of transport – problems of organ allocation

In general, the transport of fluid throughout the entire plant involves three plant organs – roots, shoots and leaves. The total mass, M_{Tot} , of a plant can be modelled to represent three major organs so that

$$M_{\text{Tot}} = M_R + M_S + M_L \quad (3)$$

where M_R , M_S and M_L are the mass of the root, stem and leaf, respectively (Enquist & Niklas 2002; Niklas and Enquist 2002). Similarly, one can model the transport 'cost' per leaf in terms of total hydrodynamic resistance, Z_{Tot} , of fluid moving throughout the entire plant xylem network to the leaves. Here Z_{Tot} is the total xylem path resistance and is simply the summation of the root and shoot xylem resistance or Z_R and Z_S , respectively,

$$Z_{\text{Tot}} = Z_R + Z_S \quad (4)$$

If xylem stem and root resistance per unit photosynthetic area is a function of organ mass then both Eqns 2 and 3

show that any change in the allocation to either organ with increases in plant size should have concomitant changes in the hydrodynamic cost in supplying resources to leaves. For example, an increase in plant size might lead to an increase in leaf area. If leaves are to be supplied with an adequate supply of resources (water, nutrients, etc.) then increases in leaf mass necessitates increases in root mass. Thus, an increase in size brings about problems of allocation that must be reconciled with the cost of resistance per unit leaf. According to Eqns 2 and 3, if there is strong selection to minimize the total cost of resource transport, Z_{Tot} , then any changes in a given organ resistance must be compensated by alteration in the other component resistances (see also Givnish 1986a). For example, biomechanical constraints limit how the relative proportions of stem and leaf biomass are partitioned with changes in plant size (Niklas 2000). These proportional changes are reflected in allometric scaling relationships of the form $Y = Y_0 M^b$, where Y is the trait of interest (leaf mass), Y_0 is a constant of proportionality, M is plant mass and b is the exponent. Further, as is argued below, if with changes in plant size, the total network resistance is minimized, so that the value of Z_{Tot} is approximately constant, then any changes in the composition of one organ must be matched by compositional changes in another organ.

A GENERAL ALLOMETRIC MODEL FOR THE EVOLUTION OF 'OPTIMAL' PLANT FORM AND FUNCTION

A new theory for the structure and function of plant form hypothesizes that many of the fundamental principles that have guided the integration of physiological and anatomical attributes are reflected in how plant traits scale with plant size (Enquist *et al.* 1998; West, Brown & Enquist 1999a, b; Enquist & Niklas 2002; and Niklas and Enquist *in press*). This general allometric model assumes that the minimization of hydrodynamic resistance reflects selection for increased plant size and a concomitant increase in metabolic potential available for allocation to growth and reproduction. This argument is reminiscent of Murray's 'principle of minimum work' (Murray 1926) and Taylor and Weible's concept of economy of design or 'symmorphosis' (Taylor & Weibel 1981).

A central premise of the West, Brown and Enquist model is that selection to minimize the cost of transporting resources through the body has resulted in an optimal design, which allows for increased survival and/or reproductive output. Such a design is reflected in allometric scaling relationships with characteristic exponents. Thus, how attributes of organisms change with their size (allometry) hold clues to the fundamental principles dictating the evolution of form, function and diversity. Specifically, as argued below, selection to minimize hydrodynamic resistance has resulted in the evolution of vascular plant form characterized by two lines of allometric evidence: (1) the allometric tapering of xylem conduits so that xylem conduits scale with branch radius with an exponent greater than or equal

to 1/6; and (2) an isometric scaling relationships between roots and stems (i.e. $M_R \propto M_S$).

A general model for the origin of allometric scaling relationships

Recently, West *et al.* (1999a, b) (WBE) highlighted the general importance of transport through vascular networks in setting the foundation for many allometric scaling relationships in biology. The WBE model assumes that evolution by natural selection has acted in a uniform fashion to (1) maximize the effective surface areas over which resources are exchanged with the environment (i.e. photosynthetic surface area) but that (2) the internal transport distances or the total energy required to transport resources through the body is minimized (West, Brown & Enquist 1997, West *et al.* 1999a, b). The WBE model further assumes that (3) the fundamental 'units' involved in resource transport (leaves, terminal xylem size, capillaries, cytochrome oxidase, etc. see West *et al.* 1999a) are invariant with size. Here the term 'invariant' does not mean that leaf size cannot vary across individuals or species but that there is no dependence of leaf size with changes in organismal size *per se*. It is also important to note that any deviation from these principle assumptions will lead to calculable deviation in allometric relationships. Thus the WBE model provides a baseline for understanding the origin of allometric relationships and the causes of residual variation from predicted trends.

