

Does water transport scale universally with tree size?

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Summary

1. We employed standardized measurement techniques and protocols to describe the size dependence of whole-tree water use and cross-sectional area of conducting xylem (sapwood) among several species of angiosperms and conifers.
2. The results were not inconsistent with previously proposed 3/4-power scaling of water transport with estimated above-ground biomass. However, for a given size, angiosperms transported considerably greater quantities of water than conifers.
3. In the angiosperms studied, the scaling of water transport with sapwood area, stem diameter and above-ground biomass was best described by sigmoid functions rather than a power function, consistent with the previously reported size dependence of other processes such as growth.
4. At least three distinct species groupings for relationships between sapwood area and stem basal area were observed. Scaling of sapwood area with stem radius was well described by a power function of the form $Y = Y_0 X^b$. However, exponents obtained for two of the three species groups differed significantly from a recently proposed theoretical value of 2.33.

Key-words: allometric scaling, hydraulic architecture, sap flow, sapwood, xylem anatomy

Functional Ecology (2005) **19**, 558–565

doi: 10.1111/j.1365-2435.2005.01017.x

Introduction

Trees typically increase in size by three to four orders of magnitude from the seedling to adult stage. Scaling of organism functional traits with body size provides insights concerning evolutionary constraints on relationships between form and function. Recent proposals that scaling of water transport and other physiological and life-history traits in plants follows universal quarter-power allometric relationships (West, Brown & Enquist 1997; Enquist, Brown & West 1998; West, Brown & Enquist 1999; Enquist *et al.* 1999; Enquist 2002) have inspired a great deal of discussion and controversy (Becker, Gribben & Lim 2000; Meinzer, Goldstein & Andrade 2001; McCulloh, Sperry & Adler 2003; Kozlowski & Konarzewski 2004; Robinson 2004). If proven to be universal, or even ubiquitous, the allometric relationships proposed by West and colleagues (WBE model) are likely to be powerful tools for identifying and understanding broad-scale convergence in plant functioning. Two key assumptions in the theoretical derivation of the WBE model include (1) a volume-filling, fractal-like vascular network that minimizes total hydraulic resistance; and (2) nearly invariant size of terminal conducting elements (vessels and

tracheids) with increasing plant size (West *et al.* 1999). However, these assumptions are not likely to be strictly true over the broad range of sizes encompassed by trees and the range of habitats they occupy (Apple *et al.* 2002; McCulloh *et al.* 2003; McCulloh & Sperry 2005).

The major phylogenetic groups of trees also exhibit fundamental differences with regard to the structure of the basic conducting elements of their water-transport tissue. Gymnosperms, most of which are conifers, possess tracheids: elongated cells that are hydraulically connected with overlapping adjacent tracheids through numerous pits that traverse thickened cell walls. Although angiosperms also possess tracheids, their primary conducting elements consist of relatively short vessel members of varying length, which have perforated end walls and occur in vertical files to form columnar vessels that tend to be wider than tracheids and up to 1 m or more in length. The hydraulic conductivity of vessels is closely related to their diameter, whereas the conductivity of tracheids is determined largely by their length, which is an index of the number of interconnecting pits (Pothier *et al.* 1989; Jean-Christophe Domec, Oregon State University, unpublished data). In addition to these fundamental differences between angiosperms and conifers, there are also broad differences in water-conducting systems among species within each group. Especially important with respect to relationships between total size and water flux in woody plants is the fact that the

cross-sectional area of wood that actually conducts water (the sapwood) relative to the total area of stemwood is highly variable among species and among plants of different sizes, or in different growth environments within species. This variability is addressed in the WBE model, which predicts a universal scaling exponent of $7/3$ for the relationship between stem radius and the area of conducting xylem (Enquist *et al.* 2000). However, universal allometry of conducting xylem with stem size would not account for the enormous radial variation in xylem functional properties such as hydraulic conductivity and sap flux that exists in trees (e.g. Jiménez *et al.* 2000; Spicer & Gartner 2001). The implications of this radial non-uniformity within and across species for the size dependence of water transport in trees are not clear.

Scaling of water transport with plant size may also be influenced by water stored in plant tissues (capacitance), which can contribute significantly to daily xylem water flux (Goldstein *et al.* 1998). In trees, daily reliance on stored water varies among species and with size (Meinzer *et al.* 2003; Phillips *et al.* 2003). Although greater capacitance may increase total water flux over a 24 h cycle, it is likely to reduce rather than increase maximum instantaneous rates of water flux (James *et al.* 2003; Meinzer *et al.* 2003). If rates of water transport are to be used as a surrogate for variation in metabolic rates with plant size (Enquist *et al.* 1998), the consequences of capacitance raise the question of whether both instantaneous and integrated rates are equally appropriate indices of concurrent variation in metabolism.

