

Patterns in hydraulic architecture and their implications for transport efficiency

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Summary We evaluated whether patterns in hydraulic architecture increase transport efficiency. Five patterns are identified: area-preserving branching; variable trunk versus twig sap velocity; distally decreasing leaf specific conductivity (K_L) and conduit diameter; and a decline in leaf specific conductance (k_L) of the entire plant with maturation. These patterns coexist in innumerable combinations depending on the ratio of distal/proximal conduit number (F). The model of West and colleagues does not account for this diversity, in part by specifying $F = 1$ and requiring a specific conduit taper derived from the incorrect premise that k_L is constant with plant size. We used Murray's law to identify the conduit taper that maximizes k_L for a given vascular investment. Optimal taper requires the ratio of distal/proximal conduit diameter to equal the ratio of distal/proximal K_L . The smaller these ratios, the greater the k_L . Smaller ratios are achieved by an increase in F . Conductivity and diameter ratios < 1 and $F \geq 1$ in plants are therefore consistent with maximizing conducting efficiency. However, the benefit of increasing F requires area-increasing conduit branching, potentially leading to mechanical instability of trees. This trade-off may explain why tree stems were relatively inefficient with F near 1 and limited conduit taper compared with vine stems or compound leaves with $F > 1$ and greater taper. Within trees, the anatomies of a coniferous and a diffuse-porous species were less efficient than that of a ring-porous species, presumably because the latter allows conduit area to increase distally without also increasing total xylem area. This is consistent with decelerating sap velocities from trunk to twigs in ring-porous trees versus accelerating velocities in other types. In general, the observed architectural patterns are consistent with the maximization of transport efficiency operating within mechanical constraints.

Keywords: da Vinci's rule, leaf specific hydraulic conductivity, Murray's law, WBE model.

Introduction

Martin Zimmermann coined the term "hydraulic architecture" in 1978 to refer to the spatial pattern of hydraulic resistances in the xylem of a plant's branch system. Flow resistance is the pressure drop per volume flow rate of the transpiration stream. High resistance is costly either because the plant must function

at a more negative pressure, or because gas exchange is restricted to minimize the drop in negative pressure. The latter behavior of pressure regulation has been shown to limit CO₂ fixation (Meinzer and Grantz 1990, Sperry and Pockman 1993, Meinzer et al. 1995, Saliendra et al. 1995, Hubbard et al. 2001). This mode of hydraulic constraint has been implicated in limiting the maximum height of trees (Mencuccini and Grace 1996, Ryan and Yoder 1997) and in causing declines in productivity in old growth forests (Yoder et al. 1994, Hubbard et al. 1999, Tyree 2003). Models of ecosystem fluxes are beginning to include canopy pressure regulation to better predict adjustments in canopy CO₂ fixation in response to soil and atmospheric drought (Williams et al. 1996). Carbon and water fluxes are coupled in plants, and insights from hydraulic architecture ultimately lead to a more mechanistic understanding of the limits on plant carbon uptake.

The boldest claim for the significance of hydraulic architecture is that it underlies the quarter-power scaling laws in biology (West et al. 1997, 1999, Enquist et al. 2000). Whether or not this claim is true, its proponents have introduced an important concept: namely that hydraulic architecture conforms to the "energy minimization" principle. Accordingly, the xylem resistance is the lowest possible for a given investment in vascular tissue (West et al. 2000). The West et al. model has had a large impact and has been extended to make predictions about the maximum height of trees (West et al. 1999), plant resource use and population density (Enquist et al. 1998, Enquist and Niklas 2001, Niklas et al. 2003) and plant growth patterns (Enquist et al. 1999, Niklas and Enquist 2002, 2003).

We begin our review with an overview of major patterns in hydraulic architecture. This provides the basis for evaluating the model of West et al. (1997). We discuss recent work that uses Murray's law to test for energy minimization (McCulloh et al. 2003, 2004). We conclude by considering how patterns in hydraulic architecture influence transport efficiency. Our review does not discuss methods or principles of water transport, which others have comprehensively covered (Tyree and Ewers 1991, Cruiziat et al. 2002).

Patterns in hydraulic architecture

The artist and engineer Leonardo da Vinci did perhaps the earliest work in hydraulic architecture. In the 1500s, da Vinci hy-

pothesized that trees must preserve the total area of their branches across junctions in order to supply their leaves with water (Richter 1970). The modern equivalent of da Vinci's rule is the pipe model, which assumes that each unit of leaf area is associated with a unit "pipe" of wood of a fixed cross-sectional area running from root to leaf (Shinozaki et al. 1964a, 1964b). The prediction of the pipe model of constant leaf area per unit xylem area results in area-preserving branching within the canopy, which is consistent with da Vinci's rule. Below the canopy, the pipe model predicts that the xylem area will increase because of the build-up of disused pipes that had been attached to shed leaves. Measurements by Shinozaki et al. (1964b) show that whole-stem area is preserved across branch points within the canopy and that stem area increases in the major branches and trunk below the crown.

Other measurements also support da Vinci's rule, at least within the canopy. Huber (1928) compared the ratio of total xylem cross-sectional area (A_x) to the leaf mass supplied by the stem at various points in young *Abies concolor* (Gord.) Lindl. ex Hildebr. and *Picea* sp. trees to exclude non-transporting heartwood. He found that this ratio (dubbed the "Huber value" by Zimmermann 1978a) was generally constant within crowns, aside from the higher values found in the leader, presumably resulting in a better hydraulic supply to the leader than to the side branches. Aside from the leader, the general constancy of the Huber value within the canopy is consistent with da Vinci's area-preserving rule. Horn (2000) also found area-preservation in branches from the trunk through the large branches, but observed a possible trend of increasing area in the small distal branches (Figure 1). Overall, however, a major architectural pattern is the widespread occurrence of area-preserving branching.

Why should plants follow da Vinci's rule? The pipe model is neutral on this question and provides no insight. Although widely cited as such (Tyree and Ewers 1991, West et al. 1997, 1999, Enquist et al. 2000), the pipe model is not a hydraulic model. It is a biomass allometry model with no assumptions about the anatomy of the unit pipe, and no particular implications concerning either hydraulics or biomechanics.

Da Vinci derived his rule from the explicit assumption that water flows with "equal rapidity" throughout the tree (Richter 1970, Zimmermann 1983). For a constant sap velocity, A_x must be constant at every level in the tree. This is because the volume flow rate (Q) is conserved across branch ranks, so maintaining equal mean velocities (v) requires constant cross-sectional area of conduits (A_c):

$$Q = vA_c \quad (1)$$

Although da Vinci did not mention it, he implicitly assumed that the cross-sectional area of the piping is proportional to the total xylem cross-sectional area ($A_c \propto A_x$). In those pre-microscope days, the anatomical complexity of wood was probably not appreciated. Although Huber measured only A_x , most of the measurements that test da Vinci's rule have been made on the total stem area (e.g., Figure 1), which makes yet a further assumption that A_c is also proportional to the cross-sectional area of the entire stem, including the pith, phloem and periderm.

