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Hydraulic constraints in the functional scaling of trees

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Summary I conducted a literature survey to assess the available information on relationships between size—expressed in terms of diameter and dry biomass—and hydraulic efficiency of woody structures at different scales, from stem segments to whole trees. Three data sets were constructed: the first described the relationship between segment diameter and hydraulic conductivity (k_h; kg m s^{-1} MPa^{-1}) in four species; the second, for the same four species, described the intraspecific trajectories of change in total hydraulic conductance (G; kg s^{-1} MPa^{-1}) during ontogeny, i.e., from saplings to mature trees, thereby providing a comparison between allometric scaling laws at the scales of segments and whole trees; the third comprised pooled means for nine species that described the interspecific trajectory of change in G with tree size.

The scaling coefficients obtained were compared with predictions made with an architectural fractal-like model incorporating tissue-specific hydraulic architecture parameters (West et al. 1999). When data on segment k_h were examined, the fractal-like model closely predicted the scaling of k_h with segment diameter in four species. However, the model failed to predict accurately in all species the intraspecific scaling at the branch and whole-tree levels, and consistently overestimated the scaling coefficients. The results suggest that ontogenetic changes in tree size during the life cycle of one tree may result in tradeoffs between optimal hydraulic supply to the existing leaf area and maintenance costs of the supporting xylem tissue. The model of West et al. (1999) may be useful for understanding broad interspecific patterns, but not for understanding more subtle ontogenetic changes.

Keywords: allometry, biomass allocation, fractals, hydraulic conductance, xylem.

Introduction

Since plants began colonizing land about 400 million years ago, an extraordinary variety of life forms has evolved. Fossil evidence shows that plants have achieved progressively greater size (e.g., Niklas 1994); tree species achieving heights in excess of 100 m illustrate this evolutionary trend. Limits to height growth may emerge because of requirements for mechanical support of stems and for water transport from the soil to the leaves. The existence of tall trees indicates how far plants have succeeded in circumventing these height constraints, although it is unclear whether this has caused tradeoffs.

Whereas quantitative data comparing the mechanical and hydraulic properties of extant and extinct phyla are limited (e.g., Raven 1977, Niklas 1994), ontogenetic changes (i.e., from seedling to mature tree) in hydraulic and biomechanical parameters are now being determined (e.g., Pothier et al. 1989, Yang and Tyree 1994, Mencuccini et al. 1997). During growth, tree structural parameters change considerably. For instance, the ratios of leaf area to leaf mass, leaf to root area, or leaf to xylem sapwood area have been reported to change significantly as trees mature and age (e.g., Mencuccini and Grace 1996*a*, Niinemets 1997*a*, 1997*b*, Brouat et al. 1998, Vanninen and Mäkelä 1999). Functional parameters such as stomatal conductance, leaf-level photosynthetic rates and ^{13}C discrimination during photosynthesis also change considerably with age (e.g., Yoder et al. 1994), thus raising the question of what type of relationship, if any, exists between changes in structural and functional properties as trees age.

The study of how plant properties change as a function of size is known as allometry (e.g., Broad 1998), although the terms functional allometry (Gould 1966) and scaling (Niklas 1994) have also been used where the emphasis was on the functional nature of the relationships studied. The study of the scaling of plant properties with size has recently attracted much interest because current mechanistic models of tree and forest stand growth are, almost without exception, based on empirical allometric coefficients rather than on the mechanistic description of partitioning processes or on predictions based on optimal allocation theories. As such, they are strongly limited in their predictive scope.

Recently, however, a few exceptions have emerged. For instance, Magnani et al. (2000) have proposed that trees allocate carbon to leaves or sapwood in the most economical (i.e., optimal) way. When leaves are produced in excess, the xylem conductive capacity to each leaf decreases, thereby increasing the risk of hydraulic failure. As a result, more xylem is produced to restore the previous optimal equilibrium, with root sapwood preferred over shoot sapwood if the return in overall tree conductive capacity is greater.

Following an allometric scaling approach, West et al. (1999) proposed that plant foliage display and the vascular system can be described by means of fractal geometry. By assuming that natural selection acts on plants to maximize surface area and minimize internal transport distance, they showed that the branching networks linking xylem vessels from trunks to petioles achieve optimality. They were able to predict the scaling of many functional and structural properties as a function of size. In other papers (West et al. 1997, Enquist et al. 1998), these authors claimed that their model responded to the requirements of a universal scaling law valid for all living organisms, the so-called "quarter-power" law. The approach proposed by West et al. (1999) has many merits. It describes the plant's hydraulic system in a more realistic fashion than the pipe model theory (Shinozaki et al. 1964), because fundamental details such as the complexity of branching and the systematic differences observed in xylem anatomy between different plant organs (vessel or tracheid diameters frequently tend to increase systematically from branches to stems to roots) are retained. However, whether this model will be of use to forest ecologists and plant physiological ecologists is still uncertain. Crucial tests of the robustness of this theory against independently collected data have yet to be performed. Initial tests were attempted by Becker et al. (2000) and Becker and Gribben (2001), who compared the scaling factors predicted by the model of West et al. (1999) with a published data set (Zimmermann 1978) describing changes in vessel diameter with height above ground. However, the few plants studied by Zimmermann (1978) were only 6–9 m tall, which limited the conclusions that could be reached about scaling with plant size.

The fractal geometry model was also tested against published data by F. Magnani et al. (IMGPF-CNR, Florence, Italy, unpublished results). They concluded that vessel tapering (i.e., the systematic increase in vessel diameter from branches to roots) was unlikely to be constant during tree growth, as assumed by West et al. (1999).

Here, I present an overview of the literature on tree hydraulic conductance and the relationship between hydraulic conductance and biomass allocation. First, I present results showing how aboveground hydraulic conductance scales with plant size across extant woody phyla, and how it scales with plant size within species during the ontogenetic transition from seedlings to mature trees. These data are then used to discuss the implications of the model of West et al. (1999).

Theory

The biomass in water transport tissues can yield different hydraulic returns depending on how allocation to different organs takes place. For instance, assume a simplified one-dimensional unbranched catena of whole-plant hydraulic conductance (G; kg s^{-1} MPa^{-1}). Hydraulic conductance is operationally defined with the Ohm's law analogy as:

$$G = \frac{F}{\Delta P}, \tag{1}$$

where F is flux of liquid water in wood xylem and ΔP is the pressure drop driving water flux.

