Tapered conduits can buffer hydraulic conductance from path-length effects

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Summary The model of West, Brown and Enquist showed that total hydraulic resistance in trees can be independent of path length, provided that vascular conduits taper sufficiently. This model assumes that the tree branch network is volume-filling, so that segment lengths increase exponentially from tree top to base. We show that partial buffering of hydraulic resistance from path-length effects can occur even for moderate tapering, and that this effect is stronger when segment lengths are fixed. Still needed are measurements of tracheary size and hydraulic resistance designed to test this model, which shows how hydraulic limitation of tree height growth may be mitigated.

Keywords: conduit diameter, hydraulic limitation, hydraulic resistance, tree height.

Maggs (1964) suggested that excessive distances between shoot apices and roots prohibited efficient transport between these parts, causing a decline in growth, and the theoretical analyses of Friend (1993) provided limited support for this idea. Recently, Ryan and Yoder (1997) advocated increased hydraulic resistance with increasing path length as the most promising explanation for the cessation of tree height growth with age. In a critical review, however, Becker et al. (2000) concluded that there was little evidence to support the hypothesis that hydraulic resistance increases with increasing tree height. They suggested that leaf:sapwood area ratio, rather than path length, may dominate in determining whole-plant conductance (reciprocal of resistance).

A central tenet of Ryan and Yoder’s (1997) version of the “hydraulic limitation” hypothesis is that the increase in xylem path length with tree height leads to an increase in total hydraulic resistance owing to friction. Although this is the expectation when conduits have constant diameter, it has been shown theoretically that if conduits taper sufficiently, then the total resistance of a tube (representing a linear series of vessels) from the base of the trunk to a petiole becomes independent of total tube length (Enquist et al. 1999, West et al. 1999).

The diameters of tracheids and vessels increase basipetally in both trunks and branches, usually being greatest in roots (Zimmermann 1983). The potential consequence of this tapering is to ensure a comparable supply of resources to all leaves, regardless of their height on the plant (Enquist et al. 1999, West et al. 1999).

Our objective was to illustrate the relationship between resistance and path length for various degrees of taper to stimulate interest in testing the model of West et al. (1999), which has important implications for the current debate concerning hydraulic limitation of tree height growth. The original theoretical model specified that tree branches constitute a volume-filling network, which means that branch segments decrease in length exponentially toward the tree top (Enquist et al. 1999, West et al. 1999). In other words, each branch segment is a constant multiple of its predecessor’s length for specified parameters. We show that the independence of hydraulic resistance from path-length effects also applies to a simpler (though not necessarily more realistic) branching architecture, thus demonstrating that the model’s result does not depend on a fractal-like organization of branch segment lengths.

The resistance, $R_k$, of a single conduit within any stem segment (k) is given by the Hagen-Poiseuille formula:

$$R_k = \frac{8\eta l_k}{\pi a_k^4},$$  \hspace{1cm} (1)

where $\eta$ is dynamic viscosity (1.0 × 10^{-6} m^2 s^{-1} for water at 20 °C), $l_k$ is length of the conduit in segment k, and $a_k$ is the conduit’s radius (Nobel 1983, Niklas 1992). This formula applies to capillary flow and neglects the substantial contribution (50–70%) of pit membrane resistance to total resistance, which fortunately does not affect relative comparisons of resistance (Nobel 1983, Niklas 1992).

The total resistance of a tube running from the trunk base (Level 0) to a petiole (Level N) through successive stem segments is defined as $R_{TOT} = \Sigma_{k=0}^{N} R_k$. West et al. (1999) showed that for $a > 1/6$, $R_{TOT} \approx R_N / [1 - n^{1/3} - 2^a]$, where $R_N$ is resistance of a conduit in the petiole, $n$ is the number of daughter branches per parent branch (2 in most plants and always 2 throughout this paper), and $a$ specifies the degree of tapering.
as the ratio of conduit radii $a_{k+1}/a_k = n^{-\tau/2}$. In the model of West et al. (1999), conduits are of uniform diameter within a segment, but conduit diameter increases basipetally from one segment to the next. Details of this derivation may be found in West et al. (1999). Briefly, the result depends on the assumption that $\tau$ is independent of $k$, which then specifies the scaling of branch radii and conduit radii, and that the branch network is volume-filling, which in turn specifies the scaling of branch lengths. The important consequence is that, because $R_N$ is invariant, $R_{TOT}$ is also constant and independent of total tube length or plant height (Enquist et al. 1999, West et al. 1999).

The general expression for $R_{TOT}$ can be simplified from that of the original formulation (West et al. 1999), while retaining all of that model’s features and assumptions, to illustrate better the dependence on total tube length $l_{TOT}$. Both $R_{TOT}$ and $l_{TOT}$ can be expressed, without approximation, in dimensionless form as:

$$Y = R_{TOT}/R_N = \left[\frac{n^{(N+1)/(N-\frac{3}{2})-1}}{n^{(N+1)/(N-\frac{3}{2})-1}}\right]^{\frac{1}{N+1}}, \quad \widetilde{\alpha} \neq 1/6,$$  

(2a)

and

$$X = l_{TOT}/l_N = [n^{(N+1)/(\frac{3}{2})-1}]/[n^{(N+1)/(\frac{3}{2})-1}],$$  

(2b)

If we fix $n = 2$ and define $\delta = 1 - \frac{1}{6}a$ and $\phi = \frac{n^{\delta}}{3}-1$, then eliminating $N$ between Equations 2 and 3 yields the desired relationship between $Y$ and $X$ in the form:

$$\phi Y = (1+cX)^{\delta} - 1, \quad \delta \neq 0,$$  

(4)

where $c = 2^{1/3} - 1 = 0.260$.