More than 400 years after da Vinci, the first measurements of sap velocity refuted his assumption that it is constant from trunk to twig. Huber and Schmidt (1936) found that sap velocity in diffuse-porous birch increased from the trunk to the distal branches. Andrade et al. (1998) have also observed this pattern in five diffuse-porous species co-occurring in the tropics, and McDonald et al. (2002) later measured the same velocity profile in conifers. In contrast, Huber and Schmidt (1936) found that sap velocity in ring-porous ash and oak decreased slightly from the trunk to the small branches. These measurements indirectly reveal the distribution of conduit area from the trunk to the leaves, because of the conservation of flow (Equation 1). In diffuse-porous species and conifers, the conduit area profile must decrease distally, while in oak and ash it must increase slightly. Variable conduit areas do not contradict the area-preserving branching pattern, which applies to total stem or xylem area. Conduits make up only approximately 6–55% of the total xylem area in angiosperms and 90–94% in conifers, and not all conduits are necessarily functioning

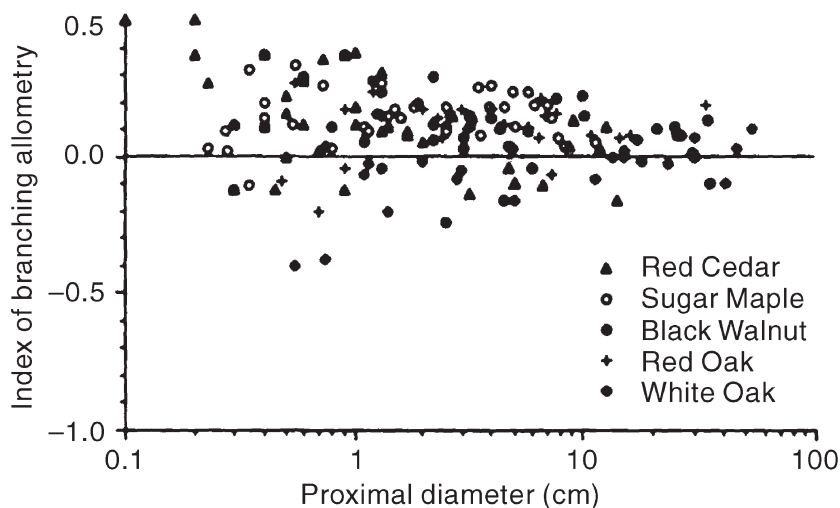


Figure 1. The preservation of stem cross-sectional area across branch points. In symmetrically bifurcating branches, Horn (2000) calculated an index of branching allometry that equals 0 for area-preserving branching, > 0 for area-increasing branching and < 0 for area-diminishing branching. Figure is from Horn (2000); used with permission.

(Zimmermann 1978a, Gartner 1995). The velocity data, combined with the trend toward area-preserving branching, indicate that the functional conduit area can vary independently of total stem area.

Although only a few species have been tested, the contrast of the velocity profiles in ring-porous oak and ash versus the diffuse-porous species and a conifer suggests a second architectural pattern. Ring-porous species in general may have higher velocities in the trunk than the branches, and diffuse-porous and coniferous species may have lower velocities in the trunk than in the branches. The fact that these velocity profiles undermine da Vinci's rationale for area-preserving branching leaves no mechanical or hydraulic basis for the tendency of plants to follow da Vinci's rule.

Martin Zimmermann (1978a) established a third architectural pattern. He measured the hydraulic conductivity of stem segments throughout several trees. Conductivity (K) is a length-independent measure of conducting capacity:

$$K = \frac{Q}{\Delta P/l} \quad (2)$$

where $\Delta P/l$ is the pressure gradient driving flow. To relate conducting capacity to leaves supplied by the stem segment, he divided K by the total leaf area (A_L) irrigated by the stem segment. This quotient is referred to as the leaf specific conductivity ($K_L = K/A_L$). The general pattern from a large number of studies on a wide variety of tree species is an exponential rise in K_L as stem diameter increases in a tree proximally from minor branches to the trunk (Figure 2; Zimmermann 1978a, Tyree et al. 1983, 1991, Ewers and Zimmermann 1984, Zotz et al. 1997). Although there can be great variability when branches of the same size are compared, and the leader often has higher K_L values than lateral branches (Zimmermann 1978a, Cochard et al. 1997), the general pattern is clear when a wide range of diameters is compared. Trees may approximate area-preserving branching, but they certainly do not show velocity- or conductivity-preserving branching. The uncoupling of conductivity and cross-sectional area is caused by changes in conduit number and diameter in stems of different sizes.

The general constancy of A_x and the pattern of declining conductivity mean that there must be a decrease in the conductivity per xylem area (the xylem specific conductivity, $K_s = K/A_x$) moving from the trunk to minor branches. Anatomically this means there is either a decrease in the number of conduits per area (conduit density) or a decrease in conduit diameter as water flows towards the leaves, or both. Available data suggest conduit densities are either relatively constant (James et al. 2003, K.A. McCulloh, unpublished results), or increase with height (Gartner 1995, Lemoine et al. 2002). In contrast, there is strong evidence for conduit diameters narrowing distally (Figure 3; Zimmermann 1978a, 1983, James et al. 2003, McCulloh et al. 2004). Distal tapering of conduit diameters constitutes a fourth general pattern of hydraulic architecture.

The relationship between the observed patterns of velocity (and conduit area), K_L , and conduit taper are diagrammed in Figure 4. This graph will be referred to frequently (see also

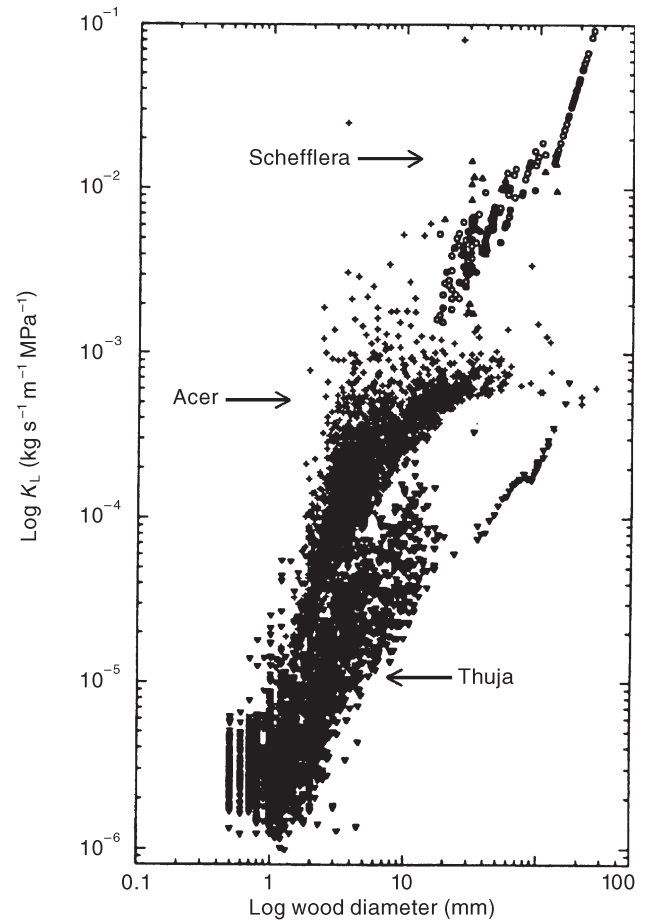


Figure 2. The relationship between leaf specific conductivity, K_L , and wood diameter (= cambium diameter). There is a pronounced trend for values of K_L to increase with stem diameter within a tree. The trend is consistent across diverse tree types including a temperate conifer (*Thuja occidentalis*), a temperate, diffuse-porous tree (*Acer saccharum*) and a tropical tree (*Schefflera morototoni*). Figure is from Tyree et al. (1991); used with permission.