Following on from the above principles of plant form and function come two critical predictions. First, the total photosynthetic surface area (which is approximated by total leaf area or leaf mass) is predicted to scale to the 3/4 power of total plant mass ($M_L \propto M_T^{3/4}$). Second, the total cost of transport (hydrodynamic resistance per unit leaf area) of fluid moving through plant stems is independent of total transport distance or plant size. Together, these two central predictions ramify to cause numerous other related anatomical and physiological allometric relationships (see West *et al.* 1999b and Enquist *et al.* 2000; Enquist & Niklas 2002; Niklas and Enquist, in press, for a complete listing of predicted relationships). Unique allometric exponents and intercepts characterize these allometric relationships.

Optimal allometric long-distance transport

West, Brown & Enquist (1999a) model the total resistance of the above-ground hierarchical branching vascular network (i.e. the stem or Z_S) as the summation of all the resistances of all the xylem conduits in each branching level (from the trunk, branching level 0, to the petiole, branching level N). The WBE model for plants assumes that the xylem network is composed on identical xylem conduits or 'tubes' of equal length running continuously in parallel from trunk to petiole (files of 'vessels' connected in series). Further, the model allows for possible changes in xylem 'tube' dimensions between branching levels. While

the model is a deliberate oversimplification of a more complex morphology it provides a starting point for more complex modeling (Enquist *et al.* 2000). Additional detail of the WBE model is given in West, Brown & Enquist 1999a; see also Enquist *et al.* 2000). Given these assumptions, the resistance (Z) of a single conduit (i) or 'tube', Z_i , within any branch segment, k , is governed by the Hagen-Poiseuille equation (Eqns 1 and 2; see also Zimmerman 1983; Nobel 1983). The total resistance of each branch 'tube' (a given xylem vessel or tracheid) can then be summed across each branch segment on a given plant with N branching generations to give a resistance of the entire xylem pathway. Therefore the total resistance running from the trunk to the petiole for a given 'tube' can be shown to be described by a general equation

$$Z_i = \sum_{k=0}^N Z_k^i = \left[\frac{1 - [(n^{1/3} - 1)l_T/l_N]^{(1-6\bar{a})}}{1 - n^{(1/3-2\bar{a})}} \right] [Z_N] \quad (5)$$

where Z_N is the resistance of the petiole, l_N is the length of a petiole, l_T is the total 'tube' or path length (from the base of the trunk to the petiole) and n is the branching ratio (number of daughter branches stemming from each parent branch), which is assumed to be approximately constant throughout the plant. As outlined by Enquist *et al.* (2000) additional sources of fluid resistance (pit membranes, vessel perforation plates and branch junctions, etc.) can be incorporated into the model. However, empirical patterns of resistance associated with these other important anatomical features do not appear to influence the general scaling predictions (Enquist, West & Brown 2000).

Equation 4 shows that when l_T is much larger than l_N , and if there are at least several branching generations, the total resistance of each xylem pathway, Z_i , depends critically on the exponent that dictates xylem vessel tapering with branching level which is reflected in the value of \bar{a} (for additional mathematical details see West *et al.* 1999b; Enquist *et al.* 2000). Here \bar{a} reflects how the xylem conduit area (a_k) tapers from parent to daughter branch (or from the base of the stem to the leaf petiole) and is defined as

$$a_{k+1}/a_k \equiv n^{\bar{a}/2} \quad (6)$$

The model assumes that \bar{a} is independent of branching level (k) and the dimensions of the petiole are independent of plant size (number and size of xylem elements supplying each leaf does not significantly vary with plant size).

Given these assumptions Eqn 4 shows that if there is no tapering of xylem dimension ($\bar{a} = 0$) the total hydrodynamic resistance increases with plant height. However, Eqn 4 has the remarkable property that if the value of \bar{a} is approximately equal to or greater than 1/6 (and that the network has more than a few branching generations) then the total tube resistance is constant, independent of both the number of branchings, N and the total path length, l_T , of the branch (see also Becker *et al.* 2000). Therefore, with a sufficient degree of tapering of xylem dimensions the total resistance of the tube, Z_i , will be a constant value with path length or size (West, Brown & Enquist 1999a). If then the

size of a leaf (i.e. l_N) remains approximately constant with changes in plant size and the number of xylem tracheids/vessels supplying a leaf is also a constant then the hydrodynamic resistance per unit leaf area will also be independent of plant size. Such tapering of xylem radii is exactly what is needed to solve the problem of ensuring that all leaves have comparable rates of resource supply independent of total branch length. If the xylem dimensions across vascular plants follow such a simple scaling law then the implications are profound. In particular, a scaling-law for the tapering of xylem dimensions across vascular plants (tracheids in gymnosperms and vessels in angiosperms) which follow the predictions of the WBE model would suggest that hydrodynamic resistance has been a general constraint on the evolution of plant vascular diversity.