The validity of quarter-power allometric models that predict the size dependence of whole-plant water transport remains uncertain because reliable and consistent empirical data over a broad range of plant size are scarce. Furthermore, some allometric functions may be biologically more appropriate than others when different measures of plant size, such as mass, basal stem diameter and basal sapwood area, are employed. For example, growth (Hunt 1982; Thomas, Jasienski & Bazzaz 1999), maintenance respiration (Meir & Grace 2002), and other metabolic indicators (Niinemets 2002) are widely reported to follow sigmoid or asymptotic trajectories with increasing plant size. A survey of published maximum rates of whole-tree water use found a range of 10–150 kg day⁻¹ in the 5–10 cm stem diameter class, and 52–349 kg day⁻¹ in the 37–42 cm stem diameter class (Wullschleger, Meinzer & Vertessy 1998). This variation is not necessarily inconsistent with quarter-power allometric models if it results in a random error around predicted relationships, although a very large error would tend to diminish the predictive power of the model. However, in order to assess whether the natural variation is consistent with universal scaling predictions, and to understand the ramifications of these predictions, it must be determined whether the substantial variation in measured fluxes over small diameter ranges reflects true differences in allometric relationships among species or species groups, with the

mean value tending to the quarter-power prediction, whether variation is a result of natural random variation among species and sites, or whether it is a result of different measurement techniques under different environmental conditions. These, of course, are not mutually exclusive.

In field-grown trees, rates of water use are most commonly estimated from measurements of sap flow (Granier 1987; Hatton & Vertessy 1990), although other techniques involving isotope tracers, lysimeters and ventilated chambers have also been employed (Dye, Olbrich & Calder 1992; Kalma, Thorburn & Dunn 1998; Wullschleger *et al.* 1998). All these methods have significant practical and theoretical constraints, particularly when applied to large trees. For example, in estimating whole-tree water use based on measurements of sap flow, both radial and circumferential variation in flow must be taken into account (Jiménez *et al.* 2000; Nadezhdina, Cermak & Ceulemans 2002).

In the present study we employed standardized sap flow-measurement techniques and protocols to determine relationships between tree size, amount of active xylem (sapwood) and rates of water transport for 65 individuals of 23 tropical and temperate angiosperm and conifer species growing in eight different sites. The basal stem diameter of the trees studied ranged from 0.04 to 1.67 m. We asked: (i) Do total daily water transport and the amount of conducting xylem scale universally with tree size?; (ii) Is scaling of daily water flux with tree biomass consistent with $3/4$ -power allometric functions?; (iii) Is the size dependence of water transport significantly different among vessel- and tracheid-bearing species?; and (iv) Based on our empirical data and existing knowledge about the size dependence of other plant functional traits, what are the most appropriate types of function for describing scaling of water transport with different measures of tree size?

Materials and methods

RESEARCH SITES AND SPECIES

Measurements were made on five conifer and one angiosperm tree species growing in five temperate sites in the north-western USA, and 17 angiosperm species in three tropical sites (Table 1). The temperate sites were an old-growth Ponderosa Pine forest, a Grand Fir stand and an oak woodland in Oregon, and an old-growth Douglas Fir/Western Hemlock stand and a 24-year-old Douglas Fir stand in Washington. The tropical sites were seasonally dry forests in Panama and a tropical savanna near Brasilia, Brazil.

WHOLE-TREE WATER TRANSPORT

Water flux was measured as sap flow using the heat-dissipation technique (Granier 1987). Pairs of sensors (James *et al.* 2002) were installed at one to five depths in the sapwood near the base of the trunk (James *et al.*

Table 1. Tree species and sites in which daily water transport and sapwood area were measured