Figure 5) and needs careful explanation. The horizontal axis quantifies the trend for narrower conduits moving from trunk to twig (conduit taper) as the ratio of distal to proximal conduit diameter. A smaller ratio means greater taper. The vertical axis quantifies the drop in K_L from trunk to twig as the ratio of distal over proximal K_L : the smaller this conductivity ratio, the greater the drop in conductivity. Both ratios are determined for the same distal/proximal branch rank comparison. A plant with a single x -axis taper ratio can have different y -axis conductivity ratios (or vice versa) by adjusting how its number of conduits changes across the two branch ranks. For example, increasing the number of conduits from proximal to distal rank will cause less of a drop in the conductivity (greater y -axis conductivity ratio) for the same x -axis taper than if the number of conduits was the same across the ranks.

The solid curve in Figure 4 shows the relationship between conduit taper and conductivity ratio for trees with constant sap velocity, and hence constant conduit area (equal Σr^2) through-

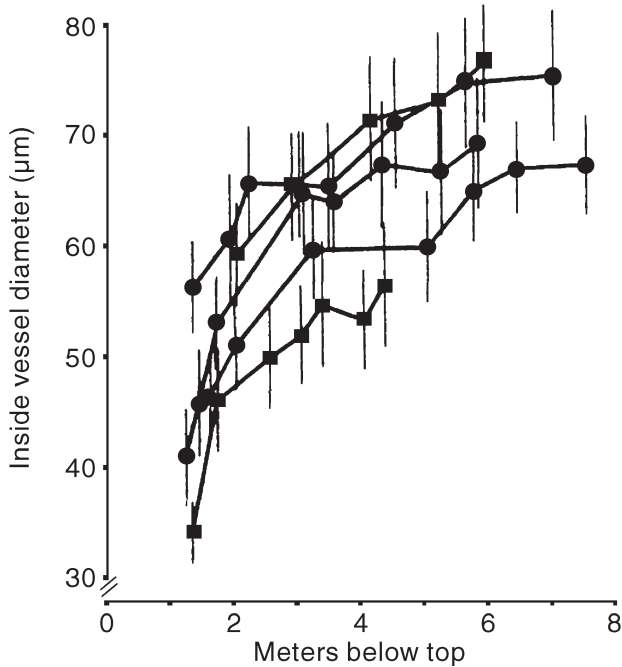


Figure 3. The inside tangential diameters of the largest vessels from the most recent growth rings versus the distance from the apex of the tree. Symbols: three birch individuals (●) and two poplars (■). The narrowing of conduit diameter with distance from the trunk is typical for woody plants. (Zimmermann 1983, McCulloh et al. in press). Figure is based on Zimmermann (1978a); used with permission.

out. Coniferous and diffuse-porous species, with increasing velocity and decreasing conduit area from trunk to twig, will fall below the constant area curve (Figure 4, – area, + velocity). Ring-porous trees with decreasing velocity and increasing conduit area will be above the curve (Figure 4, + area, – velocity).

The advantages usually attributed to the observed K_L pattern reflect the way that these conductivities determine the overall hydraulic conductance from trunk to leaf. Hydraulic conductance (k) is a length-dependent measure that represents the conductivity integrated over the length of the flow path ($k = Q/\Delta P$). If conductivity is constant, doubling the flow path will halve conductance. Hydraulic conductance can also be expressed per leaf area supplied ($k_L = k/A_L$).

By having the lowest conductivities in the minor branches at the end of the flow path, plants can control the distribution of water regardless of how far it must travel (Zimmermann 1978a). Low conductivities at the downstream end result in similar values of total root–leaf conductance despite different path lengths. The advantages of this are numerous. The higher values of K_L in the leader will result in a lower pressure difference required to move a given amount of water to a fast growing leader than to the side branches. Under favorable conditions, this can result in a better water supply to the leader than to the side branches, even though the path length to the leader may be several times that to the lower branches (Zimmermann 1978a, 1978b, Ewers and Zimmermann 1984). Under water limiting conditions, branches with lower K_L values will be

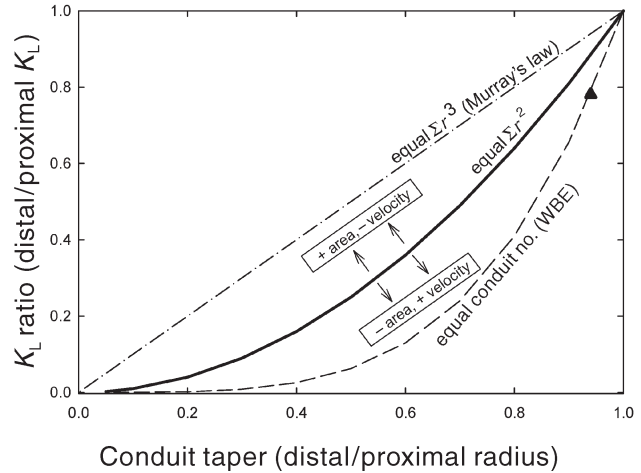


Figure 4. The relationship between conduit taper across branch ranks and the corresponding leaf specific conductivity (K_L) ratio. The solid line shows the relationship when conduit area, and therefore sap velocity, is constant from trunk to twigs. Above this line, conduit area increases distally and sap velocity declines (+ area, – velocity). Below this line, conduit area diminishes distally and sap velocity increases (– area, + velocity). The dashed line is for trees with an equal number of conduits from trunk to twigs, as assumed in the WBE model. The triangle identifies the conduit taper across adjacent ranks assumed by WBE for a bifurcating branching structure. The dash-dot line shows the 1:1 relationship conforming with Murray's law. Xylem networks on this line maximize hydraulic conductance per fixed vascular volume and branching architecture.

more water stressed. This stress will be manifest as either greater stomatal closure or lower xylem pressures. Either response can lead to preferential loss of low-conductance branches. This controlled dieback improves the water balance of the remaining crown (Tyree and Sperry 1988).

A fifth architectural trend is for a decrease in whole-shoot k_L as plants mature (Rust and Roloff 2002, Mencuccini 2003). Meinzer and Grantz (1990) and Saliendra et al. (1995) observed three- to fourfold declines in the k_L values of sugarcane and birch associated with maturation from the juvenile to adult stage. In birch, the drop in k_L was the result of the increased path length of larger trees (Saliendra et al. 1995). The decline in k_L with maturation imposes stress because a plant must either reduce its stomatal conductance to maintain leaf water balance, or experience progressively more negative leaf water potential as it ages (Hubbard et al. 1999, Barnard and Ryan 2003). The hydraulic costs associated with increased plant height have been implicated in declines in forest productivity with age (Yoder et al. 1994, Hubbard et al. 1999, Schäfer et al. 2000, Tyree 2003) and in limits to tree height (Mencuccini and Grace 1996, Ryan and Yoder 1997, Koch et al. 2004).

Table 1 summarizes the architectural patterns we have discussed. It is not an exhaustive list, but includes the basic trends. Characterizing architectural patterns is important, but interpreting their meaning is equally so. We consider some functional consequences of architectural patterns after discussing the innovative work of West and colleagues.