EMPIRICAL SUPPORT FOR OPTIMAL XYLEM TAPERING

There are several examples in the literature indicating that xylem vessels taper from the base of the trunk to the leaf (see Zimmerman 1983; Aloni 1987; Gartner 1995 and references within). Nevertheless, the functional scaling relationship quantifying the degree of tapering within a given branch, within an individual over ontogeny, between differing taxa, or over evolutionary time is not known. In order to assess whether the degree of tapering of xylem dimensions accords with the critical predictions of the WBE model I assembled from the literature a diverse but yet preliminary data-set across both extant and fossil plants. The data-set covers inter- and intraspecific variation in xylem dimensions (area, radius) as a function of branch diameter (D_k) in both angiosperms and gymnosperms. Investigation of xylem dimensions within gymnosperms and angiosperms thus provide two independent sources to assess independent evolution of allometric scaling of xylem dimensions (i.e. tracheids versus vessels). As is shown below, empirical data appear to match the predicted scaling relationships.

Static intraspecific scaling

Ewers & Zimmermann (1984) report the dimensions of xylem tracheids across branches which differ in size within an individual gymnosperm (*Tsuga canadensis*). Data range from larger basal stems to more peripheral and smaller terminal branches. Least Squares Regression analysis (Model I regression) on \log_{10} transformed data shows that tracheid diameter scales with branch size [slope = 0.312, 95% confidence interval (CI) = 0.341–0.285, $r^2 = 0.981$, $n = 23$, $F = 525.69$, $P < 0.0001$; Fig. 1]. The observed exponent, 0.308, is within the bounds predicted by the WBE model suggesting that the total hydrodynamic resistance would be independent of path length. In addition, utilizing data from Zimmermann (1978) for two angiosperms (*Betula papyrifera* and *Populus grandidentata*) Becker & Gribben (2001) show that the observed tapering of xylem

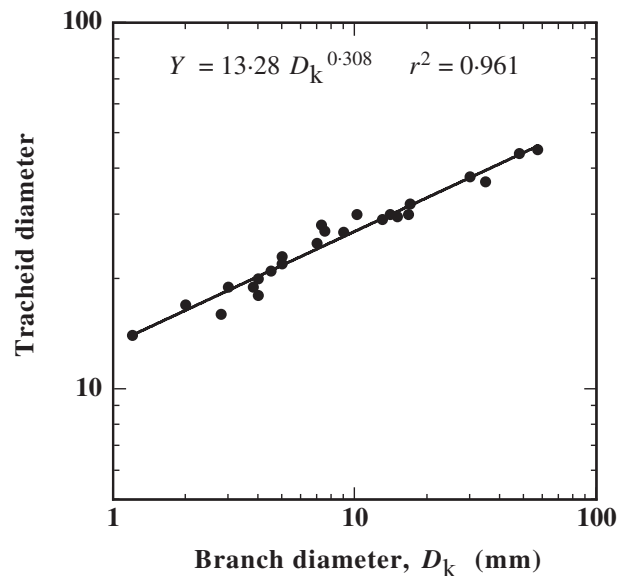


Figure 1. The intraspecific scaling of tracheid diameter (From Ewers & Zimmermann 1984) with increasing branch size within a gymnosperm (*Tsuga canadensis*). Data are taken from within a given individual so that variation in stem diameter reflects variation from the base of the tree to the terminal branches. As shown by Ewers and Zimmermann, tracheid dimensions increase with branch size. The observed relationship is best fitted by a power function. The observed exponent is within the range predicted for hydrodynamic resistance to be approximately constant along the branching vascular network.

vessel elements with plant height is consistent with the WBE model.

Ontogenetic scaling of xylem dimensions within a given branch

Within plants, characterized by secondary growth, increases in stem size is achieved through the addition of sequential secondary growth as marked by annual rings. The WBE model predicts that during ontogeny as a given stem increases in size (i.e. stem radius, r_k , or diameter, D_k) the average radius or area of the xylem elements within each growth ring of a given branch should increase. Assembled intraspecific data (from Noshiro & Suzuki 2001) for ontogenetic changes in the average cross-sectional area of vessels, within four separate species of *Rhododendron*, provide support for the WBE model (Fig. 2, Table 1). Because the vessel density per unit area is an approximate constant (see Fig. 18, Noshiro & Suzuki 2001) the cross-sectional area of vessels reflects the cross-sectional area of a given vessel. Although the range in branch size across each species is somewhat small (approximately one order of magnitude in stem diameter which limits statistical power), across species, there is a significant increase in vessel area with increases in stem diameter. Further, for each species, statistical analysis indicates that the 95% confidence intervals for the scaling exponent include the predicted value of 1/6 or greater (Table 1). However, there does appear to be signif-

Table 1. Least Squares (Model I) regression statistics for the intraspecific relationship between stem radius (cm) and vessel area (mm^2) for six species of *Rhododendron*. Except for *R. hodgsonii* and *R. cinnabarinum* each regression statistic is significant of the 0.05 level. *Min* and *max* refer to the minimum and maximum stem diameter size respectively.