Tree species	Family	Diameter (m)	<i>n</i>
Temperate woodland, Corvallis, OR, USA (44°34' N; 123°15' W; alt. 90 m)			
<i>Quercus garryana</i> Dougl. ex Hooke	Fagaceae	0.20–0.64	6
Deschutes National Forest, OR (44°27' N; 121°43' W; alt. 970 m)			
<i>Abies grandis</i> (Dougl.) ex D. Don	Pinaceae	0.54	2
Metolius Research Natural Area, OR (44°30' N; 121°37' W; alt. 940 m)			
<i>Pinus ponderosa</i> Dougl. ex Laws	Pinaceae	0.19–0.93	6
Wind River Canopy Crane, WA (45°49' N; 121°57' W; alt. 355 m)			
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Pinaceae	0.81–1.67	6
<i>Thuja plicata</i> Donn ex D. Don	Cupressaceae	0.95–1.48	4
<i>Tsuga heterophylla</i> (Raf.) Sarg.	Pinaceae	0.32–0.94	7
Wind River Experimental Forest, WA (45°49' N; 121°57' W; alt. 370 m)			
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Pinaceae	0.20–0.22	4
Tropical forest, Barro Colorado Island, Panama (09°10' N; 79°51' W; alt. 50 m)			
<i>Abuta racemosa</i> (Thunb) Tr. & Planch	Menispermaceae	0.12	1
<i>Anacardium excelsum</i> (Bertero & Balb.) Skeels	Anacardiaceae	0.74	1
<i>Entada monostachya</i> DC.	Fabaceae	0.25	1
<i>Guatteria dumetorum</i> Fries	Annonaceae	0.30–0.68	2
<i>Hura crepitans</i> L.	Euphorbiaceae	0.60–0.64	2
<i>Luehea seemanii</i> Tr. & Planch	Tiliaceae	0.40–0.83	4
<i>Platymiscium pinnatum</i> (Jacq.) Dug.	Fabaceae	0.33–0.49	2
<i>Pseudobombax septenatum</i> (Jacq.) Dug.	Bombacaceae	1.30	1
<i>Quararibea asterolepis</i> Pitt.	Bombacaceae	0.37	1
<i>Trichilia tuberculata</i> C. DC.	Meliaceae	0.23	1
<i>Viola surinamensis</i> (Rol.) Warb.	Myristicaceae	0.51	1
Tropical forest, Panama City, Panama (09°10' N; 79°51' W; alt. 13 m)			
<i>Anacardium excelsum</i> (Bertero & Balb.) Skeels	Anacardiaceae	0.98	1
<i>Cordia alliodora</i> (Ruiz & Pav.) Cham.	Boraginaceae	0.34	1
<i>Ficus insipida</i> Willd.	Moraceae	0.65	1
<i>Schefflera morototoni</i> (Aubl.) Maguire, Steyerl. & Frodin	Araliaceae	0.47	1
Tropical savanna, Brasilia, Brazil (15°56' S; 47°53' W; alt. 1100 m)			
<i>Kielmeyera coriacea</i> Mart.	Clusiaceae	0.04–0.08	3
<i>Miconia ferruginata</i> DC.	Melastomataceae	0.04–0.08	3
<i>Schefflera macrocarpum</i> (C. & S.) Seem.	Araliaceae	0.05–0.06	3

2003; Meinzer, Woodruff & Shaw 2004) at ≈ 1.5 m. The temperature difference between the continuously heated and unheated reference sensor was measured every minute, and 10-min means were recorded with a data logger (CR10X, Campbell Scientific, Logan, UT, USA) equipped with a 32-channel multiplexer. Several days of continuous data were recorded for each tree to estimate maximum daily sap flow on clear days with high atmospheric vapour pressure deficit and minimal soil water deficit. The maximum values reported here represent means of at least three to five of the highest daily totals, depending on the length of the measurement period and the weather conditions during the measurement period for each individual. The mass flow of water (F ; g s^{-1}) corresponding to each pair of sensors was calculated as $F = vA$ where v is water flux ($\text{g m}^{-2} \text{s}^{-1}$) and A (m^2) is the cross-sectional area of sapwood calculated as the ring area centred on the sensor tip and extending to midway between two sensors of successive depth. Whole-tree water transport was calculated by summing the mass flow through successive rings of sapwood associated with each pair of sensors (James *et al.* 2002). The number of depths at which sensors were installed depended on the diameter of the stem and the sapwood thickness estimated from prior observa-

tions. In larger trees with sensors installed at multiple depths in the sapwood, the sapwood inner boundary was estimated by extrapolating the radial profile of axial flow to zero flow. In smaller stems (< 10 cm diameter) with one pair of sap-flow sensors, the sapwood inner boundary was determined from distribution of injected dye carried in the transpiration stream (Meinzer *et al.* 1999).

DATA ANALYSIS

Relationships between sapwood area and tree size were evaluated with respect to both stem basal area and radius. Because the dependence of sapwood area on stem radius was non-linear and appeared to conform to a power function, an equation of the form $Y = Y_0 X^b$ was fitted to the data, where Y is sapwood area, Y_0 is a normalization constant, X is stem radius, and b is the allometric scaling exponent. Relationships between water transport and tree size were evaluated with respect to three size indices: basal sapwood area; stem diameter; and above-ground biomass. Published allometric equations were used to estimate above-ground biomass from basal stem diameter. For the tropical angiosperms and *Quercus garryana*, biomass (kg) was calculated as $0.094D^{2.618}$ (Enquist 2002) where D is

diameter in cm. For the conifers, biomass was estimated from species-specific equations given in Table 4 of Jenkins *et al.* (2003). The appropriateness of sigmoid *vs* power functions to describe the dependence of water transport on plant size was compared (see below).