Hydraulic conductivity of individual stem segments of unitary length (k_h; kg m s^{-1} MPa^{-1}) and specific conductivity (or permeability, k_s; kg m^{-1} s^{-1} MPa^{-1}) can then be derived from Darcy's law as:

$$k_h = A_{sw} k_s = \frac{\eta l G}{\rho_w}, \tag{2}$$

where ρ_w is water density, A_{sw} is conducting sapwood area, η is dynamic water viscosity and l is path length.

If all new biomass is used to increase the length of the catena with no increase in diameter (d), then the relationship between biomass (M) and G will take the following form, assuming that k_s does not change during growth:

$$G \propto M^{-1}. \tag{3}$$

If, instead, all new biomass is used to increase the cross-sectional area with no increase in length, then:

$$G \propto M^{1} \tag{4a}$$

or

$$G \propto d^{2}, \tag{4b}$$

assuming no loss to heartwood.

Finally, growth in diameter may compensate for growth in height, so that no change in G over time is apparent:

$$G \propto M^{0} \tag{5a}$$

or

$$G \propto d^{0}. \tag{5b}$$

These three scenarios illustrate possible extremes in scaling relationships between hydraulic properties and physical dimensions of trees. They are realistic only in that analogous situations may occur in real trees. For instance, the first scenario may occur in a plant competing with its neighbors in height growth and experiencing no increase in leaf area over time, with the result that there is a continuous decline in water supply capacity to a fixed amount of foliage. The second scenario may entail a continuous increase in leaf area over time, but at the cost of no height growth. In the third scenario, height growth occurs without an increase in leaf area, and the hydraulic supply to the existing foliage remains constant. Because we have assumed constant k_s, in all cases the scaling of k_h with segment diameter (D) will be:

$$k_h \propto D^{2}. \tag{6}$$

A number of factors are unaccounted for in this simplistic analysis. First, k_s normally increases during growth as a result of increases in tracheid or vessel diameter and length. This results in radial changes in anatomical properties from pith to bark, rather than constant cross-sectional values. Second, sapwood area is gradually lost to heartwood during growth. Third, whereas a tree is a highly complex architectural object, the previous analysis simplified its representation to that of a single unbranched (and untapered) resistor. Finally, there are systematic differences in anatomical features among plant organs (branches, stems, roots) that are likely to determine, at least partially, overall plant hydraulic efficiency (e.g., Tyree and Ewers 1991, West et al. 1999, Comstock and Sperry 2000).

Nonetheless, these expressions are useful because they give possible boundary values for the allometric scaling of hydraulic properties. This may help in understanding the range of variability expected in the scaling coefficients when more sophisticated models are employed. For instance, the scaling of G against M should be expected to range, at most, between –1 and +1, and more likely, between 0 and +1, i.e., a rather narrow range.

As described in the Introduction, West et al. (1999) recently proposed a model based on fractal geometry to describe the plant vascular system (cf. Becker et al. 2000 and F. Magnani et al., unpublished data, for further details on applications to trees). The model makes predictions about the scaling of plant hydraulic characteristics with M and D, based on the assumption that scaling of morphological features (such as branch length and diameter) and anatomical features (such as vessel diameter) follow stationary laws (i.e., the allometric law is identical for all branches, independent of branching order or size).

According to their model, k_h should scale with segment mass (M) as:

$$k_h \propto M^1. \tag{7a}$$

Whole-plant hydraulic conductance should instead scale as (Enquist et al. 2000):

$$G \propto M^{3/4} \propto M^{0.750}, \tag{8a}$$

predicting the well-known "quarter-power" law. The same relations could be expressed as a function of diameter:

$$k_h \propto D^{8/3} \propto D^{2.667}, \tag{7b}$$

because of the progressive increase in tracheid or vessel diameter with increases in cross-sectional area (i.e., D^2), despite heartwood formation, and:

$$G \propto D^{2.00}, \tag{8b}$$

i.e., the progressive increase in tracheid or vessel size with cross-sectional area perfectly counteracts the progressive increase in path length. In other words, G is simply a function of the increasing cross-sectional area. It should be noticed that the model of West et al. (1999) makes no provision for differences in the hydraulic scaling against diameter of branches as opposed to trees. Instead, a common regression coefficient is anticipated. Although the equations provided by West et al. (1999) are more complicated than Equations 7 and 8, the authors concluded that the latter should represent a good approximation of the system under typical parameter values. Equation 8b was not presented explicitly in West et al. (1999), but can be derived from the scaling of whole-branch resistance (Z_o) against plant mass (see above and Enquist et al. 2000, Table 1) and the reported scaling of diameter against plant mass.

Materials and methods

Literature-derived data sets

Data sets of whole-plant hydraulic conductance and plant biomass were obtained from the literature. The search was conducted in accordance with the following criteria: (1) hydraulic conductance was measured directly or estimated from whole-plant transpiration rates (or sap flow rates), transpiring leaf water potential and soil water potential (or pre-dawn leaf water potential); (2) for those data sets for which water potential measurements at the plant base were available, aboveground hydraulic conductance was calculated; in some instances, direct measurements of aboveground hydraulic conductance were also available; (3) plant biomass was measured either directly or from information available in the original publication and locally derived, species-specific allometric equations; and (4) for the aboveground hydraulic conductance data, aboveground biomass (leaf excluded) was calculated, and for the whole-plant hydraulic conductance data, whole-plant biomass was calculated as the sum of aboveground biomass (leaf excluded) and coarse root biomass.

Three major data sets were constructed. The first contained data on the relationships between D and k_h among four species (*Acer rubrum* L., *A. saccharum* Marsh., *Pinus sylvestris* L. and *P. banksiana* Lamb.). The second was based on data for the same four species and documented the intraspecific relationships between aboveground hydraulic conductance (the conductance of the entire pathway from the base of the bole to all the branch tips in parallel, G_{ag}; kg s^{-1} MPa^{-1}) and tree size-related variables (i.e., stem diameter and total biomass), thereby illustrating how these parameters vary during ontogeny (i.e., from saplings to adult trees). The results for jack pine (*P. banksiana*) should be considered with caution, because aboveground hydraulic conductance was estimated only from measurements in the trunk. For two of the four species, data were also available at the branch level, to characterize the allometric scaling of branch hydraulic conductance (the conductance of the pathway from the base of the branch to all the tips in parallel, G_{br}; kg s^{-1} MPa^{-1}) against branch basal diameter.