Species	<i>b</i>	95% CI	Y_0	95% CI	r^2	Min	Max	<i>n</i>
<i>R. arboreum</i> Sm.	0.190	0.124–0.255	2.54	2.48–2.54	0.658	0.87	19.6	21
<i>R. hodgsonii</i> Hook. f.	0.092	–0.014–0.198	2.63	2.56–2.68	0.157	0.5	7.2	20
<i>R. campanulatum</i> D. Don	0.137	0.020–0.254	2.57	2.52–2.63	0.264	0.5	4.9	19
<i>R. cinnabarinum</i> Hook. f.	0.085	–0.025–0.197	2.72	2.69–2.77	0.134	0.5	6.7	19
<i>R. campylocarpum</i> Hook. f.	0.253	0.146–0.360	2.53	2.46–2.60	0.577	0.5	13.9	20
<i>R. wightii</i> Hook. f.	0.195	0.227–0.164	2.57	2.55–2.58	0.916	0.5	6.2	18

Data were provided by Noshiro and Suzuki (see Noshiro & Suzuki 2001) and were \log_{10} transformed. For each species, the observed tapering of vessel area as reflected in the allometric exponent *b* is within the range predicted by the WBE model indicating that total hydrodynamic resistance is independent of plant size. The regression intercept, Y_0 , is also listed. Note, although the fitted slope or exponent for each species overlap some species differ significantly in their allometric intercepts (compare *R. arboreum* and *R. wightii*). CI, confidence interval.

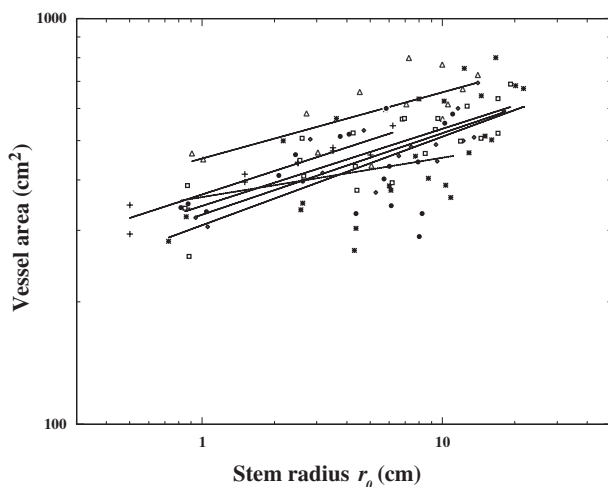


Figure 2. The ontogenetic scaling of intraspecific vessel area with increasing branch size across six species of angiosperms (*Rhododendron* sp.). Each intraspecific plot represents the change in vessel area as a function of ontogenetic changes in stem diameter (Data are from Noshiro & Suzuki (2001); □, *R. arboreum*; ◆, *R. hodgsonii*; ●, *R. campylocarpum*; △, *R. cinnabarinum*; ★, *R. campanulatum*; ×, *R. wightii*). The fitted scaling relationships across and within each species are within the range predicted for hydrodynamic resistance to be approximately constant along the vascular network.

icant variation in the allometric intercept, Y_0 between species (Table 1). Such variation in the intercept may indicate important differences in xylem anatomy reflecting differing ecological environments (e.g. Carlquist 1975; Baas 1986). Nevertheless, even though species may differ in their allometric intercepts their exponents do not differ.

Indirect support via total hydrodynamic resistance

Indirect support for the minimization of xylem path resistance is seen in experiments measuring the total resistance of fluid as it passes from branch to branch throughout a

given tree. Figure 3 shows the total hydrodynamic resistance of the stem xylem network for two angiosperm individuals of *Acer saccharum* (data from Yang & Tyree (1993) – as plotted in West, Brown & Enquist (1999a)). The plots show the effect of sequentially removing branches of increasing size (radius r_k) on the proportion of total network resistance remaining, R_k . If the xylem network is optimized for long-distance transport so that resistance per unit leaf area is independent of plant size then observed values should fall at or below the 1/6 curve predicted by the general allometric model (see details listed in West, Brown & Enquist 1999a). The predicted ranges of values are in excellent agreement with data from each individual. Note, the pipe model (Shinozaki *et al.* 1964), where there is no tapering of xylem dimensions (where $\bar{a} = 0$), clearly does not fit the data.