Ordinary least squares (OLS) regression analyses were performed on linear or log-transformed data using SAS (Proc MIXED, SAS version 9.1, SAS Institute, Cary, NC, USA). Reduced major axis (RMA) regressions were generated on the same data set for comparison (Bohonak & van der Linde 2004). Slopes and intercepts of log-transformed data were compared for significant differences between species groupings based on ANOVA (Proc MIXED). For non-linear data, curve parameters, their standard errors and 95% confidence intervals, and Akaike's information criterion (AIC), were estimated using non-linear regression (Proc NLMIXED). *t*-tests were used to test if power function exponents were significantly different from proposed theoretical values at the 95% significance level. Differences in AIC values ($\Delta_{\text{AIC}} = \text{AIC}_i - \text{AIC}_{\text{min}}$) were used to compare the ability of sigmoid *vs* power functions to describe the dependence of water transport on basal sapwood area and stem diameter. Values of $\Delta_{\text{AIC}} < 2$ reflect little difference in the appropriateness of the two functions, whereas $4 < \Delta_{\text{AIC}} < 7$ reflects a considerably poorer fit using the function being compared, and $\Delta_{\text{AIC}} > 10$ suggests that it is highly unlikely that the alternative function is appropriate (Burnham & Anderson 2002).

Results

Although basal sapwood area was significantly correlated ($P \leq 0.001$) with stem basal area when data for all species were combined, basal area was not a robust predictor of sapwood area for the combined data set ($R^2 = 0.45$). However, there appeared to be three distinct species groupings within the overall data set, and ANOVA confirmed that these three groupings were significantly different ($P \leq 0.05$), with strong linear relationships between sapwood area and basal area (Fig. 1a). Parameter estimates for these relationships based on OLS or RMA regression were similar, generally within 10% of one another. Among the 17 tropical angiosperm species studied, about 72% of the stem basal

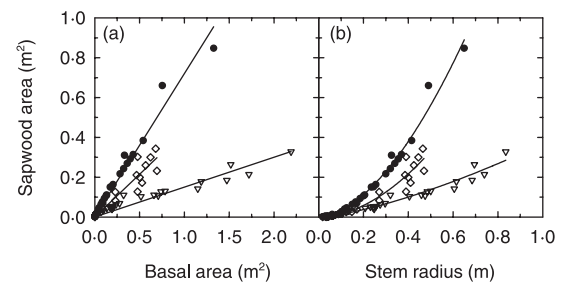


Fig. 1. Basal sapwood area in relation to (a) total stem basal area and (b) stem radius for several angiosperm and conifer species (Table 1). Lines in (a) are least-squares regressions with slopes of: 0.72 ($R^2 = 0.97$, $P < 0.0001$) for tropical angiosperms (●); 0.43 ($R^2 = 0.83$, $P < 0.0001$) for the conifers *Abies grandis*, *Pinus ponderosa* and *Tsuga heterophylla* (◇); and 0.15 ($R^2 = 0.96$, $P < 0.0001$) for the temperate angiosperm *Quercus garryana* and the conifers *Pseudotsuga menziesii* and *Thuja plicata* (▽). Curves in (b) are power functions fitted to the data (Table 2).

area comprised sapwood for trees with stems ranging up to 1.3 m in diameter. In contrast, sapwood constituted 43% of stem basal area in the temperate conifers *Abies grandis* (Grand Fir), *Pinus ponderosa* (Ponderosa Pine) and *Tsuga heterophylla* (Western Hemlock), and only 15% of stem basal area in the temperate angiosperm *Quercus garryana* (Oregon White Oak) and two other temperate conifers, *Pseudotsuga menziesii* (Douglas Fir) and *Thuja plicata* (Western Redcedar). Fitted exponents for power functions describing the relationship between sapwood area and stem radius (Fig. 1b) ranged from 1.42 to 1.90 for the three species groupings identified above (Table 2). Exponents for two of the three groups shown in Table 2 differed significantly from the value of 2.33 proposed in a recent allometric model (Enquist 2002).

When maximum daily water flux was plotted as a function of basal sapwood area or stem diameter (Fig. 2), both three- and four-parameter sigmoid functions generally yielded good fits to the data (Δ_{AIC} values, Table 3). The one exception was the considerably poorer fit obtained with the three- *vs* four-parameter sigmoid function for the dependence of water flux on sapwood area in *P. menziesii*. For the angiosperms and *P. menziesii*, a power function of the form $Y = Y_0 X^b$ proved to be a poor model compared with the sigmoid function for

Table 2. Parameters of power functions ($Y = Y_0 X^b$) fitted to relationships between sapwood area and stem radius (Fig. 1b) and between water transport and above-ground biomass (Fig. 3) for different groupings of angiosperms and conifers