The third data set was based on data for nine species and documented the equivalent allomorphic (i.e., interspecific) relationship between G_{ag} and d. Because ontogenetic curves were not available for all species, only the largest individuals measured were considered for analysis. Frequently, this represented an average of several individuals for which physiological properties were measured in the field during one or more seasons. Because of the paucity of available data, no attempt was made to group results by phylogenetic distance or to stan-

Table 1. Summary of the data used to construct the relationships between whole-plant hydraulic conductance and tree physical variables (i.e., diameter and biomass). For the four species in bold face, intraspecific changes during ontogeny were documented separately, and the values given here refer to the largest trees measured.

Species	Leaf area (m^2)	Stem diameter (cm)	Height (m)	Aboveground biomass (g)	Aboveground sapwood biomass (g)	Total biomass (g)	Aboveground hydraulic conductance (g s^{-1} MPa^{-1})	Total hydraulic conductance (g s^{-1} MPa^{-1})	Reference
Pseudotsuga menziesii (Mirb.) Franco	256.86	50.00	55.00	1,680,636[1]	658,533[1]	2,184,827[1]	10.156[2]	4.4493	Waring and Running 1978
P. menziesii	45.50	16.12	14.20	81,311[3]	–	103,473[3]	–	2.7300	Borghetti and Vendramin 1987
Pinus banksiana	**57.75**	**34.54**	**15.30**	**433,574**[4]	**159,420**[4]	–	**1.754**	–	Pothier et al. 1989
Picea sitchensis (Bong.) Carrière	25.50	11.30	11.00	25,080[5]	23,292[5]	33,237[5]	0.202	0.1681	Hellqvist et al. 1974
Pinus sylvestris	**84.27**	**41.00**	**24.00**	**517,952**[6]	**299,232**[6]	**671,669**[6]	**5.277**	**4.7399**[7]	Mencuccini and Grace 1996*a*, 1996*b*
Pinus contorta Dougl. ex Loud.	2.32	4.40	4.50	3,500	3,500	4,600	–	0.0579	Running 1980*a*, 1980*b*
P. contorta	19.08[8]	16.80	–	55,501[9]	52,730[9]	–	–	0.630	Pataki et al. 2000
Acer rubrum	**104.50**	**17.81**	**20.00**	**107,683**[10]	**93,276**[10]	–	**4.688**	–	Yang and Tyree 1994
Acer saccharum	**88.70**	**16.65**	**20.00**	**164,342**[10]	**122,426**[10]	–	**3.486**	–	Yang and Tyree 1994
Malus pumila Mill.	4.14	–	3.00	24,429[11]	24,429[11]	30,857[11]	0.270	0.1338	Landsberg et al. 1975
M. pumila	0.53	6.00	1.00	350	350	700	0.025	0.0090[12]	Landsberg et al. 1976
Acer campestre L.	4.55	–	6.30	8,566	–	11,221	–	0.2203	Kuppers 1984, 1985
Quercus petraea L. ex Liebl.	19.53[13]	11.25	14.80	47,157[13]	–	51,882[13]	–	0.4874	Breda et al. 1993
Pinus ponderosa Dougl. ex P. Laws. & C. Laws. (old trees)	150	76.0	33.00	2,325,496[14]	945,792[14]	–	–	2.50	Yoder et al. 1994, Hubbard et al. 1999
P. ponderosa (young trees)	–	23.00	10.00	162,032.7[14]	100,812.6[14]	–	–	0.9891	Yoder et al. 1994, Hubbard et al. 1999

[1] Equations as in Grier and Logan (1977); [2] ratio of aboveground conductance to whole-plant conductance based on water potential rates measured in Bauerle et al. (1999); [3] estimates from site-specific allometry; [4] site-specific equations as in Hegyi (1972); [5] equations as in R.R. Matthews (Forest Research, Alice Holt, Farnham, U.K., personal communication); [6] site-specific equations as in Ovington (1957); [7] estimated from Roberts (1977) at the same site; [8] leaf/sapwood area ratio as in Kaufmann and Troendle (1981); [9] biomass equations as in Gholz et al. (1979); [10] equations as in Ribe (1973) (cited in Ter-Mikaelian and Korzukhin 1997) and Pausch et al. (2000) for *A. rubrum*, and Chapman and Gower (1991) for *A. saccharum*; [11] data for apple trees of same age and graft type and similar rootstock (J. Palmer, HortResearch, Motueka, New Zealand, personal communication); [12] estimated from data from Experiment 1, between 1200 and 1400 h; [13] site- and age-specific equations as in Breda et al. (1995) and Drexhage et al. (1999); [14] equations as in Gholz et al.

dardize the sample size for different phylogenetic groups. In some publications, the values were obtained directly by the authors, whereas in other publications the figures were analyzed with image analysis software (ImageTool, University of Texas) to estimate the original values.

All values of hydraulic conductance were corrected for hydrostatic gravitational effects by means of the known values of total plant height.

Table 1 lists the sources consulted to construct the three data sets, together with references to the appropriate literature for biomass estimation, when relevant.

Statistical analysis

Scaling of hydraulic properties against physical characteristics (i.e., diameter and biomass) of stem segments, branches or whole trees was obtained by regression analysis. Ordinary least squares (OLS) regression analysis is not the most appropriate method when Y and X are both random variates subject to error. Although the topic is far from resolved (e.g., Sokal and Rohlf 1995), when the estimation of the functional relationship between two covariates is sought, OLS coefficients are normally presented together with the coefficients of either major axis or reduced major axis (RMA) regression; the latter is preferred when the two covariates do not have the same units (but cf. Wolpoff 1985). The rationale for calculating OLS regression coefficients in this analysis is that one can consider the physical variables employed here (i.e., diameter and biomass) to be the causal variables determining xylem hydraulic conductance. Therefore, the regressions can be considered to be of the predictive type, for which OLS regression is the most appropriate approach (e.g., Sokal and Rohlf 1995).

Numerically, the regression coefficient of the RMA regression, b^{RMA}, will always be larger than the regression coefficient of OLS regression, b^{LS}, because it is obtained by dividing b^{LS} by Pearson's correlation coefficient (r).

The standard error, s_b, of b^{RMA} was calculated according to Ford and Corruccini (1985) as:

$$s_\mathrm{b} = \frac{s_\mathrm{Y}^2}{s_\mathrm{X}^2}\left(\frac{1-r^2}{N}\right), \qquad (9)$$

where s_Y^2 and s_X^2 are the standard deviations squared of Y and X, respectively, and N is sample size.