Scaling of xylem dimensions throughout the fossil record

The fossil record shows that across three major clades and grades of vascular plants (pteridophytes, gymnosperms, angiosperms) there has been an increase in plant size and stature (e.g. see Niklas 1997; Enquist *et al.* 2001 and references therein). The fossil record also shows that with increasing size there has been a concomitant increase in the dimensions of xylem elements (Niklas 1984). It is unclear, however, if the increase in xylem dimensions reflects taxonomic differences, ecological differences (Carlquist 1975), or allometric constraints of long-distance transport associated with increases in plant size.

In order to assess if the observed evolutionary increase in xylem radii reflects an allometric response to changes in plant size as predicted by the WBE model, data on the relationship between branch size and tracheid radius were assembled from the paleo literature (Niklas 1984, 1994). Data for the maximum stem diameter and average recorded tracheid diameter recorded for some of the earliest tracheophytes during four geologic time periods (Upper Silerian, Lower Devonian, Mid Devonian and Upper

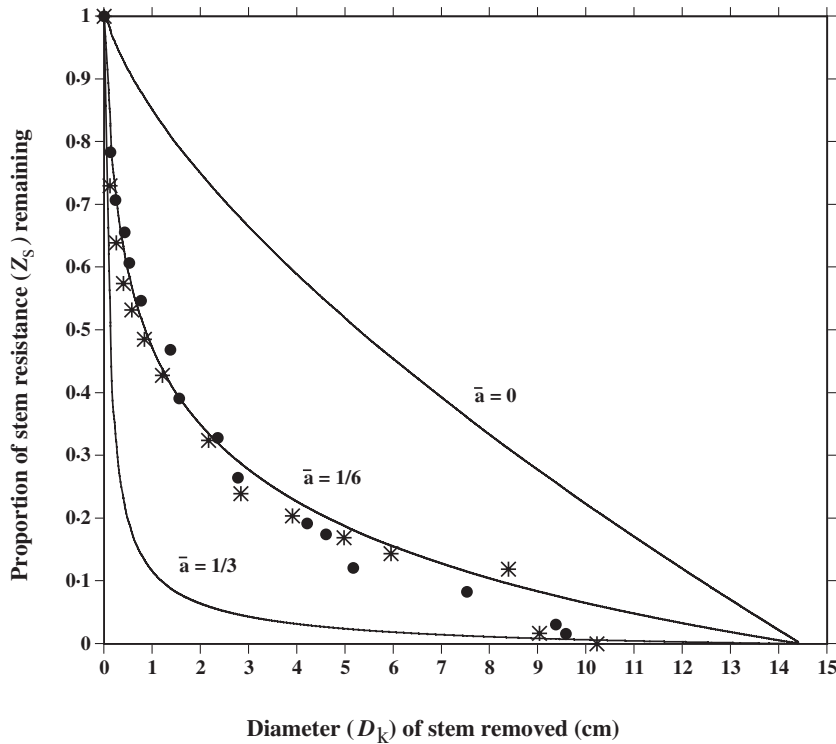


Figure 3. Total resistance of shoot xylem network for two individuals of *Acer saccharum* [data from Yang & Tyree (1993) – as plotted in West, Brown & Enquist (1999a)]. The plots show the effect of sequentially removing branches of increasing size (radius r_k) on the proportion of total network resistance remaining (R_k). If the xylem network is optimized for long-distance transport so that resistance is minimized then observed values should fall near or below the 1/6 curve predicted by the general allometric model. The predicted range of values are in excellent agreement with the data that represent two trees.

Devonian) were each recorded. Both data-sets were published independently of one another (Niklas 1984, 1994). Unfortunately, because of the resolution of the data, there are only four data points for the relationship between stem diameter and tracheid diameter through time. Nevertheless, when plotted together on logarithmic axes there is an increasing trend in average tracheid diameter with the evolution of increased plant size (Fig. 4). The observed exponent is within the range predicted by the WBE model (slope = 0.381, 95% CI = -0.057 to 0.821, $r^2 = 0.875$, $n = 4$, $F = 14.00$, $P = 0.064$, constant = 0.886, 95% CI = 0.04–1.73; Fig. 4).