	<i>n</i>	Y_0	SE	<i>b</i>	SE	R^2	Predicted <i>b</i>
Sapwood area <i>vs</i> stem radius							
Tropical angiosperms	30	1.90	0.089	1.76	0.056	0.98	2.33*
<i>Quercus garryana</i> , <i>Pseudotsuga menziesii</i> , <i>Thuja plicata</i>	54	0.37	0.014	1.42	0.060	0.96	2.33*
<i>Abies grandis</i> , <i>Pinus ponderosa</i> , <i>Tsuga heterophylla</i>	15	1.23	0.474	1.90	0.433	0.83	2.33
Water transport <i>vs</i> biomass							
Angiosperms	36	0.83	0.341	0.69	0.043	0.91	0.75
Conifers	29	0.11	0.136	0.74	0.125	0.66	0.75

Asterisks following predicted values of *b* indicate significant differences from observed values at $P \leq 0.05$. Predicted values of *b* obtained from Enquist *et al.* (2000).

Table 3. Comparison of non-linear power and sigmoid function fits to data and parameters for ordinary least-squares regression for log-transformed data from Figs 2 and 3

	Non-linear fit (Δ AIC)			Linear fit (OLS regression)			
	2-par power	3-par sigmoid	4-par sigmoid	Intercept	SE	Slope	SE
Water transport vs sapwood area							
Angiosperms	12	6	0	2.91a	0.048	0.86a	0.030
<i>Pseudotsuga menziesii</i>	33	24	0	2.63b	0.145	0.78a	0.120
<i>Abies grandis</i> , <i>Pinus ponderosa</i> , <i>Tsuga heterophylla</i> , <i>Thuja plicata</i>	3	0	2	2.46b	0.114	1.00a	0.119
Water transport vs stem diameter							
Angiosperms	17	0	2	2.65a	0.056	1.57a	0.076
Conifers	1	0	3	1.81b	0.070	0.95b	0.199
Water transport vs biomass							
Angiosperms	17	7	0	0.12a	0.086	0.60a	0.035
Conifers	0	1	2	0.19a	0.265	0.43b	0.065

Lower Δ AIC values indicate a better fit. Δ AIC values >4 indicate a poorer fit. Intercept and slope values followed by different letters within columns are significantly different at $P \leq 0.05$ based on ANOVA.

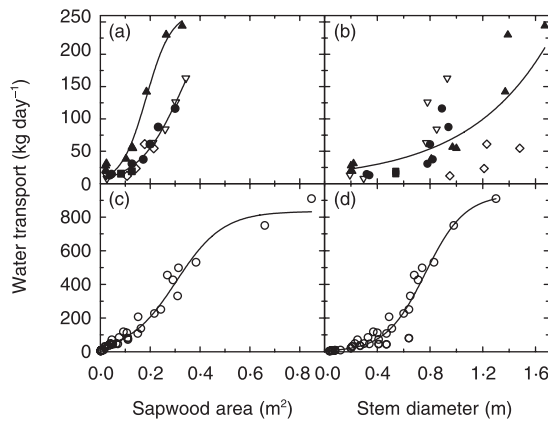


Fig. 2. Maximum daily water transport per tree in relation to basal sapwood area and basal stem diameter for (a,b) five coniferous and (c,d) 18 angiosperm species. (a,b) *Abies grandis* (■), *Pinus ponderosa* (▽), *Pseudotsuga menziesii* (▲), *Thuja plicata* (◇), *Tsuga heterophylla* (●). (c,d) 18 angiosperm species (○) listed in Table 1. Four-parameter sigmoid regressions are fitted to the data ($y = y_0 + a / (1 + e^{-[(x-x_0)/\beta]})$).

describing the relationship between water transport and sapwood area (Δ AIC values >10, Table 3). Similarly, sigmoid functions were much more appropriate models than a power function for characterizing the dependence of water transport on stem diameter in angiosperms. For the conifers, however, all three models appeared to be almost equally appropriate to characterize this relationship. ANOVA of intercepts for linear regressions of log-transformed data indicated significant differences between angiosperms and conifers for the dependence of water transport on both sapwood area and stem diameter (Table 3). There were also significant differences between the regression slopes for angiosperms and conifers for the dependence of water transport on stem diameter.