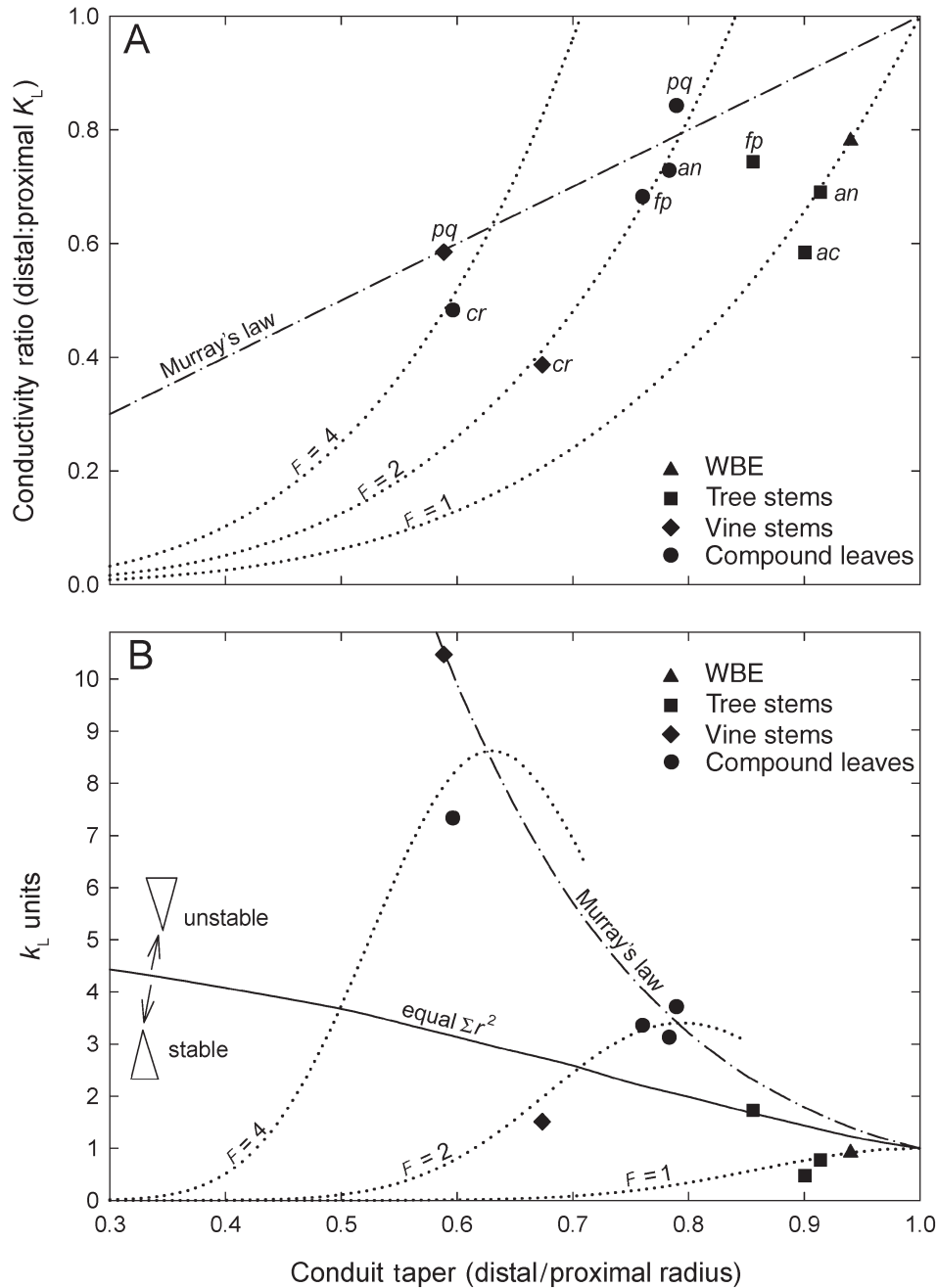


Figure 5. (A) Conductivity ratio versus conduit taper. Dash-dotted line is the 1:1 Murray's law relationship. Dotted lines represent different conduit furcation numbers (F), the ratio of cross-sectional conduit number in adjacent distal versus proximal stems. As F of adjacent ranks is increased from the West et al. (WBE) model value (i.e., of 1) to 4 (dotted curves $F = 1, 2, 4$), more taper is required (= smaller ratio) for the same conductivity ratio. Symbols show adjacent rank data for species measured by McCulloh et al. (2003, 2004) and for the architecture assumed in the WBE model (▲). Tree stems are from *Fraxinus pennsylvanica* Marsh. (*fp*, ring-porous), *Acer negundo* L. (*an*, diffuse-porous) and *Abies concolor* (*ac*, conifer). Vine stems are from *Parthenocissus quinquefolia* (L.) Planch. (*pq*) and *Campsis radicans* (L.) Seem. ex Bur. (*cr*). Compound leaves are from the same species. Stem ranks were defined by annual increments of extension growth and leaf ranks were petiole versus petiolule comparisons. For McCulloh et al. (2004) data (stems of *fp*, *an* and *ac*), conductivity ratios were measured directly and taper estimated from F . For McCulloh et al. (2003, 2004, all comparisons), conductivity ratio was estimated from the Hagen-Poiseuille equation and taper determined from mean conduit diameters. Symbols are pooled means from both studies. (B) Hydraulic conductance (k_L) versus conduit taper. The k_L was calculated for fixed branching architecture

(five bifurcating ranks of equal length) and constant vascular volume. The maximum k_L for a given F (dotted $F = 1, 2, 4$ curves) is achieved at Murray's law (dash-dotted curve). The k_L was arbitrarily set equal to 1 for the Murray optimum when $F = 1$. Increasing F leads to increasing conducting efficiency. For fixed investment and branching architecture, tree stems (■) and WBE (▲) are much less efficient than vine stems and compound leaves. Efficiency of tree stems may be limited by the need to stay on or below the area-preserving curve for conduits (solid "equal Σr^2 " curve) to maintain a mechanically stable area profile. Vine stems and leaf xylem show area-increasing conduit branching and greater hydraulic efficiency, consistent with no mechanical constraint on their xylem structure.

The West et al. (WBE) model

West et al. ("WBE," 1997, 1999) have developed a model of hydraulic architecture to predict various quarter-power scaling laws, including the scaling of metabolic rate with body mass to the three-fourths power. Their most recent version for plants

(West et al. 1999, Enquist et al. 2000) included the following assumptions of branching structure and hydraulic architecture. (1) The branching pattern is self-similar, meaning that all branches of a given rank have equal length and give rise to an equal number of daughter branches. This is similar to the re-

Table 1. A list of some of the patterns in hydraulic architecture.

Patterns in hydraulic architecture
1. Stem-area-preserving branching (“da Vinci’s rule”)
2. Sap velocities increase distally in diffuse-porous and coniferous species; sap velocities decrease distally in ring-porous species
3. Leaf specific hydraulic conductivity increases exponentially with stem diameter
4. Conduit diameter increases with stem diameter
5. Leaf specific hydraulic conductance declines from the juvenile to the mature developmental stage

peating bifurcation of a *Psilotum* shoot, for example. This shoot structure has no main axis and every leaf is equidistant from the base of the tree. (2) Daughter branches are shorter than the parent branch by a specific ratio (e.g., 0.79 for bifurcating branching). (3) The number of functional conduits is equal at every level, meaning the trunk has the same number of functional conduits as all petioles combined. (4) The conduit diameter tapers just enough to ensure the hydraulic resistance of the trunk-to-leaf flow path is independent of length. This means that the hydraulic conductance per leaf area is constant with plant size. (5) The final branch of the network is size invariant. (6) Branch length scales with branch diameter to the two-thirds power as required for elastic similarity of mechanical support (McMahon 1973). From the specifics of their self-similarity assumption (1), this requires area-preserving branching, which, when combined with a fixed number of tapering conduits, results in the proportion of nonconducting xylem (i.e., heartwood) increasing from trunk to twig. (7) Within the constraints of this architecture, the hydraulic resistance is minimized according to the energy minimization principle.