Plotting the allometric relationship between stem diameter and tracheid diameter for an extant gymnosperm *Tsuga canadensis* (Fig. 1) and for fossil early tracheophytes (Fig. 4) on the same graph reveals that both extant and paleo samples fall on the same allometric function (slope = 0.307, 95% CI = 0.280–0.335, $r^2 = 0.961$, $n = 24$, $F = 546.29$, constant = 1.123, 95% CI = 1.09–1.15, $P < 0.0001$; Fig. 5). Although there appears to be slight deviation for some of the earliest vascular plants (e.g. the diminutive *Cooksonia* sp.) within the Upper Silurian, the observed scaling exponent for the combined data-sets (Figs 1 & 4) is indistinguishable from fitted regressions for each independent data-set. Although the paleo data are preliminary, the presence of a common allometric scaling law for both extant and fossil plants suggests that the rapid size diversi-

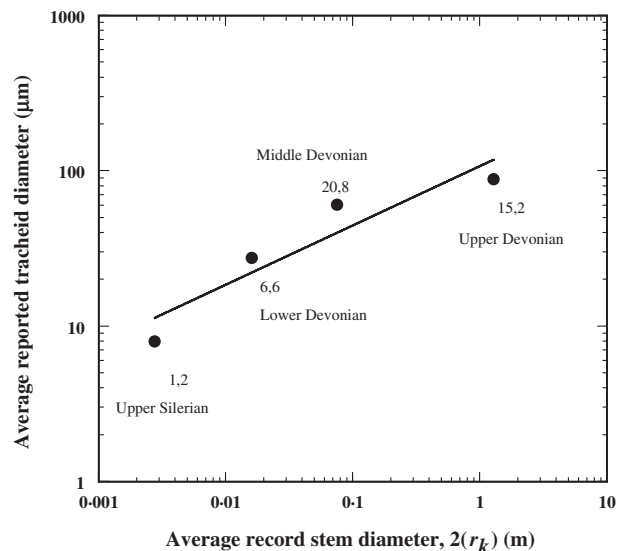


Figure 4. Plot of increase of fossil tracheid diameter with increases in plant size as recorded by stem diameter. Values of stem diameter for each paleo time period are record diameters recorded for that time. Time periods range from the Upper Silurian to the Upper Devonian. Numbers next to each data point reflect the sample size of tracheid and stem diameter data-set, respectively. Similarly, average tracheid size for each time period is an average for maximum values reported in the literature. Data from K. J. Niklas (1994, 1997).

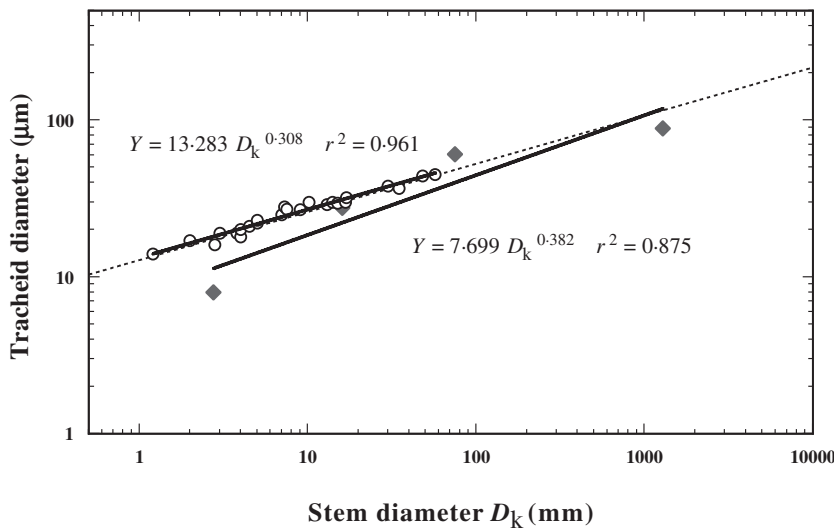


Figure 5. Plot of diameter and tracheid diameter within an extant gymnosperm *Tsuga canadensis*, \circ and the increase of tracheid size and stem size through the fossil record (\blacklozenge data from K. J. Niklas). The observed scaling relationship for both data sets are indistinguishable from one another. The combined allometric relationship for the extant gymnosperm and for fossilized tracheids and stem size is $a_k = 12.807 D_k^{0.307}$ (fitted dotted line). The 95% confidence intervals for this combined allometric relationship is not significantly different from the fossil allometry. The similarity between the allometry for extant species and the fossil data suggests that the diversification of the early vascular plants was guided by similar allometric constraints.

fication by some of the earliest vascular plants was guided by selection to minimize vascular resistance through the xylem network as predicted by the WBE model.