Power functions fitted to the relationship between total daily water transport and estimated above-ground biomass (Fig. 3a) yielded exponents of 0.69 and 0.74

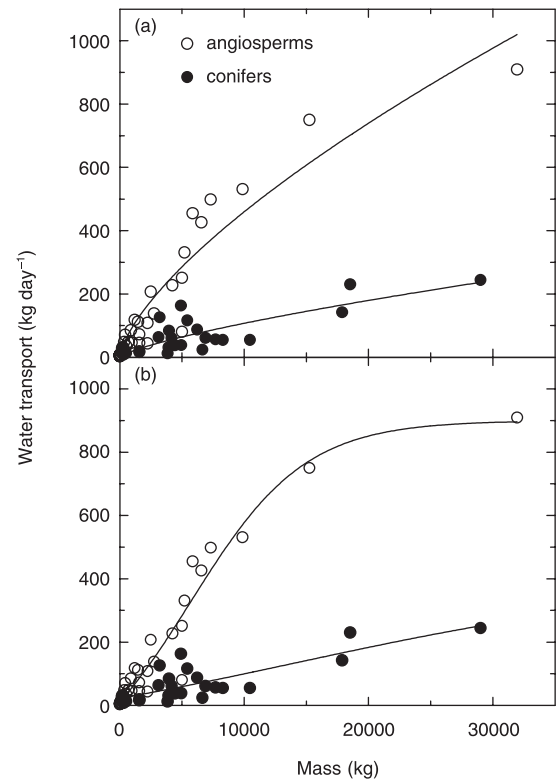


Fig. 3. Scaling of total daily water transport with estimated above-ground biomass in 18 angiosperm and five coniferous species. Curves are (a) power or (b) four-parameter sigmoid functions fitted to the data (Tables 2 and 3).

(Table 2) for the angiosperms and conifers, respectively, which were not significantly different from a theoretical value of 0.75 proposed earlier (Enquist *et al.* 1998). Nevertheless, OLS regression slopes of log-transformed data differed significantly (Table 3), indicating a marked difference in the size dependence of water transport among the angiosperms and conifers studied. Comparison of the fits obtained with the power function and sigmoid models indicated that, for the angiosperms,

the power function yielded a poor fit compared with the sigmoid functions, whereas for the conifers the three models yielded nearly identical fits (Table 3). These conclusions are readily visible graphically in Fig. 3(b), which shows that the sigmoid function provides a closer fit to the angiosperm data than the power function in Fig. 3(a). For the angiosperms, estimates of total daily water transport obtained with the fitted power function were about 20–75% greater than those obtained with the fitted sigmoid function over the range of mass from 100 to 3500 kg (diameter ≈ 15–55 cm), a common range of tree size in many forest stands. The estimates were generally within 20% of each other for smaller and larger sizes. However, for angiosperm trees > 30 000 kg (diameter > 125 cm), increasing divergence between estimates would occur.

Discussion

Our results are not inconsistent with universal 3/4-power scaling of water transport with tree mass among angiosperms and conifers, two groups differing markedly in their xylem structure and hydraulic properties. Nevertheless, sigmoid functions provided superior fits to the angiosperm data. For the conifers studied, the fits obtained with the sigmoid and power function models appeared to be indistinguishable, but this may have resulted from the greater scatter in the conifer data rather than fundamental differences in the trajectory of water transport with increasing plant mass. Regardless of the model or measure of plant size employed, vessel-bearing angiosperms transported considerably greater quantities of water than tracheid-bearing conifers at a given plant size.

Although a power function of the form $Y = Y_0 X^b$ appeared to be an adequate model for scaling of water transport with mass, the sigmoid trajectories of water transport with increasing sapwood area and tree diameter were not consistent with an earlier proposal (Enquist *et al.* 1998) that total xylem water transport (kg day^{-1}) scales universally with plant stem diameter (D) according to a power function of the form $0.257D^{1.778}$. Furthermore, when the data, presented in Fig. 3, of Enquist *et al.* (1998) are plotted in their original non-linear form, it is seen that the point representing the largest stem diameter suggests an asymptotic increase in water transport with diameter, whereas the point representing the next largest diameter would suggest an exponential increase in water transport if the data for the larger diameter were not included. The mechanistic and theoretical basis for selecting an exponential growth function over an asymptotic function to describe these data thus seems unclear. If the appropriate model for describing the dependence of water transport on stem diameter and sapwood area is a sigmoid function, then use of a power function with an exponent > 1 would clearly lead to increasing overestimates of water transport above a critical diameter threshold and an exponent < 1 would lead to overestimates of water transport at small stem diameters.

Sigmoid trajectories of water transport with increasing stem diameter and sapwood area are consistent with the size dependence of other processes such as growth, photosynthesis and respiration (Hunt 1982; Thomas *et al.* 1999; Meir & Grace 2002; Mencuccini 2002; Niinemets 2002). Furthermore, abundant evidence that stomata increasingly limit transpiration and photosynthesis as trees grow above a threshold size (Bond 2000; Ryan *et al.* 2000; McDowell *et al.* 2002; Niinemets 2002) provides compelling reasons to believe that power functions predicting exponential increases in water transport with increasing tree diameter (Enquist *et al.* 1998) may be biologically inappropriate, even though they may appear to represent overall trends in certain data sets adequately. We conclude that sigmoid functions whose parameters may be specific to groups of species or individual species may be universally applicable for describing trajectories of water transport with certain indices of plant size. The nature of the appropriate allometric scaling model will thus depend on the measure of tree size employed.