Tests of significance of the difference between two regression coefficients were performed with standard ANOVA for b^{LS} and by calculating the z-statistics, as in Ford and Corruccini (1985), for b^{RMA}:

$$z = \frac{b_1^{\mathrm{RMA}} - b_2^{\mathrm{RMA}}}{(s_1^2 + s_2^2)^{1/2}}, \qquad (10)$$

where b_i^{RMA} are the two RMA regression coefficients to be compared and s_i^2 are the standard deviations squared for the two groups. Differences between observed and theoretical regression coefficients were tested with a standard t-test, with the appropriate standard errors for b^{LS} and b^{RMA}.

Further tests were performed following the approach based on residual analysis outlined in Dodds et al. (2001). Briefly, to test whether a theoretical slope fitted the data correctly, a nonlinear regression approach was used to estimate, with maximum likelihood techniques, the intercept of the log–log line with slope equal to the expected theoretical slope. The residuals from this line of theoretical slope were then calculated and plotted against stem diameter or aboveground biomass. If the regression between independent variable and residuals was significant, it was concluded that the line of theoretical slope did not represent the best expression of the functional scaling between the variables. In all cases, this residual analysis approach gave the same results as the t-tests. Therefore, it will not be presented here.

Results

Intraspecific ontogenetic patterns

For Scots pine (*P. sylvestris*, Mencuccini and Grace 1996*b*) and red maple (*A. rubrum*, Yang and Tyree 1994), data were available relating k_h and G to the respective segment, branch or tree diameters (Figures 1a and 1b, respectively). In the case of Scots pine, the slope of the ontogenetic relationship between segment diameter and segment hydraulic conductivity (b = 2.55) was significantly higher than the slope of the regression between branch diameter and branch hydraulic conductance (b = 1.92, P < 0.001), and this slope was also significantly higher than the slope of the regression between tree diameter

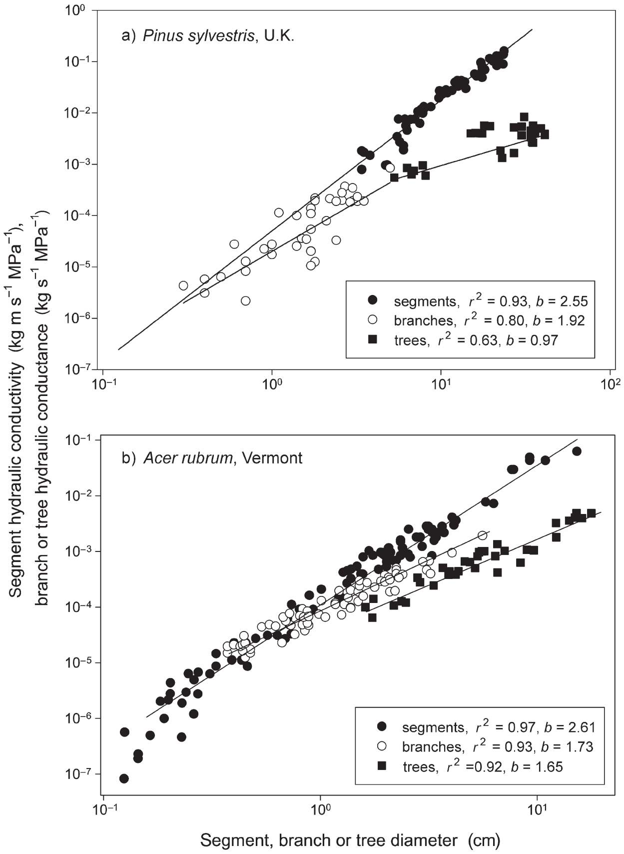

Figure 1. (a) Linear regressions of segment hydraulic conductivity (●), branch hydraulic conductance (○) or aboveground whole-tree hydraulic conductance (■) against segment, branch or tree diameter, respectively, for Scots pine in Thetford, U.K. (data from Mencuccini and Grace 1996*a*, 1996*b*). The slopes of the three regressions were significantly different from one another (P < 0.001). (b) Regressions as in (a) for red maple in Vermont, USA. The regression for segments had a significantly (P < 0.001) greater slope than the regressions for branches and trees. These last two did not have significantly different slopes (P > 0.05), but the intercepts were significantly different from one another (P < 0.001). Both data sets suggest that, at the segment scale, the scaling between dimensional and hydraulic properties was consistent with the requirements of an optimal architectural, fractal-like model. However, at the branch and tree scales, scaling of hydraulic conductance with diameter was too slow to be accounted for by this fractal-like model.

at breast height and whole-tree aboveground hydraulic conductance ($b = 0.97$, $P < 0.001$, Tables 2 and 3). In the case of red maple, the ontogenetic slope referred to segment conductivity was significantly higher ($P < 0.001$) than those referred to branch and whole-tree conductances (b = 2.61, 1.73 and 1.65 for segments, branches and trees, respectively), whereas the regression slopes referred to branch and whole-tree conductances were not significantly different from one another ($P > 0.05$, Tables 2 and 3). However, these last two regressions significantly differed in their regression intercepts, with the branch regression shifted upward compared with the whole-tree regression ($P < 0.01$, ANCOVA). In both cases, therefore, there was evidence that moving in scale upward from segments to trees resulted in substantial reductions in the relevant hydraulic term with respect to a constant diameter, especially for large diameters.

When the ontogenetic slopes were compared with the theoretical values expected from the West et al. (1999) fractal-like model (Table 2), significant disagreement was observed for all regressions except the segment regressions (expected value of $b = 2.67$; see Equation 7a) and the branch regression for Scots pine (expected value of $b = 2.00$; see Equation 8a). In other words, at the whole-tree scale and, for one species, at the branch scale as well, the model of West et al. (1999) significantly overestimated the ontogenetic slopes, whereas it appeared to accurately predict the regression slope at the segment scale. It should be noted that this conclusion holds whether one examines OLS or RMA regression coefficients (Table 2), suggesting that the interpretation is robust, despite doubts about what is the best method for estimating the functional relationships between covariates subject to random errors (cf. Mencuccini and Magnani 2000).

Pooling the available data for four species (sugar maple (*A. saccharum*), red maple, Scots pine and jack pine; Tyree and Sperry 1988, Pothier et al. 1989) at the segment and whole-tree levels (Figure 2) highlighted the similarities in the overall ontogenetic scaling patterns across species. In all cases, the ontogenetic scaling of hydraulic conductivity with segment diameter followed rather closely the theoretical predictions of the model of West et al. (1999) (i.e., $b = 2.67$; Equation 7a). In contrast, the ontogenetic scaling of aboveground hydraulic conductance with plant diameter, although it appeared to be similar across the four species, followed a different trajectory, with a common slope much lower ($P < 0.001$) than that predicted by the fractal model (i.e., $b = 2.00$; Equation 8a, Table 4).