The dashed line in Figure 4 shows the conduit taper versus conductivity relationship for a WBE-type tree with a constant number of conduits at every level (assumption 3). The triangle on this curve corresponds to the specific conduit taper assumed in the WBE model for adjacent ranks for a bifurcating branch system (assumption 4). Comparing taper across more distant ranks (e.g., twig versus trunk) would move the triangle down the dashed line, because the taper would be amplified. The WBE line falls below the equal area and velocity line (solid line), meaning that conduit area will decrease and velocity will increase from trunk to twig.

The WBE model has generated much interest and some criticism. Dodds et al. (2001) claimed that the energy minimization principle could be achieved regardless of whether the network is fractal. Moreover, when the assumption that the network is a fractal is relaxed, the model no longer predicts three-fourths-power scaling of metabolic rate with body mass. Further critique by Kozłowski and Konarzewski (2004) claimed that the assumption of size-invariance of the final branch (assumption 5) results in metabolic rate scaling directly with body mass, not to the three-fourths power. Both pa-

pers also question whether three-fourths-power scaling exists between metabolic rate and body mass.

A more basic limitation of the WBE model is that few, if any, plants develop according to their assumptions. Leaves are not equidistant from the base of the tree and apical dominance of a central axis is the rule rather than the exception (assumption 1). Daughter branches are not known to be shorter than the parent branch by a specific ratio (assumption 2). Most conduits are much shorter than the plant, which means that the number of conduits running in parallel is not necessarily constant with height (assumption 3, McCulloh et al. 2003). This is true even for *Psilotum nudum*, which otherwise might be a plant with WBE structure (Schulte et al. 1987, McCulloh and Sperry 2005). The assumption that hydraulic resistance is independent of plant height (assumption 4) is also inconsistent with data, which show decreasing k_L with size (Meinzer and Grantz 1990, Saliendra et al. 1995, Rust and Roloff 2002, Mencuccini 2003). Moreover, this assumption seems maladaptive: why should a 1-m sapling be penalized with the same high resistance as its 100-m parent? Such a sapling would quickly be outcompeted by rival saplings with less taper and lower resistance than their parents.

Not surprisingly, some predictions of the WBE model are incompatible with observations. The model predicts decreasing conduit area and increasing sap velocity from trunk to twig (Figure 4, dashed line). While this is qualitatively consistent with diffuse-porous and coniferous trees, it is inconsistent with the velocities of ring-porous trees, which slow distally (Huber and Schmidt 1936, Andrade et al. 1998, McDonald et al. 2002). The model requires that the proportion of nonconducting wood area must increase from the trunk to the minor branches. This is necessary to make the tapering of a constant number of conduits compatible with area-preserving branching (assumption 6). The model predicts that trees will become height limited when the basal sapwood area is forced to rise to 100% of the trunk cross-sectional area. However, in real trees, the heartwood area increases with age and does not approach 0% in the trunks of the tallest trees (Hazenbergh 1991, Sellin 1994, Yang et al. 1994, Alemayehu et al. 1998, Paques 2001, Rigling et al. 2002, Perez Cordero and Kanninen 2003).

Despite these shortcomings, the WBE approach has introduced important concepts to the study of hydraulic architecture. Its authors were the first to imply that patterns in hydraulic architecture have evolved to minimize the energy associated with water transport. They were also the first we know of to consider quantitatively the important and potentially conflicting interaction between hydraulic architecture and biomechanical stability. Future work should pursue these concepts in line with a more anatomically and morphologically realistic representation of architecture.

Murray’s law and energy minimization

Murray’s law provides a useful starting place for analyzing the energy minimization principle in plants. Derived by Cecil Murray for animal cardiovascular systems in 1926, this law predicts that blood vessels should taper to maintain propor-

tionality between the volume flow rate (Q) and the sum of the conduit radii cubed (Σr^3) at every branch level in order to maximize hydraulic conductance for a given investment in vascular tissue volume. For networks with constant Q at all branch levels, Murray's law predicts conservation of Σr^3 . In deriving his law, Murray assumed that the wall thickness of the vessels was negligible and that a cost of the vascular system was in the metabolic maintenance of the blood. He further assumed that the flow was laminar and the conductivity of the piping was proportional to the Hagen-Poiseuille value. Importantly, Murray's law does not predict how the branch system ramifies or the lengths of individual branches. Rather, it predicts only the optimal tapering for a given branching architecture and investment. This is less ambitious than the WBE model, which specifies both taper and architecture. However, because the branching architecture does not necessarily conform to the WBE conditions, the more limited approach of applying Murray's law may be more informative.

Despite the differences between animal and plant vascular networks, Murray's law is applicable to xylem given a few additional assumptions. Unlike animals, the major cost of the xylem is not the fluid, but in the thick walls necessary to withstand the compressive forces caused by the negative pressures associated with plant water transport. The proportionality between conduit dimensions (the ratio of wall thickness to conduit width) and cavitation resistance shown by Hacke et al. (2001) means that for a given cavitation resistance, the total wall volume should be proportional to the total lumen volume, and Murray's law will still apply (McCulloh et al. 2003). The conductivity of plant conduits is substantially less than the Hagen-Poiseuille value because of the added resistance of the conduit end walls. Recent work, however, indicates that end walls contribute approximately half of the total resistance to flow across a wide range of conduit sizes (Sperry et al. 2005). This means that the conductivity is still roughly proportional to the Hagen-Poiseuille value, as required for Murray's law to be valid. Finally, it must be assumed that the xylem conduits do not provide mechanical support to the plant in addition to their transport role. Murray's law does not take into account any mechanical benefit of conduit structure and is inappropriate for cases where conduits have multiple functions. Given these assumptions, Murray's law predicts the optimal conduit taper for a given architecture and investment will conserve Σr^3 in xylem conduits.

A hydraulic architecture that follows Murray's law has a conduit taper (distal/proximal radius) that is exactly equal to the conductivity ratio (distal/proximal K_L) as shown by the dash-dotted 1:1 line in Figure 4. Plants that fall on this line will have a conduit area profile that increases from trunk to twig, like an inverted cone, and velocities that decrease distally. For the WBE architecture with equal conduit numbers, Murray's law is achieved only if the conduits do not taper (Figure 4, intersection of dash-dotted and dashed curves). This non-tapering and energy-minimizing structure is what WBE assumed in their first version of the model (West et al. 1997). Adding taper in their revised version (West et al. 1999) moved their architecture off the Murray's law optimum and sacrificed efficiency.

The possibility that the number of conduits in parallel can vary from trunk to twig complicates the application of Murray's law. The "furcation number" (F) is defined as the ratio of functional conduit number in daughter branches to adjacent mother branches. In animals, where a single tube ramifies to form the vascular system, F must be ≥ 2 . In plants, the large number of short conduits in parallel means that F is not necessarily ≥ 2 , nor the WBE value of 1. The only a priori restriction is that F must be > 0 . The dotted curves in Figure 5A show how F influences the conductivity versus conduit taper relationship (for adjacent branch ranks). The $F = 1$ curve is the WBE model. Increasing F to 2 or 4 steepens the relationship, requiring more taper for the same conductivity ratio (Figure 5A, $F = 2$ and $F = 4$ curves).

Furcation number is important, because, like conduit taper, it influences the conductance per unit investment of the vascular system. The dotted curves in Figure 5B show how the conductance of a vascular system of constant volume and identical branching architecture changes with taper and F . With F fixed, the optimal (maximum) conductance is reached at the Murray's law taper. This is seen in the correspondence between the taper at peak conductance of the dotted curves in Figure 5B, and the taper where the dotted furcation curve and the Murray's law line intersect in Figure 5A. Figure 5B also shows that as F is increased (while vascular volume and branch architecture are held constant), the Murray's law maximum increases. Networks with higher F in combination with Murray's law taper are more efficient. This results from fewer, wider conduits in the trunk that ramify into numerous, narrower conduits distally.