LONG-DISTANCE TRANSPORT AND THE INTEGRATION OF PLANT ORGANS – ROOTS AND STEMS

Selection to minimize whole – plant resistance associated with increased transport distances have also hypothesized to be reflected is the partitioning of root and stem biomass. As noted above, because of biomechanical constraints alone, an increase in plant size necessitates a reconciliation in how biomass is allocated between plant organs. As a consequence potential selection to minimize total plant vascular resistance associated with long-distance transport will probably also influence how biomass is allocated between plant organs as plants increase in size. In other words, allocation to roots and stems should reflect selection to minimize the hydrodynamic cost of whole plant transport resistance. Pearsall (1927), building upon Huxley's 1924) hypothesis of constant differential growth ratios, highlighted that the allometric integration of roots and stems should reflect a general principle of optimal allometric growth and allocation. Building upon these observations Enquist & Niklas (2002) and Niklas & Enquist (2002a, b) have extended the predictions of the WBE model toward understanding how biomass and metabolic production are partitioned and allocated to plant roots, stems and leaves, respectively.

The WBE model assumes that the amount of resource used per individual plant, approximates metabolic demand or gross photosynthesis B . Since B is predicted to scale proportionally to total leaf biomass, M_L , the WBE model predicts that the surface areas over which resources are exchanged with the environment (e.g. leaf surface area, which correlates with M_L) is proportional to the $3/4$ power of the total plant mass, M_T , so that $B \propto M_L \propto M_T^{3/4}$ and $M_L \propto D_S^2$, where D_S is stem diameter (West, Brown &

Enquist 1999a, Enquist *et al.* 2000). Empirical studies confirm that plant metabolic rate scales as the $3/4$ -power of total plant biomass M_T (which equals the sum of M_L , M_S and M_R) and that metabolic rates scales isometrically with respect to M_L (Niklas & Enquist 2001, 2002a,b). Enquist and Niklas (2002) note that $B = \beta_1 M_T^{3/4} = \beta_1 (M_L + M_S + M_R)^{3/4}$ where $B = \beta_2 M_L$, where values of β are a constant but may reflect species or taxon specific variation. Here, β_1 and β_2 include units of year^{-1} . Furthermore, $M_L = \beta_3 (M_L + M_S + M_R)^{3/4}$, where $\beta_3 = \beta_1/\beta_2$. Again, values of b are allometric constants, which may vary across taxa or even individuals. For example, β_3 is a measure of the proportion of the total biomass that is partitioned to leaves, whereas β_2 and β_2 reflect the intensity of metabolism per unit leaf mass and whole plant mass, respectively.

Using the above framework, Enquist & Niklas (2002) solve for how each plant organ (M_L , M_S and M_R) will scale with respect to each other by imposing a minimization 'cost' constraint. Specifically, in order for the hydrodynamic resistance associated with long-distance transport to be minimized (as in the WBE model) the total volume of fluid absorbed and transported by roots through stems per unit time must also be conserved. In other words, it is assumed that the volume of fluid transported per unit time in the root is always a constant fraction of the fluid transported in the stem. Under this constraint, in addition with the allometric prediction that $M_L \propto M_{\text{tot}}^{3/4}$, Enquist and Niklas (2002) predict that root biomass (M_R) and above-ground biomass (M_A) should scale directly proportionally to one another so that $M_S \propto M_R$ (see also Huxley 1924; Pearsall 1927). In particular, using the notation of Enquist & Niklas (2002), the relationships between all three major plant organs can then be expressed as general allometric allocation rules where,

$$M_L = \beta_{12} M_S^{3/4} \quad (7)$$

$$M_L = \beta_{13} M_R^{3/4} \quad (8)$$

$$M_S = (\beta_{12}/\beta_{13}) M_R \quad (9)$$

Again, the values of β_{12} and β_{13} are allometric constants, reflecting potential taxon or individual differences in the proportion of biomass that is allocation between roots and stems, and potentially differences in tissue quality (e.g. tissue density; see Enquist & Niklas 2002). A large global compendium of stem, root and leaf biomass from numerous studies support the model's predictions (Enquist & Niklas 2002; Niklas & Enquist 2002a, b). In general, both herbaceous and woody species appear to conform to the predictions from the model.