Some of the species studied are known to exhibit substantial species- and size-specific variation in intrinsic capacitance and daily reliance on internally stored water (Goldstein *et al.* 1998; Meinzer *et al.* 2003; Phillips *et al.* 2003). Although withdrawal of water from internal storage compartments leads to lags between changes in transpiration and changes in sap flux near the base of the tree, this phenomenon is not expected to influence the size dependence of total daily water transport unless overnight recharge is incomplete, leading to progressively increasing internal water deficits and stomatal restriction of transpiration. Because we explicitly selected maximum rates of water transport for our analyses, the individuals from which data were collected in this study were not experiencing severe water deficits, and overnight recharge of storage appeared to be complete as indicated by rates of sap flow falling to zero prior to dawn.

Consistent with many earlier studies, we found wide variation in the relationship between the cross-sectional area of stems and the area of conducting xylem. This, in addition to numerous studies that document significant radial and circumferential variations in xylem function within individual trees, suggests that all xylem is not functionally equivalent, which violates some of the assumptions of universal allometric scaling models (West *et al.* 1999). In two of the three species groupings, scaling exponents for the relationship between sapwood area and stem radius differed significantly from a recently proposed theoretical value of 7/3 (Enquist *et al.* 2002). More data are needed to determine whether the mean scaling exponent of 1.69 reflects 5/3-power or 7/4-power scaling of conducting area with stem radius.

Our results further suggest that the relative amount of conducting vs non-conducting xylem at a given stem diameter was not determined solely by the presence of

vessels vs tracheids as primary conducting elements. It is unlikely that site environmental conditions played a significant role in determining the size dependence of water transport capacity because the *P. ponderosa* trees were growing in a semiarid site with high atmospheric evaporative demand, yet relative amounts of sapwood area at a given size were similar to those observed in *T. heterophylla* trees growing in a moist forest with lower evaporative demand. Moreover, the size dependence of sapwood area was different in *T. heterophylla* from that in *P. menziesii* and *T. plicata* although the individuals sampled for all three species occurred in the same forest stands. It is probable that the relationship between cross-sectional area of active xylem and tree size is governed by multiple features of hydraulic architecture operating over a broad range of scale, from the transport efficiency of individual conducting elements, to the overall ratio of leaf area, to sapwood area for the entire tree.

Quarter-power allometric scaling models (Enquist 2002) have reinvigorated interest in universal constraints that lead to convergence in functioning at multiple scales from plant to ecosystem. The challenge is to understand the mechanistic basis of these models and to identify the relevant structural and functional traits that determine whether there is convergence or divergence among species with regard to allometric scaling relationships for water transport and other functional attributes.

Acknowledgements

This research was supported by the USDA Forest Service Ecosystem Processes Program, the National Science Foundation (IBN), the Western Regional Center (WESTGEC) of the National Institute for Global Environmental Change (NIGEC) through the US Department of Energy (Cooperative Agreement No. DE-FC03-90ER61010), and the Wind River Canopy Crane Research Facility located within the Wind River Experimental Forest, T. T. Munger Research Natural Area in Washington State, USA. The facility is a cooperative scientific venture between the University of Washington, the USDA Forest Service Pacific Northwest Research Station and Gifford Pinchot National Forest. We are grateful to Manuela Huso for statistical advice.

References

- Apple, M., Tiekotter, K., Snow, M. *et al.* (2002) Needle anatomy changes with increasing tree age in Douglas-fir. *Tree Physiology* **22**, 129–136.
- Becker, P., Gribben, R.J. & Lim, C.M. (2000) Tapered conduits can buffer hydraulic conductance from path-length effects. *Tree Physiology* **20**, 965–967.
- Bohonak, A.J. & van der Linde, K. (2004) RMA: software for reduced major axis regression, Java version. www.kimvdlinde.com/professional/rma.html
- Bond, B.J. (2000) Age-related changes in photosynthesis of woody plants. *Trends in Plant Science* **5**, 349–353.

- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multitmodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, USA.
- Dye, P.J., Olbrich, B.W. & Calder, I.R. (1992) A comparison of the heat pulse method and deuterium tracing method for measuring transpiration from *Eucalyptus grandis* trees. *Journal of Experimental Botany* **43**, 337–343.
- Enquist, B.J. (2002) Universal scaling in tree and vascular plant allometry toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiology* **22**, 1045–1064.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. *Nature* **395**, 163–165.
- Enquist, B.J., West, G.B., Charnov, E.L. & Brown, J.H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**, 907–911.
- Enquist, B.J., West, G.B. & Brown, J.H. (2000) Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. *Scaling in Biology* (eds J.H. Brown & G.B. West), pp. 167–198. Oxford University Press, Oxford, UK.
- Goldstein, G., Andrade, J.L., Meinzer, F.C. *et al.* (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell & Environment* **21**, 397–406.
- Granier, A. (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology* **3**, 309–320.
- Hatton, T.J. & Vertessy, R.A. (1990) Transpiration of plantation *Pinus radiata* estimated by the heat pulse method and the Bowen ratio. *Hydrological Processes* **4**, 289–298.
- Hunt, R. (1982) *Plant Growth Curves: The Functional Approach to Plant Growth Analysis*. University Park Press, Baltimore, MD, USA.
- James, S.A., Clearwater, M.J., Meinzer, F.C. & Goldstein, G. (2002) Variable length heat dissipation sensors for the measurement of sap flow in trees with deep sapwood. *Tree Physiology* **22**, 277–283.
- James, S.A., Meinzer, F.C., Goldstein, G. *et al.* (2003) Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* **134**, 37–45.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S. & Birdsey, R.A. (2003) National-scale biomass estimators for United States tree species. *Forest Science* **49**, 12–35.
- Jiménez, M.S., Nadezhdina, N., Cermak, J. & Morales, D. (2000) Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiology* **20**, 1149–1156.
- Kalma, S.J., Thornburn, P.J. & Dunn, G.M. (1998) A comparison of heat pulse and deuterium tracing techniques for estimating sap flow in *Eucalyptus grandis* trees. *Tree Physiology* **18**, 697–705.
- Kozłowski, J.K.M. & Konarzewski, M. (2004) Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? *Functional Ecology* **18**, 283–289.
- McCulloh, K.A. & Sperry, J.S. (2005) Patterns in hydraulic architecture and their implications for transport efficiency. *Tree Physiology* **25**, 257–267.
- McCulloh, K.A., Sperry, J.S. & Adler, F.R. (2003) Water transport in plants obeys Murray's law. *Nature* **421**, 939–942.
- McDowell, N.G., Phillips, N., Lurch, C., Bond, B.J. & Ryan, M.G. (2002) An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology* **22**, 763–774.
- Meinzer, F.C., Goldstein, G., Franco, A.C. *et al.* (1999) Atmospheric and hydraulic limitations on transpiration in Brazilian cerrado woody species. *Functional Ecology* **13**, 273–282.
- Meinzer, F.C., Goldstein, G. & Andrade, J.L. (2001) Regulation of water flux through tropical forest canopy trees: do universal rules apply? *Tree Physiology* **21**, 19–26.

- Meinzer, F.C., James, S.A., Goldstein, G. & Woodruff, D. (2003) Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell & Environment* **26** (1147–1155).
- Meinzer, F.C., Woodruff, D.R. & Shaw, D.C. (2004) Integrated responses of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection. *Plant, Cell & Environment* **27**, 937–946.
- Meir, P. & Grace, J. (2002) Scaling relationships for woody tissue respiration in two tropical rain forests. *Plant, Cell & Environment* **25**, 963–973.
- Mencuccini, M. (2002) Hydraulic constraints in the functional scaling of trees. *Tree Physiology* **22**, 553–565.
- Nadezhdina, N., Cermak, J. & Ceulemans, R. (2002) Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors. *Tree Physiology* **22**, 907–918.
- Niinemets, U. (2002) Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. *Tree Physiology* **22**, 515–535.
- Phillips, N.G., Ryan, M.G., Bond, B.J., McDowell, N.G., Hinckley, T.M. & Cermák, J. (2003) Reliance of stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology* **23**, 237–245.
- Pothier, D., Margolis, H.A., Poliquin, J. & Waring, R.H. (1989) Relation between the permeability and anatomy of jack pine sapwood with stand development. *Canadian Journal of Forest Research* **19**, 1564–1570.
- Robinson, D. (2004) Scaling the depths: below-ground allocation in plants, forests and biomes. *Functional Ecology* **18**, 290–295.
- Ryan, M.G., Bond, B.J., Law, B.E. *et al.* (2000) Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia* **124**, 553–560.
- Spicer, R. & Gartner, B.L. (2001) The effects of cambial age and position within the stem on specificity conductivity in Douglas-fir. *Trees* **15**, 222–229.
- Thomas, S.C., Jasienski, M. & Bazzaz, F.A. (1999) Early vs. asymptotic growth responses of herbaceous plants to elevated CO₂. *Ecology* **80**, 1552–1567.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.
- West, G.B., Brown, J.H. & Enquist, B.J. (1999) A general model for the structure and allometry of plant vascular systems. *Nature* **400**, 664–667.
- Wullschlegel, S.D., Meinzer, F.C. & Vertessy, R.A. (1998) A review of whole-plant water use studies in trees. *Tree Physiology* **18**, 499–512.

Received 13 September 2004; revised 7 January 2005; accepted 26 April 2005