The analysis in Figure 5 provides a new explanation of why plants have tapering conduits and declining conductivities moving from trunk to twig: this structure increases hydraulic efficiency. Reducing conductivity ratio and steepening taper in proportion moves plants to the lower left of Figure 5A and thus to higher hydraulic conductance per unit investment (upper left, Figure 5B). This is true regardless of whether plants manage to follow Murray's law exactly. A corollary is that F should be close to 1, if not greater. If plants had no conduit taper, or widened their conduits distally in combination with constant or increasing conductivities, they would move to the upper right of Figure 5A and to lower conducting efficiencies (lower right, Figure 5B), even if they obeyed Murray's law. This maladaptive hydraulic architecture would also be associated with an F value much less than 1. This advantage of conduit taper and declining conductivity complements its previously recognized significance in terms of controlling water supply and managing water stress as discussed earlier.

To provide a preliminary assessment of where real xylem networks fall with respect to F and conduit taper, we plotted data from earlier studies (McCulloh et al. 2003, 2004) in Figure 5. Taper and conductivity ratio are shown for adjacent ranks in Figure 5A. Taper versus relative hydraulic conductance is shown in Figure 5B, assuming for comparison the same total volume of conduits and branching topography used to calculate the dotted furcation trajectories. Furcation numbers in Figure 5 are not standardized for variation in branching

pattern and so differ from values reported earlier for these data (McCulloh et al. 2003, 2004).

The data are consistent with expected hydraulic patterns in showing a conduit taper (diameter ratio < 1) and decreasing conductivity (conductivity ratio < 1). Also as expected, F values were near 1 or above. The data generally fall on or somewhat below the Murray's law 1:1 optimum, rather than above it.

Overall, there is a strong trend for the xylem of free-standing trees to have the lowest F and thus the lowest conducting efficiency, as compared with the high F and high efficiencies of vine stems and compound leaves of the same vine and tree species. This trend suggests that constraints on F and taper limit the transport efficiency of free-standing stems relative to vines and leaves. We consider this constraint in the next section.

Hydraulic efficiency versus mechanical stability

There is a basic conflict between optimizing transport and maintaining mechanical stability. The solid curve in Figure 5B (equal Σr^2) represents the xylem network with area-preserving branching of its xylem conduits. Xylem networks above this curve, although benefiting from greater conductance, show area-increasing branching of conduits. If there is even a loose proportionality between conduit area and total xylem area, this will correspond with a small diameter trunk supporting a wider collective branch area. Such an "inverted cone" area profile is mechanically unstable, regardless of branching architecture, simply because this structure would be top-heavy. For mechanical stability, branching should be at least area-preserving (da Vinci's rule), if not area-diminishing.

Vines and compound leaves can escape this trade-off because in both cases the xylem conduits are not significantly involved in structural support. Vines remain aloft by clinging to other plants, and compound leaves are supported largely by turgor pressure and non-vascular sclerenchyma or collenchyma. Accordingly, the vine and leaf data fall above the constant area curve in Figure 5B. These xylem networks are free to exploit the greater efficiency of high F in combination with near-optimal Murray tapering despite area-increasing branching of conduits. In contrast, the tree stem data generally lie below the constant area curve, consistent with the need to maintain area-preserving or even area-decreasing branching of xylem conduits. However, this mechanically "safe" structure comes at the price of reduced conducting efficiency.

Within the three tree species (Figure 5), the data indicate a trend toward higher F and greater efficiency moving from the conifer (*Abies concolor*), to a diffuse-porous angiosperm (*Acer negundo*) and finally to a ring-porous angiosperm (*Fraxinus pennsylvanica*). These data are consistent with the different velocity profiles between these tree types. Both the diffuse-porous and conifer species lie below the constant conduit area line (Figure 5B, equal Σr^2) with decreasing area and increasing velocities from trunk to twig. In contrast, the ring-porous species lies just above this constant area line, indicating constant or slightly decreasing velocity distally. The switch to

a decelerating velocity profile in ring-porous trees is thus a functional correlate of increasing conducting efficiency. The data predict that the velocity profiles of the xylem of vines and compound leaves should resemble that of the xylem of ring-porous trees, but with an even greater deceleration of sap velocity moving distally. However, we know of no velocity measurements with which to evaluate this prediction.

The trend toward greater efficiency in trees with ring-porous wood versus other trees is associated with a decrease in the percentage of xylem area occupied by xylem conduits. In conifers, conduits make up over 90% of the wood area, versus about 25% in diffuse-porous trees, and only about 10% in the xylem of ring-porous trees (McCulloh et al. 2004). This progressive decoupling of hydraulic and mechanical functions may leave the conduit network free to achieve area-preserving or even area-increasing conduit branching as required for maximum conducting efficiency, while the overall xylem area remains area-preserving or even area-diminishing for best mechanical support. This inference posits that the proportion of conducting area versus total xylem area will increase from trunk to twig in ring-porous trees, a trend opposite to assumption 6 for the WBE architecture.

Figure 5B poses a conundrum with respect to the tree stem data. Stems could maintain the same mechanically stable area-profile simply by shifting to the left on this graph while keeping the same position relative to the solid constant area curve (i.e., near the *Campsis radicans* (L.) Seem. ex Bur. vine stem data point). This would require increasing their taper and their F . Although this shift would find them relatively farther from the Murray optimum, it would nevertheless increase their conducting efficiency without altering the area profile. There are several possible adverse consequences with this configuration. Such high taper may be unsustainable in the highly branched shoot structure of trees. A taper of 0.7 (distal/proximal radius) for adjacent branch ranks, if sustained across 10 branch levels, results in a trunk vessel 25 times the diameter of a leaf vessel. Such large diameters may be developmentally impossible, either because of limits to cell size or because of limitations inherent in ring-like circumferential growth from a cambium (McCulloh et al. 2004). Even if such large vessels were developmentally possible, they may be mechanically vulnerable and certainly would be more vulnerable to freezing-induced cavitation (Davis et al. 1999, Pittermann and Sperry 2003), if not to cavitation induced by water stress (Sperry and Tyree 1990, Hargrave et al. 1994, Lo Gullo et al. 1995). In addition, high F in highly branched tree stems would decrease the number of vessels running in parallel in the trunk relative to the rest of the tree. Having fewer trunk vessels means less redundancy in the event of local dysfunction to the trunk network.

That vines generally have wider vessels than trees is consistent with their having greater taper and higher F . Mechanical vulnerability of large vessels would have little adaptive significance for vines, and many have anomalous cambial growth that may accommodate development of exceptionally large vessels. In addition, vine stems may be less branched than trees and hence would have less amplification of taper and furcation over multiple branch ranks.

Concluding perspectives on architectural patterns

Consideration of the energy minimization principle and Murray's law in the context of anatomy and mechanics provides new insight into the architectural patterns summarized in Table 1. The only valid explanation for why plants might follow da Vinci's rule of area-preserving branching may be that it sets the limit to a mechanically stable area-profile. Even better from the mechanical point of view would be area-diminishing branching (Keller and Niordson 1966), a pattern that may apply better to the trunk and its major branches below the crown (Shinozaki et al. 1964b). More precise measurements of how total stem area, xylem area and conduit area change with branching in different plant functional types would be useful in the analysis of the effects of area profile on mechanical stability.