The form of Equation 4 indicates that, if the degree of taper $\widetilde{\alpha} = 0$ ($\delta = 1$), the total hydraulic resistance increases linearly with total path length. For $0 < \widetilde{\alpha} < 1/6$ ($1 > \delta > 0$), the total resistance continues to increase with path length, although progressively less rapidly. The limiting case occurs at $\widetilde{\alpha} = 1/6$ ($\delta = 0$), when it can be shown from Equation 2b that the increase in $Y$ with $X$ is logarithmic.

On the other hand, when $\widetilde{\alpha} > 1/6$ ($\delta < 0$), Equation 4 can be written as: $\phi Y = 1 - 1/(1+cX)^{\phi}$. This shows that, for large X, the total resistance (relative to $R_N$) approaches an asymptotic value of $1/\phi l = (1-n^{\frac{\delta}{3}})^{-1}$ as total path length increases. This behavior is indicated in Figures 1 and 2, obtained by direct calculation of the series (Equation 1).

Calculation of $R_{TOT}$ by summation of Equation 1, applied to successive segments from tree top to base for realistic values of conduit length and radius in the petiole, illustrates that although $\widetilde{\alpha} > 1/6$ represents the threshold degree of tapering for total resistance to become virtually independent of path length, substantial independence is possible for $\tau$ as small as 0.1 (Figure 1). This effect is more evident when segment lengths are fixed (Figure 2), rather than being constrained to increase exponentially in a basipetal direction according to the fractal-like, volume-filling model. It can be shown mathematically that this is a general result for segments of arbitrary fixed length if $\widetilde{\alpha} > 0$. For other cases of conduit-length ratios (i.e., $l_{k+1}/l_k = n^{-b}$, for $0 < b < 1/3$), the approach to the asymptotic resistance is intermediate in rapidity to the fractal-like and fixed segment-length models for any specified $\widetilde{\alpha} > 1/6$.

Figure 1. Relationship between total hydraulic resistance and total tube length for various degrees of tube taper $\tau$ (specified in the right margin). All plots are for $l_N = 0.05$ m and $a_N = 10 \mu$m, the length and radius, respectively, of the ultimate (petiolar) conduit. Segment length (horizontal spacing between points) increases exponentially from tree top to base (left to right), according to a volume-filling model (Enquist et al. 1999, West et al. 1999); i.e., $l_{k+1}/l_k = n^{(N-k)/3}$, where the number of daughter branches $n = 2$. Conduit radii in the basal segments were 10, 14, 20, 32 and 80 $\mu$m, respectively, for tubes with increasing degree of taper. These are realistic values for diffuse- and ring-porous trees (Nobel 1983).

Figure 2. Relationship between total hydraulic resistance and total tube length for various degrees of tube taper $\tau$ (specified in right margin) when segment length $l_k$ is fixed at 1 m and conduit radius in the ultimate segment $a_N = 10 \mu$m.
Because hydraulic resistance is inversely proportional to the fourth power of conduit radius, but only linearly dependent on path length (Equation 1), sufficiently large increases in conduit radius can offset path-length effects. If resistance owing to non-laminar flow increases in approximately linear fashion with path length, this would displace the curves in Figures 1 and 2 upward, without substantially altering their shapes. Thus, conduit tapering would still buffer hydraulic resistance from path-length effects. However, even for \( \alpha > 1/6 \), hydraulic resistance is predicted to increase slightly with path length in small branches with fine conduits, and ontogenetically from sapling to adult (Figures 1 and 2).

Suitable data for estimating \( \alpha \) are limited because most investigators have not measured conduit diameters in successive stem segments. From the ratios of the radii of the widest tracheids in the outer growth ring of a trunk–branch junction in eastern hemlock (Tsuga canadensis (L.) Carr.) (Ewers and Zimmermann 1984, Table 1), we calculated an \( \alpha \) of 0.25, which would be more than sufficient to ensure the independence of total hydraulic resistance from effects of path length. Measurements of hydraulic resistance and branch and conduit dimensions designed to test the applicability of the model proposed by Enquist et al. (1999) and West et al. (1999) are needed. Empirical verification of the model would be facilitated if conduit taper could be expressed as a function of path length, rather than stem segments.

The theoretical maximum height of trees is about 100 m, but this estimate is very sensitive to petiolar parameters such as radius and total number and radii of conduits. Also, the degree of conduit taper \( \alpha \) must approach its optimal minimum value of 1/6 (Enquist et al. 1999, West et al. 1999). Failure of trees to reach the maximum height predicted from their petiolar parameters and \( \alpha \) would imply that either the model is incomplete (e.g., in failing to account for the propensity of wide conduits to embolization or the resistances attributable to non-laminar flow), or that tree height growth is not ultimately limited by hydraulic path-length effects.

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References