Interspecific allomorphic patterns

When aboveground hydraulic conductance was plotted against stem diameter (Figure 3) or aboveground biomass (Figure 4) for seven species, significant log–log relationships were observed. The interspecific data set spanned more than one order of magnitude for diameter and more than three orders of magnitude for biomass, i.e., more than half the span of the ontogenetic data sets from saplings to mature trees (Figures 3 and 4).

A significant difference was observed between ontogenetic and allomorphic (i.e., interspecific) relationships when data were plotted against biomass ($P < 0.05$, Table 4), with the allomorphic relationship having a steeper slope (i.e., $b^{LS} = 1.87$ and $b^{RMA} = 2.78$, respectively) than the combined ontogenetic relationships (i.e., $b^{LS} = 1.19$ and $b^{RMA} = 1.32$, respectively; Table 5). However, when data were plotted as a function of stem diameter, no significant difference was evident between the two, even if the trend was similar, because of the large scatter apparent in the allomorphic relationship (Tables 4 and 5).

Independent of whether data were plotted against diameter or biomass, the allomorphic relationships did not appear to differ significantly from the theoretical expectations of the fractal model, which predicted $b = 2.00$ and 0.750 (Equations 8a and 8b), respectively ($P > 0.05$ in all cases; Table 5). However, as outlined above, almost none of the ontogenetic relationships appeared to follow the theoretical predictions, and almost all of them showed lower values than expected from the West et al. (1999) theory (Table 5). The only exception to this rule was the regression of G_{ag} against M for *A. saccharum*, whose scaling exponent did not differ significantly from the theoretical $b = 0.750$, likely as a result of the small sample size ($n = 9$). Also, none of the regression coefficients of the interspecific data set (i.e., b^{LS} and b^{RMA} for regressions against diameter or

Table 2. Allometric scaling of hydraulic conductivity (k_h) of stem segments, branch hydraulic conductance (G_{br}) and aboveground hydraulic conductance (G_{ag}) against their respective diameters. Abbreviations: LS = least square regression; RMA = reduced major axis regression; b^{LS} = regression coefficient based on OLS; b^{RMA} = regression coefficient based on RMA; s_b = standard error of the regression coefficient; P = level of probability; and n = number of samples. Symbols after standard errors of regression coefficients indicate the level of significance according to the t-test for differences between the actual slopes and the theoretical slope predicted by the fractal-like model (i.e., b = 2.67, 2.00 and 2.00 for stem segment k_h, branch G_{br} and aboveground G_{ag}, respectively): ns = not significantly different from one another ($P > 0.05$); * = significantly different at $P < 0.05$; ** = significantly different at $P < 0.01$; and *** = significantly different at $P < 0.001$. Data for *Pinus sylvestris* from Mencuccini and Grace (1996); data for *Acer rubrum* from Yang and Tyree (1994).

Species	Segment k_h							Branch G_{br}							Aboveground G_{ag}						
	OLS			RMA			n	OLS			RMA			n	OLS			RMA			n
	b^{LS}	s_b	P	b^{RMA}	s_b	P		b^{LS}	s_b	P	b^{RMA}	s_b	P		b^{LS}	s_b	P	b^{RMA}	s_b	P	
Pinus sylvestris	2.55	0.08	ns	2.63	0.08	ns	58	1.92	0.20	ns	2.26	0.19	ns	39	0.97	0.14	***	1.23	0.14	***	30
Acer rubrum	2.61	0.05	ns	2.66	0.05	ns	101	1.73	0.06	***	1.79	0.06	***	66	1.65	0.08	***	1.72	0.08	**	35

Table 3. Summary of ANOVA for pairwise comparisons between regression coefficients.

Source	df	SS	MS	*F*-Value	*P*-Value
(A) Stem segments versus branches					
Pinus sylvestris					
Among regression coefficients	1	3.484	3.484	10.15	< 0.001
Within regression	93	31.924	0.343		
z-Statistics				1.73	
Acer rubrum					
Among regression coefficients	1	18.039	18.039	85.54	< 0.001
Within regression	163	34.373	0.211		
z-Statistics				11.24	
(B) Branches versus whole trees					
Pinus sylvestris					
Among regression coefficients	1	6.303	6.303	12.99	< 0.001
Within regression	65	31.533	0.485		
z-Statistics				4.40	
Acer rubrum					
Among regression coefficients	1	0.057	0.057	0.55	ns
Within regression	97	9.996	0.103		
z-Statistics				0.69	

biomass) were significantly different from isometry (i.e., $b = 1.00$, $P > 0.05$).

For a number of species, data were available to calculate hydraulic conductance for the entire pathway from soil to leaves (G_{tot}; Table 1). When these data were plotted against total (i.e., aboveground plus belowground) biomass, the scaling regression followed a line parallel to that apparent for the G_{ag} data set (Figure 5). The regression for G_{tot} was significantly shifted downward compared with that for G_{ag}, indicating significant belowground resistance across the data set (ANCOVA, $F = 19.14$, $P < 0.0001$).

Discussion

Potential errors

There are several potential sources of error in the analyses reported in this paper. First, in only a few cases was hydraulic conductance measured directly. Most often, it was estimated from sap flow and water potentials. This introduces some error, but there is evidence to suggest that direct measurements and indirect estimates tend to agree within measurement error (e.g., Tyree et al. 1995, Mencuccini and Comstock 1999).