Hydraulically, there seems to be no reason to follow da Vinci's rule, because greater conductance for a given vascular investment can be achieved by area-increasing branching of xylem conduits (Figure 5B). The data in Figure 1 show a suggestive increase in area of the minor twigs, but because the data are for total stem area, it is unclear whether this is a result of increased conduit area relative to other tissues. Certainly the vines and compound leaves measured show area-increasing conduit branching (Figure 5, McCulloh et al. 2003). Free-standing trees may follow da Vinci's rule because it represents the best compromise between conflicting mechanical versus hydraulic optima.

The three patterns of conductivity, conduit diameter and sap velocity (Table 1, Figures 2–4) all are consistent with an energy-minimizing hydraulic architecture subject to mechanical constraints. A proportional decline in conductivity and conduit diameter from the trunk to twigs confers greater hydraulic efficiency (Figure 5). The shift from a distally accelerating velocity profile in conifer and diffuse-porous trees to a distally decelerating velocity profile in ring-porous trees is indicative of greater conducting efficiency in ring-porous wood. It remains to be seen if more extensive sampling across these contrasting wood types (including vines) reinforces these contrasting patterns in sap velocity.

The relationship between conductivity ratio and taper (Figures 4 and 5) is conceptually useful for distinguishing architecturally different xylem types and comparing their structural relationships with area profile and F . For example, Figure 4 provides a context for comparing the WBE architecture with the many alternatives. This type of plot also provides a relatively quick method of assessing the architectural type of real plants. Measuring leaf-specific conductivities of different branch ranks is relatively simple, and as long as the measured conductivity remains constantly proportional to the Hagen-Poiseuille value (Sperry et al. 2005), the measured conductivity ratio will bear the same relationship to conduit taper as calculated for the various curves in Figures 4 and 5. Measuring vessel diameter distributions is also straightforward. As long as the distributions compared are of similar shape, the taper of the population can be estimated from the mean diameter across ranks. The limited data plotted in Figure 5 need to be

confirmed with more extensive measurements made specifically for this type of analysis.

Our examination of the WBE model and the application of Murray's law to plants suggests that a comprehensive theoretical model of hydraulic efficiency has yet to be established. The WBE model, though properly ambitious in treating optimal conduit taper, branching architecture and mechanics, fails by ignoring anatomical and morphological realities such as variable F and velocity profiles, apical dominance and other features. Murray's law is too restrictive because it only solves for optimal taper for a given branching architecture and F . It does not solve for the optimal architecture where taper, branching pattern and F are all free to vary, nor does it consider mechanics. Nevertheless, both exercises have provided new insights and should help to structure further work.

The significance of any energy-minimizing design lies in minimizing the cost of transpiration to the plant. Long ago, Cowan (1982) recognized the importance of this cost for determining the optimal stomatal conductance of plants. Knowing the cost of transpiration also allows water-use efficiency, the quantity of CO_2 assimilated per quantity of H_2O transpired, to be converted to a more meaningful ratio: quantity of CO_2 assimilated per quantity of CO_2 expended to construct and support the transpiration stream. The latter more directly measures the carbon acquisition versus water loss dilemma confronted by land plants.

Accounting for the cost of transpiration is complex, and Givnish's (1986) work is the only thorough effort we know of after Cowan (1982). Although both studies were commendable in their scope, they lacked many parameters of water relations and hydraulic architecture. A challenge for the future is to apply the progress in plant hydraulics towards a cost-benefit analysis of supplying the transpiration stream (Mencuccini 2003).

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References

- Alemayehu, D., D.M. Engle, R.F. Wittwer and S. Anderson. 1998. Pattern of growth of sapwood, heartwood, and stem volume of open-grown eastern redcedar in grasslands. *South. J. Appl. For.* 22: 169–174.
- Andrade, J.L., F.C. Meinzer, G. Goldstein, N.M. Holbrook, J. Cavellier, P. Jackson and K. Silvera. 1998. Regulation of water flux through trunks, branches, and leaves in trees of a lowland tropical forest. *Oecologia* 115:463–471.
- Barnard, H.R. and M.G. Ryan. 2003. A test of the hydraulic limitation hypothesis in fast-growing *Eucalyptus saligna*. *Plant Cell Environ.* 26:1235–1245.
- Cochard, H., M. Peiffer, K. Le Gall and A. Granier. 1997. Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L.: impacts on water relations. *J. Exp. Bot.* 48:655–663.