The WBE model predicts that even if there is an increase in the dimensions of the stem (mass, M_S or length L_S) the total stem resistance per unit photosynthetic area, Z_S , is an approximate constant. Therefore, if Z_S does not vary with stem mass then $Z_S = c_S M_S^0$ where c_S is an allometric constant which may vary between taxa and individuals. If the xylem hydrodynamic resistance of the root, Z_R , is governed in a fashion similar as predicted by the WBE model then $Z_R = c_R M_R^0$. Therefore, the total path resistance through both the root and stem components, Z_{Tot} , will simply follow Eqn 4. Importantly, the total path resistance of fluid passing through the root and the stem will be a constant – independent of plant size,

$$Z_{tot} = c_R M_R^0 + c_S M_S^0 \quad (10)$$

Here, Z_{Tot} will approximate $c_R + c_S$, where the values of c_R and c_S document the magnitude of resistance for a given amount of root and shoot mass respectively. Possible variation in c_R and c_S reflect potential differences between taxa and environments (including resistance of pit membranes and density of conducting tissue which reflects the density of vessels and/or tracheids in the stem or root or variation in the resistances of pit membranes or branching junctions; see Nobel 1983; Enquist *et al.* 2000). Hence, it is expected that Z_{Tot} will likely vary due to important phylogenetic and ecological differences. However, if, as predicted by Enquist & Niklas (2002; see also Niklas & Enquist 2002a, b), $M_R \propto M_S$ then according to the WBE model, Z_{Tot} will be independent of plant size. Note, as shown in Eqn 6, if M_R and M_S do not scale isometrically with one another (an exponent greater than or less than 1.0) then Z_{Tot} will change with increases in plant size.

Analysis of a global compendium of plant organ biomass for both angiosperms and gymnosperms provide robust support for the general allometric model (Enquist & Niklas 2002). For the purposes of this paper analysis of the partitioning of biomass between roots and stems also provides support for the hypothesis of integrated allocation to minimize hydrodynamic cost. Least squares (Model I) regression on \log_{10} -transformed data for the relationship between root mass and stem mass for both angiosperms and gymnosperms indicates a slope that is essentially indistinguishable from 1.0 (gymnosperm slope = 1.05, 95% CI = 1.10–1.01, $r^2 = 0.969$, $n = 169$, $F = 2563.02$, constant = 0.457, 95% CI = 0.409–0.505, $P < 0.0001$; Angiosperm slope = 1.12, 95% CI = 1.14–1.12, $r^2 = 0.989$, $n = 345$, $F = 16541.53$, constant = 0.421, 95% CI = 0.387–0.454, $P < 0.0001$). The data indicate there is a slight deviation toward an exponent greater than

1.0. Such deviation is likely attributed to sampling error associated with sampling root biomass – especially for the largest trees. That is, as plants become increasingly larger there is an increase in the error of accurately sampling root biomass. Increased error in sampling below-ground biomass with increasing plant size will lead to a slightly increased deviation from the expected scaling exponent of 1.0. Nevertheless, the overlap between gymnosperms and angiosperms in their allometric constants indicates that both angiosperms and gymnosperms have approximately a constant amount of biomass partitioned between roots and stems.

The above treatment should be thought of as a zero-th order model for biomass partitioning between plant organs. There is a rich literature on how various biotic and abiotic variables may influence root:shoot ratios, stem:leaf ratios, etc. (e.g. see Bazazz & Grace 1997; Andrews *et al.* 1999 and references cited within). Clearly, local environmental conditions will further influence variability about allometric partitioning relationships. Nevertheless, as supported by a large compendium of global biomass data, the general allometric model appears to explain much of the resulting variation in the scaling of biomass between plant stems, roots and leaves.

CONCLUSIONS

This paper presents a general argument for the role of long-distance transport as a fundamental constraint shaping the evolution of vascular plants. In particular, I have focused on the hydrodynamic costs associated with increasing path lengths and the problem of allocation as it relates to the integration of the root and stem components of the vascular network. This argument is inherently allometric in nature. The impressive increase in the range of plant size observed within the fossil record could not have been achieved without reconciling biomechanical and hydrodynamic constraints. Here it is argued that selection to minimize the increasing costs of hydrodynamic resistance was associated with increased transport distances.

Allometric theory points to the importance of the hydrodynamics of transport in the evolution of organismal form and function (West *et al.* 1997). This theory posits that selection to minimize hydrodynamic resistance but yet maximize the scaling of leaf surface area ($M_L \propto M_{Tot}^{3/4}$) has led to the evolution of plant vascular networks characterized by allometric scaling relationships with characteristic exponents. Preliminary data on the scaling of vascular plant xylem dimensions and the partitioning of plant organ biomass appear to support the notion that the evolution of long-distance transport has been a central feature shaping plant form and function. Although the predictions of the general allometric model are in need of further testing there appears to be broad support for many of the model predictions (see Enquist *et al.* 1998; West *et al.* 1999a, b; Enquist & Niklas 2002; and Niklas & Enquist 2002a, b). Together, these studies support the notion that selection to

minimize the costs of hydrodynamic resistance has shaped the evolution of plant form and function across vascular plants. The development of a rapidly growing body of allometric theory and data from both extant and fossil plants strongly suggests that plant size is perhaps the most important attribute describing variation in plant form, function and diversity.

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