Second, biomass measurements were not obtained directly

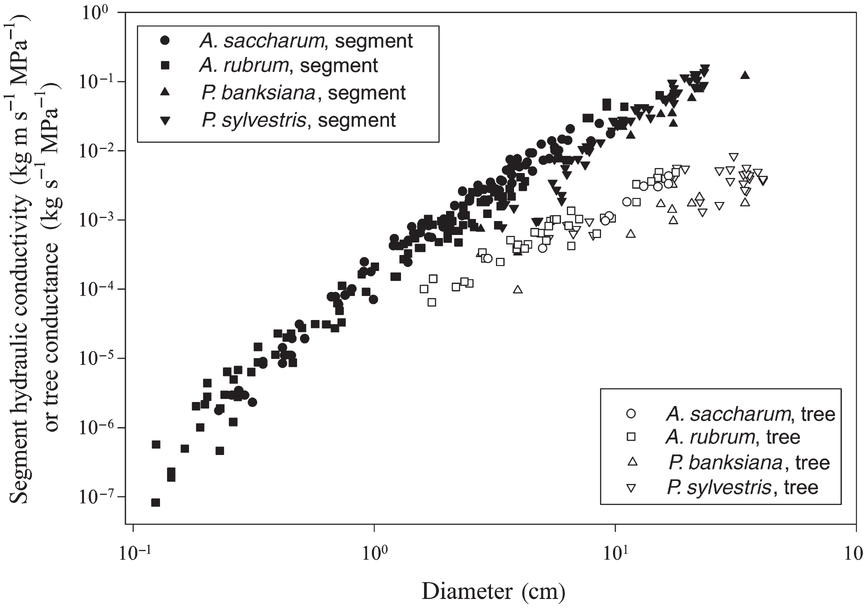

Figure 2. Combined data sets of segment-scale hydraulic conductivity (k_h; closed symbols) and tree-scale aboveground hydraulic conductance (G_{ag}; open symbols) for four species (red maple, sugar maple, Scots pine and jack pine). The combined segment-scale regression followed rather closely the predictions of the West et al. (1999) theory, whereas all four data sets at the tree scale (both separately and as a whole) showed significantly lower regression coefficients than predicted by the fractal-like theory. The similarity in the scaling across the four species is remarkable.

Table 4. Allometric scaling of aboveground hydraulic conductance (G_{ag}) against diameter at breast height or aboveground biomass. Abbreviations: OLS = least square regression; RMA = reduced major axis regression; b^{LS} = regression coefficient based on LS; b^{RMA} = regression coefficient based on RMA; s_b = standard error of the regression coefficient; and P = probability. Symbols after standard errors of each regression coefficient indicate significance of the *t*-test for differences between actual slopes and theoretical slopes predicted by the fractal-like model (i.e., b = 2.00 and 0.75 for stem diameter and biomass, respectively): ns = not significantly different from one another ($P > 0.05$); * = significantly different at $P < 0.05$; ** = significantly different at $P < 0.01$; and *** = significantly different at $P < 0.001$. Data for *Acer rubrum* and *Acer saccharum* from Yang and Tyree (1994); data for *Pinus sylvestris* from Mencuccini and Grace (1996); data for *Pinus banksiana* from Pothier et al. (1989). Interspecific data set from Table 1.

Species	Regressions against diameter						Regressions against biomass					
	OLS			RMA			OLS			RMA		
	b^{LS}	s_b	P	b^{RMA}	s_b	P	b^{LS}	s_b	P	b^{RMA}	s_b	P
Acer rubrum	1.65	0.08	***	1.72	0.08	***	0.62	0.03	**	0.65	0.03	**
Acer saccharum	1.64	0.14	*	1.68	0.12	*	0.63	0.06	ns	0.65	0.05	ns
Pinus sylvestris	0.97	0.14	***	1.23	0.14	***	0.40	0.06	**	0.50	0.05	***
Pinus banksiana	1.14	0.25	**	1.34	0.22	*	0.44	0.10	*	0.52	0.09	*
All four species	1.19	0.06	***	1.32	0.06	***	0.50	0.02	***	0.54	0.02	***
Interspecific	1.87	0.92	ns	2.78	0.78	ns	0.84	0.21	ns	0.96	0.18	ns

from the literature, but were estimated from equations obtained in studies other than those from which the analyzed data were obtained. Although an effort was made to collect site-, age- and species-specific equations, only limited confidence can be placed in those individual estimates. However, the biomass data spanned more than three to four orders of magnitude (depending on whether aboveground or total biomass was used), with the result that errors in the individual estimates do not propagate easily to the estimate of the overall slope. For example, if, in Figure 4, the biomass at each of the six largest values had been estimated with a positive error of 50%, whereas the biomass at each of the three lowest values had been estimated with a negative error of 50%, introduction of the appropriate corrections to the data would yield only a –15% change in the slope. It is more likely that each biomass value was estimated with an error of 10–30%. Furthermore, there is no reason to believe that a systematic bias (e.g., overestimates for large values and underestimates for small values) was present in the biomass estimates. If random errors were the main source of error, then the overall error of the estimated slope would be much more constrained, probably no more than 1–2%.

Finally, the whole-tree data set for *P. banksiana* suffered from methodological limitations, because estimates of aboveground hydraulic resistances were limited to the trunk and excluded branch resistance. However, inspection of Table 5 provides no evidence of a major discrepancy between the scaling coefficients for this and the other three species.

Does the "quarter-power" law apply to plant vascular systems?

It is widely held that many biological phenomena show a de-

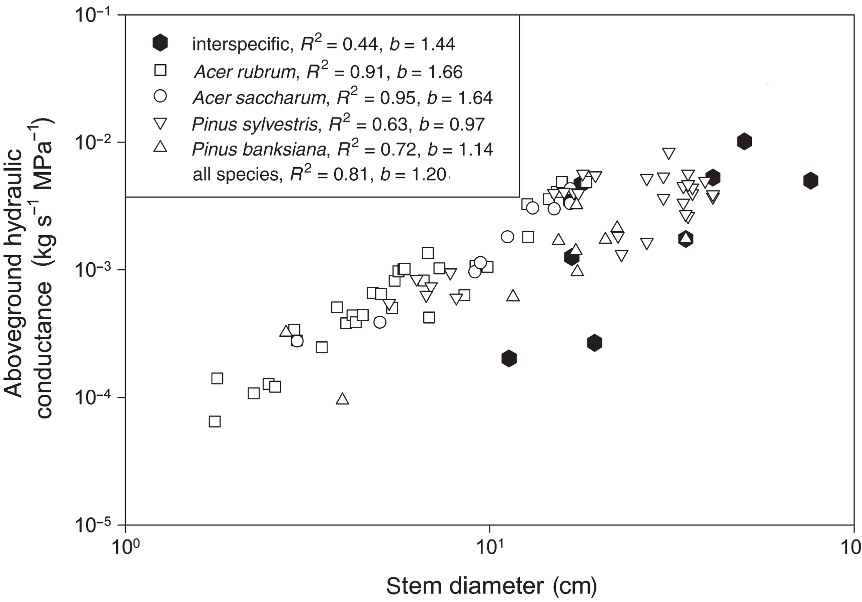

Figure 3. Regressions of aboveground hydraulic conductance against tree stem diameter for the intraspecific and interspecific data sets. The interspecific data set showed a regression slope slightly steeper than that of the combined intraspecific regression ($P <$ 0.10).