- Cowan, I.R. 1982. Regulation of water use in relation to carbon gain in higher plants. *In* Transport in Plants. Vol. 2. Eds. U. Lüttge and M.G. Pitman. Springer-Verlag, Berlin, pp 589–613.
- Cruziat, P., H. Cochard and T. Ameglio. 2002. Hydraulic architecture of trees: main concepts and results. *Ann. For. Sci.* 59:723–752.
- Davis, S.D., J.S. Sperry and U.G. Hacke. 1999. The relationship between xylem conduit diameter and cavitation caused by freeze-thaw events. *Am. J. Bot.* 86:1367–1372.
- Dodds, P., D. Rothman and J. Weitz. 2001. Re-examination of the “3/4-law” of metabolism. *J. Theor. Biol.* 209:9–27.
- Enquist, B.J. and K.J. Niklas. 2001. Invariant scaling relations across tree-dominated communities. *Nature* 410:655–660.
- Enquist, B.J., J.H. Brown and G.B. West. 1998. Allometric scaling of plant energetics and population density. *Nature* 395:163–165.
- Enquist, B.J., G.B. West, E.L. Charnov and J.H. Brown. 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401:907–911.
- Enquist, B.J., G.B. West and J.H. Brown. 2000. Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. *In* Scaling in Biology. Eds. J.H. Brown and G.B. West. Oxford University Press, Oxford, pp 167–198.
- Ewers, F.W. and M.H. Zimmermann. 1984. The hydraulic architecture of eastern hemlock (*Tsuga canadensis*). *Can. J. Bot.* 62: 940–946.
- Gartner, B.L. 1995. Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. *In* Plant Stems: Physiological and Functional Morphology. Ed. B.L. Gartner. Academic Press, New York, pp 125–149.
- Givnish, T.J. 1986. Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. *In* On the Economy of Plant Form and Function. Ed. T.J. Givnish. Cambridge University Press, Cambridge, pp 171–213.
- Hacke, U.G., J.S. Sperry, W.P. Pockman, S.D. Davis and K.A. McCulloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461.
- Hargrave, K.R., K.J. Kolb, F.W. Ewers and S.D. Davis. 1994. Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). *New Phytol.* 126:695–705.
- Hazenberg, G. and K.C. Yang. 1991. Sapwood/heartwood width relationships with tree age in balsam fir. *Int. Assoc. Wood Anat. Bull.* 12:95–99.
- Horn, H.S. 2000. Twigs, trees and the dynamics of carbon in the landscape. *In* Scaling in Biology. Eds. J.H. Brown and G.B. West. Oxford University Press, Oxford, pp 199–220.
- Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol.* 19:165–172.
- Hubbard, R.M., V. Stiller, M.G. Ryan and J.S. Sperry. 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell Environ.* 24:113–121.
- Huber, B. 1928. Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanzen. *Jahrb. wiss. Bot.* 67:877–959.
- Huber, B. and E. Schmidt. 1936. Weitere thermo-elektrische Untersuchungen über den Transpirationsstrom der Baume. *Tharandt Forst Jb.* 87:369–412.
- James, S.A., F.C. Meinzer, G. Goldstein, D. Woodruff, T. Jones, T. Restom, M. Mejia, M. Clearwater and P. Campanello. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134:37–45.
- Keller, J.B. and F.I. Niordson. 1966. The tallest column. *J. Math. Mech.* 16:433–446.
- Koch, G.W., S.C. Sillett, G.M. Jennings and S.D. Davis. 2004. The limits to tree height. *Nature* 428:851–854.
- Kozłowski, J. and M. Konarzewski. 2004. Is West, Brown and Enquist’s model of allometric scaling mathematically correct and biologically relevant? *Funct. Ecol.* 18:283–289.
- Lemoine, D., H. Cochard and A. Granier. 2002. Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L.): evidence for a stomatal control of xylem embolism. *Ann. For. Sci.* 59: 19–27.
- Lo Gullo, M.A., S. Salleo, E.C. Piaceri and R. Rosso. 1995. Relations between vulnerability to xylem embolism and xylem conduit dimensions in young trees of *Quercus cerris*. *Plant Cell Environ.* 18: 661–669.
- McCulloh, K.A. and J.S. Sperry. 2005. The evaluation of Murray’s law in *Psilotum nudum* (Psilotaceae), an analogue of ancestral vascular plants. *Am. J. Bot.* In press.
- McCulloh, K.A., J.S. Sperry and F.R. Adler. 2003. Water transport in plants obeys Murray’s law. *Nature* 421:939–942.
- McCulloh, K.A., J.S. Sperry and F.R. Adler. 2004. Murray’s law and the mechanical versus hydraulic functioning of wood. *Funct. Ecol.* 18:931–938.
- McDonald, K.C., R. Zimmermann and J.S. Kimball. 2002. Diurnal and spatial variation of xylem dielectric constant in Norway spruce (*Picea abies* [L.] Karst.) as related to microclimate, xylem sap flow, and xylem chemistry. *IEEE Trans. Geosci. Remote Sens.* 40: 2063–2082.
- McMahon, T.A. 1973. Size and shape in biology. *Science* 179: 1201–1204.
- Meinzer, F.C. and D.A. Grantz. 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant Cell Environ.* 13:383–388.
- Meinzer, F.C., G. Goldstein, P. Jackson, N.M. Holbrook, M.V. Gutierrez and J. Cavelier. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. *Oecologia* 101: 514–522.
- Mencuccini, M. 2003. The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant Cell Environ.* 26:163–182.
- Mencuccini, M. and J. Grace. 1996. Hydraulic conductance, light interception and needle nutrient concentration in Scots pine stands and their relations with net primary productivity. *Tree Physiol.* 16: 459–468.
- Murray, C.D. 1926. The physiological principle of minimum work. I. The vascular system and the cost of blood volume. *Proc. Natl. Acad. Sci. USA* 12:207–214.
- Niklas, K.J. and B.J. Enquist. 2002. On the origin of vegetative biomass partitioning of seed plant leaves, stems, and roots. *Am. Nat.* 159:482–497.
- Niklas, K.J. and B.J. Enquist. 2003. An allometric model for seed plant reproduction. *Evol. Ecol. Res.* 5:79–88.
- Niklas, K.J., J.J. Midgley and B.J. Enquist. 2003. A general model for the mass–growth–density relations across tree-dominated communities. *Evol. Ecol. Res.* 5:459–468.
- Paques, L. 2001. Genetic control of heartwood content in larch. *Silvae Genet.* 50:69–75.
- Perez Cordero, L.D. and M. Kanninen. 2003. Heartwood, sapwood and bark content, and wood dry density of young and mature teak (*Tectona grandis*) trees grown in Costa Rica. *Silva Fenn.* 37: 45–54.
- Pittermann, J. and J.S. Sperry. 2003. Tracheid diameter is the key trait determining the extent of freezing-induced embolism in conifers. *Tree Physiol.* 23:907–914.

- Richter, J.P. 1970. The notebooks of Leonardo da Vinci (1452-1519), compiled and edited from the original manuscripts. Dover, New York, 499 p.
- Rigling, A., O. Braker, G. Schneider and F. Schweingruber. 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). *Plant Ecol.* 163:105–121.
- Rust, S. and A. Roloff. 2002. Reduced photosynthesis in old oak (*Quercus robur*): the impact of crown and hydraulic architecture. *Tree Physiol.* 22:597–601.
- Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth: what keeps trees from growing beyond a certain height? *Bioscience* 47:235–242.
- Saliendra, N.Z., J.S. Sperry and J.P. Comstock. 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. *Planta* 196: 357–366.
- Schäfer, K.V.R., R. Oren and J.D. Tenhunen. 2000. The effect of tree height on crown level stomatal conductance. *Plant Cell Environ.* 23:365–377.
- Schulte, P.J., A.C. Gibson and P.S. Nobel. 1987. Xylem anatomy and hydraulic conductance of *Psilotum nudum*. *Am. J. Bot.* 74: 1438–1445.
- Sellin, A. 1994. Sapwood–heartwood proportion related to tree diameter, age, and growth rate in *Picea abies*. *Can. J. For. Res.* 24: 1022–1028.
- Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964a. A quantitative analysis of plant form—the pipe model theory: I. Basic analysis. *Jpn. J. Ecol.* 14:97–105.
- Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964b. A quantitative analysis of plant form—the pipe model theory: II. Further evidence of the theory and its implications in forest ecology. *Jpn. J. Ecol.* 14:133–139.
- Sperry, J.S. and M.T. Tyree. 1990. Water-stress-induced xylem embolism in three species of conifers. *Plant Cell Environ.* 13:427–436.
- Sperry, J.S. and W.T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* 16:279–287.
- Sperry, J.S., U.G. Hacke and J.K. Wheeler. 2005. Comparative analysis of end wall resistivity in xylem conduits. *Plant Cell Environ.* In press.
- Tyree, M.T. 2003. Hydraulic limits to tree performance: transpiration, carbon gain, and growth in trees. *Trees* 17:95–100.
- Tyree, M.T. and F.W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. *Tansley Review No. 34. New Phytol.* 119:345–360.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* 88:574–580.
- Tyree, M.T., M.E.D. Graham, K.E. Cooper and L.J. Bazos. 1983. The hydraulic architecture of *Thuja occidentalis*. *Can. J. Bot.* 61: 2105–2111.
- Tyree, M.T., D.A. Snyderman, T.R. Wilmot and J.L. Machado. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*). *Plant Physiol.* 96:1105–1113.
- West, G.B., J.H. Brown and B.J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276: 122–126.
- West, G.B., J.H. Brown and B.J. Enquist. 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400: 664–667.
- West, G.B., J.H. Brown and B.J. Enquist. 2000. The origin of universal scaling laws in biology. *In Scaling in Biology*. Eds. J.H. Brown and G.B. West. Oxford University Press, Oxford, pp 87–112.
- Williams, M., E.B. Rastetter, D.N. Fernandes et al. 1996. Modelling the soil–atmosphere continuum in a *Quercus–Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell Environ.* 19: 911–927.
- Yang, K.C., Y.S. Chen, C. Chiu and G. Hazenberg. 1994. Formation and vertical distribution of sapwood and heartwood in *Cryptomeria japonica* D. Don. *Trees* 9:35–40.
- Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40:513–527.
- Zimmermann, M.H. 1978a. Hydraulic architecture of some diffuse-porous trees. *Can. J. Bot.* 56:2286–2295.
- Zimmermann, M.H. 1978b. Structural requirements for optimal water conduction in tree stems. *In Tropical Trees as Living Systems*. Eds. P.B. Tomlinson and M.H. Zimmermann. Cambridge University Press, Cambridge, pp 517–532.
- Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, 143 p.
- Zotz, G., S. Patino and M.T. Tyree. 1997. Water relations and hydraulic architecture of woody hemiepiphytes. *J. Exp. Bot.* 48: 1825–1833.