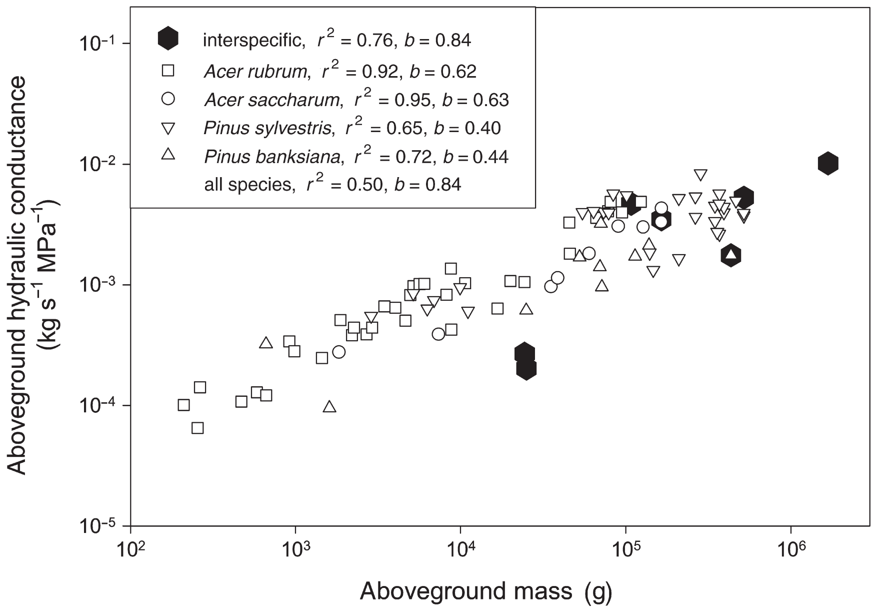

Figure 4. Linear regressions of tree aboveground hydraulic conductance against aboveground biomass for the intraspecific and interspecific data sets. The interspecific data set showed a regression slope significantly steeper than that of the combined intraspecific regression ($P < 0.001$).

pendency on whole-organism mass raised to the exponent of 3/4 (e.g., Peters 1983, Schmidt-Nielsen 1984). However, a recent comprehensive reanalysis of the classical animal data sets that are frequently invoked to prove this assertion (Dodds et al. 2001) failed to reject the geometric similarity hypothesis of $b = 2/3$ in favour of $b = 3/4$, reinforcing earlier arguments along the same lines. Therefore, doubts have repeatedly been cast on the veracity and universality of this rule in animal physiology.

In plant sciences, the dependency of physiological parameters on size has been little explored (but see Niklas 1994). Here, the sparse literature on the subject of xylem hydraulic conductance was collated in order to attempt such a scaling exercise. Because only a few data sets were available, the conclusions reached must be regarded as preliminary.

When aboveground hydraulic conductance was related to the physical dimensions of trees, the scaling exponents did not appear to follow a "3/4 power" law for biomass. Independent of the type of statistical test performed (i.e., type of regression model employed—RMA or OLS—and analysis of residuals), in three out of four cases there was a statistical significant difference between the observed ontogenetic scaling exponents against biomass and the predicted $b = 3/4$ (Table 4). The fourth case, however, which also showed a lower estimated slope than predicted by $b = 3/4$, was characterized by a relatively small sample size. Consistent with these results, all four regressions against stem diameter showed significant departures from the predicted $b = 2.00$ (West et al. 1997).

Therefore, our analyses support doubts expressed by Dodds et al. (2001) about the universality of the "3/4 power" law. The estimated hydraulic scaling against biomass for the four species analyzed here showed values more consistent with the geometrical scaling of 2/3, or even 1/2, than the assumed 3/4 (cf. Dodds et al. 2001).

Does the model of West et al. provide useful insights for plant physiology?

The arguments proposed by West et al. (1997) are powerful. Through fractal analysis, more biological information is incorporated in the model of plant structure than with the pipe

Table 5. Summary of ANOVA for the comparison of interspecific variability versus intraspecific variability in the scaling of aboveground hydraulic conductance (G_{ag}) against diameter at breast height or aboveground biomass. Abbreviation: ns = not significant.

Source	df	SS	MS	*F*-Value	*P*-Value
Scaling against stem diameter					
Among regression coefficients	1	0.808	0.808	2.392	ns
Within regression	87	29.384	0.338		
z-Statistics				1.87	
Scaling against aboveground biomass					
Among regression coefficients	1	1.653	1.653	6.600	< 0.05
Within regression	87	21.793	0.250		
z-Statistics				2.312	

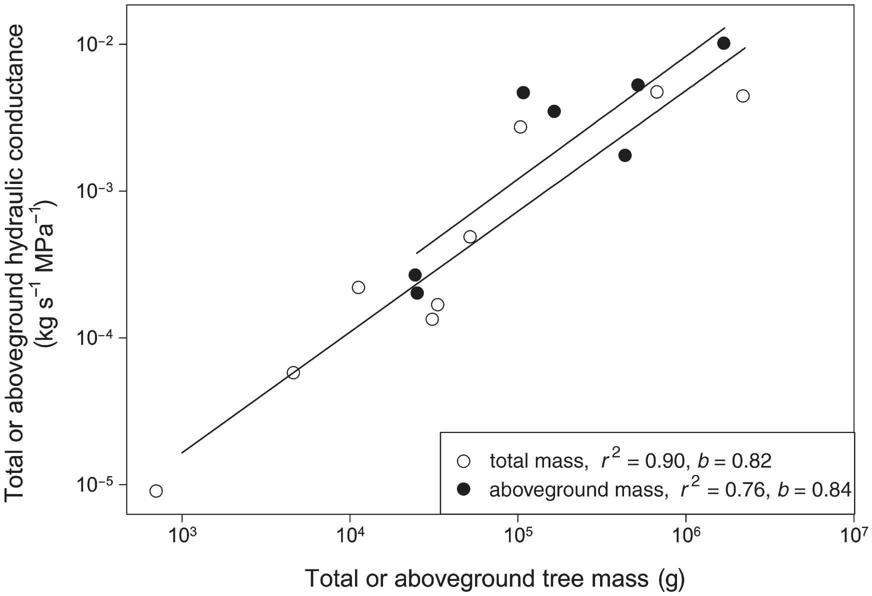

Figure 5. Linear regressions of total or aboveground hydraulic conductance against total or aboveground biomass, respectively. No significant difference was present between the slopes of the two regressions ($P > 0.05$); however, the intercept was significantly different (ANCOVA, $F = 19.14$, $P < 0.0001$), indicating a significant belowground resistance.

model theory, and a more general theoretical framework is provided. However, it is still unclear whether plant hydraulic networks can be described as fractals, given the initial assumptions of maximization of surface areas and minimization of transport distances (Dodds et al. 2001).

More specifically in relation to water transport and flow in the xylem, uncertainty exists about the degree of tracheid or vessel tapering, i.e., one of the crucial parameters needed to estimate the theoretical scaling of many hydraulic properties against size. As a consequence, the simplifications introduced by West et al. (1997) in their derivations of the equations presented in the Materials and methods may prove unnecessary.

In support of this conclusion I submit the data obtained in this work. For each of the four species considered (two pines and two maples), the model of West et al. (1999) accurately predicted the scaling of hydraulic properties at the segment scale, but failed to do so at the branch and whole-tree scales. In all four cases, the ontogenetic scaling of hydraulic conductance against diameter was slower than predicted by $b = 2.00$, suggesting that vessel tapering or biomass allocation to increase stem and branch girth over time were insufficient to compensate for the progressive increase in tree height and the loss of sapwood to heartwood.

Is there a component missing in the model of West et al., whose exclusion causes the predictions at the branch and whole-tree levels to fail? And how can the predictions be correct at the segment scale, but not at the branch and whole-tree scales? It is possible that vessel tapering is not constant during tree growth, but becomes less steep in old trees (i.e., vessel tapering is itself a function of size), resulting in the well-known plateau of vessel dimensions when plotted against cambial age within any one section (F. Magnani et al., unpublished data). A constant vessel tapering, independent of age, may be too expensive to maintain in terms of the required sapwood area, or may incur other costs related to the scaling of vulnerability to cavitation with tree size. The correct prediction of the hydraulic scaling for segments of largely different sizes would then mask more subtle age- or size-dependent scaling differences. Finally, it is possible that either or both assumptions of area-preserving and volume-filling hydraulic networks are incorrect.

When the hydraulic transport efficiencies of different species were compared (in terms of hydraulic return of their biomass), the observed allomorphic slopes (Figures 3 and 4) appeared to be closer to the theoretical predictions of the fractal model. A simple way to interpret these results is that, if the premises of the fractal model are correct, taller tree species may be no more limited hydraulically than shorter tree species. In other words, vessel tapering may have followed a common pattern across many species, so that the interspecific differences in overall size and hydraulic path length are compensated for.

However, allomorphic relationships must be interpreted cautiously, because constant ontogenetic scaling within a species (i.e., the same ontogenetic slope for all species) predicts isometric scaling in the allomorphic trajectories (White and Gould 1965). Therefore, even though the allomorphic coefficients were not significantly different from $b = 0.75$, this does not necessarily imply optimal (*sensu* West et al. 1997) scaling of the transport networks across species. Either the sample individuals were not equivalent in their developmental stage (a likely possibility, given the paucity of relevant literature), or species of different size behaved differently from one another in their ontogenetic scaling (i.e., b for the ontogenetic trajectories varied from species to species). In either case, that none of the regression coefficients of the allomorphic relationships were significantly different from isometry does not lend support to the fractal theory.

Allometric analysis is employed to describe a variety of biological scaling phenomena. It is presently unclear whether one single theoretical model can encompass all possible cases of the three major classes of scaling relationships (intraspecific static, intraspecific ontogenetic and interspecific allomorphic). The present data set suggests that the model of West et al. (1997) may be useful for describing scaling relationships of the third class, but not of the first or second.

The significance of the observed scaling

Despite these caveats, the significance of the log–log allomorphic regressions (Figures 3 and 4) is remarkable, given the diversity of life history strategies, morphological, ecological and ecophysiological properties, and especially the diversity in xylem characteristics among species, which included diffuse porous and ring-porous broadleaves and tracheid-bearing conifers (Table 1). It is likely that differences associated with xylem structure largely disappeared as a result of the magnitude of the absolute differences in plant biomass and hydraulic conductance, but it is also possible that the significant differences in transport efficiency predicted at the scale of individual conduits largely disappear when whole tissues or plants are examined. For example, Becker et al. (1999) failed to demonstrate any difference in whole-plant, leaf-specific hydraulic conductance between two distinct groups of tropical conifers and angiosperms, which differed largely when examined at the anatomical or tissue scale.

However, the intraspecific ontogenetic reductions in the hydraulic efficiency of biomass appeared to vary between pine and maple species. For pine, the observed scaling of whole-tree conductance against either diameter or biomass diverged largely from theoretical predictions, whereas for maple, the differences were more attenuated. This suggests that either methodological differences affected the final slopes, or that species behave differently in hydraulic scaling depending on the type of xylem elements that they possess.

What is the cause of the reduced water transport efficiency in large trees of the four study species? The kinds of adaptive pressures acting across species may be quite different from those acting on a single individual throughout its lifecycle. For example, it could be more advantageous for an individual to reduce its hydraulic efficiency in the later stages of its life cycle if this provided other adaptive benefits. For example, reduced hydraulic conductance could be more conducive to tight regulation of stomatal functioning during water stress, or could increase the supply of carbohydrates available for reproduction. Finally, it could result in increased fine root biomass (to increase water or nutrient uptake) or increased leaf area (to increase light interception) via altered carbon allocation strategies, although each leaf would have a more restricted water supply. Conditions envisaged in the last scenario could be beneficial in the light-limited and crowded conditions of forests.

Finally, across both species for which data were available, slopes of segment hydraulic conductivity versus segment, branch or tree diameter were lower for whole trees than for individual segments, whereas branch-level coefficients were intermediate (Figures 1a and 1b). It is unlikely that differences in sapwood/heartwood ratios were a factor contributing to these slope differences because the size range of sampled segments and branches overlapped the size range of sampled whole trees, ensuring that, for example, large stem segments with low sapwood/heartwood ratios were also sampled.

Conclusions

There are three main conclusions from these analyses. (1) Scaling of hydraulic functions in trees appears to change depending on whether stem segments, branches or entire trees are considered, with an overall similarity across the four examined species. The "quarter-power" law proposed as a scaling law for animal physiology does not appear to hold for plant vascular tissues in the species examined. (2) The model of West et al. (1999) is useful as a reference to summarize the complexity of plant vascular systems. Most of the model predictions for ontogenetic trajectories were reasonably close to the observed scaling coefficients. However, significant doubts remain as to the relevance of fractality for the description of tree architecture and the expected theoretical exponents (cf. Dodds et al. 2001). (3) Allomorphic regressions yield useful evolutionary and phylogenetic information. However, caution has to be exercised when interspecific comparisons are made, because model predictions valid for ontogenetic trajectories cannot easily be extended to predict allomorphic trajectories.

Acknowledgments

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