

LETTER

Universal hydraulics of the flowering plants: vessel diameter scales with stem length across angiosperm lineages, habits and climates

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Abstract

Angiosperm hydraulic performance is crucially affected by the diameters of vessels, the water conducting conduits in the wood. Hydraulic optimality models suggest that vessels should widen predictably from stem tip to base, buffering hydrodynamic resistance accruing as stems, and therefore conductive path, increase in length. Data from 257 species (609 samples) show that vessels widen as predicted with distance from the stem apex across angiosperm orders, habits and habitats. Standardising for stem length, vessels are only slightly wider in warm/moist climates and in lianas, showing that, rather than climate or habit, plant size is by far the main driver of global variation in mean vessel diameter. Terminal twig vessels become wider as plant height increases, while vessel density decreases slightly less than expected tip to base. These patterns lead to testable predictions regarding evolutionary strategies allowing plants to minimise carbon costs per unit leaf area even as height increases.

Keywords

Adaptation, allometry, convergence, hydraulic architecture, lianas, linear models, optimality models, vessel density, vessel taper, xylem.

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INTRODUCTION

Across angiosperms, vessels in main stems vary from a few micrometres to over half a millimetre in diameter, with slight differences in diameter markedly affecting conductance (Comstock & Sperry 2000; Cruiziat *et al.* 2002; Sperry *et al.* 2008). Given its functional importance, to understand the ecology and evolution of plant hydraulic performance it is essential to identify the main drivers of variation in mean vessel diameter across species. Mean vessel diameter has been shown to vary predictably with both climate and plant height (Wheeler *et al.* 2007; Carlquist 2012). Because maximum height also varies with climate (Moles *et al.* 2009), it is not clear whether climate or height is the main driver of variation in mean vessel diameter. Here, we provide the first test of the main drivers of global variation in average vessel diameter across the flowering plants taking into account stem dimensions, climate and habit.

Many dozens of studies over the past 50 years have documented variation in average vessel diameter across habitats (Baas & Carlquist 1985; Wheeler *et al.* 2007; De Micco *et al.* 2008; Bosio *et al.* 2010; Boura *et al.* 2011; Carlquist 2012; etc.). Vessel diameter–climate associations are usually explained as the result of selection favouring different combinations along the embolism resistance–conductive efficiency

trade-off (Lens *et al.* 2004; Carlquist 2012). Given plants of the same size, in areas subject to cold or drought, selection should favour narrow, slowly conducting but embolism-resistant vessels, whereas in warm, moist areas, it should favour wide, rapidly conducting but more vulnerable ones.

At the same time, mean vessel diameter is wider in larger plants (Fig. 1a, b; Wheeler *et al.* 2007; Carlquist 2012), a feature usually explained as the result of selection favouring the maintenance of constant hydraulic resistance as plants grow in size. Recent evidence suggests that the vessel diameter–plant size relationship is predictable across species, based on the scaling of vessel diameter against stem diameter (McCulloh *et al.* 2010; Olson & Rosell 2013; Olson *et al.* 2013), and against stem length in a limited phylogenetic and environmental sampling of angiosperms (Anfodillo *et al.* 2006; Weitz *et al.* 2006; Petit *et al.* 2008, 2010; Fan *et al.* 2009; Zach *et al.* 2010; Bettiati *et al.* 2012; Gleason *et al.* 2012; Aloni 2013). Hydraulic optimality (HO) models predict that stem length should determine whether vessels at the base of a plant are, on average, narrow or wide, regardless of environment (West *et al.* 1999; Anfodillo *et al.* 2006; Olson *et al.* 2013). HO models build on the idea that, all else being equal, resistance to conduction in a pipe increases with increasing length, because additional wall area per unit water volume and therefore friction is being added (West *et al.* 1999; Comstock & Sperry

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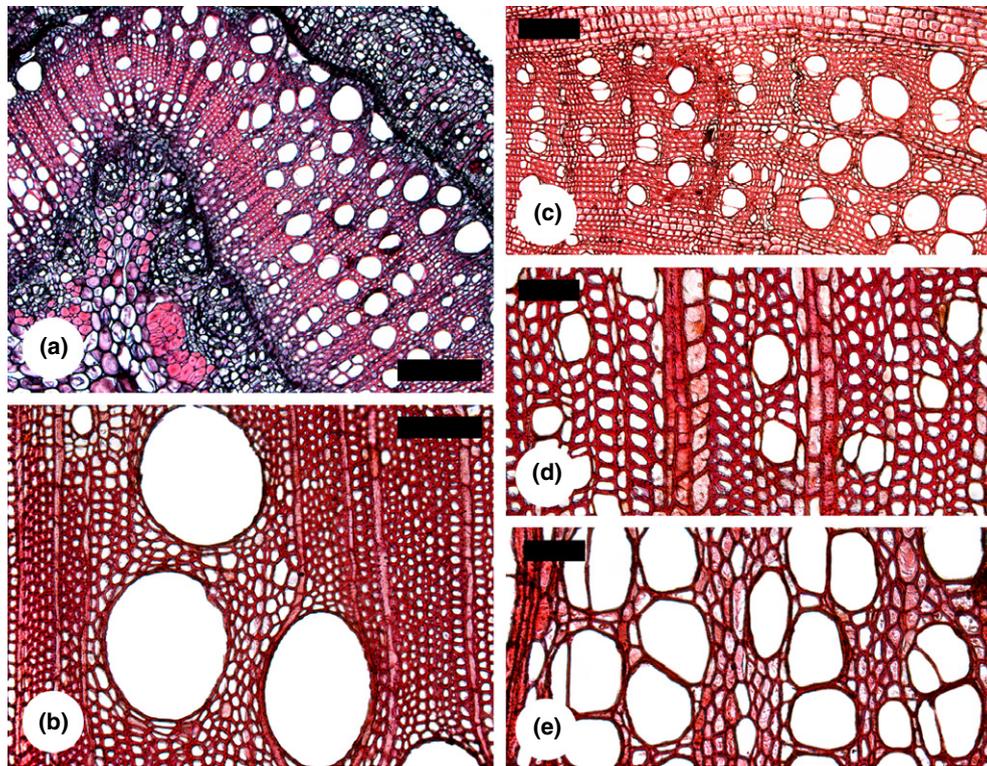


Figure 1 Vessel diameter variation. (a) Twig vessels of *Eucalyptus regnans* are much narrower than those at the stem base (b). (c) Vessels are narrow in the earliest formed secondary xylem, at the centre of the stem (at left), and become wider with each layer produced (right, *Austrobaileya scandens*). Basipetal and radial increases in conduit diameters are collectively known as Sanio's Laws. (d, e) Lianas have markedly wide vessels for a given stem diameter. (d) This 2-cm-diameter and 2.48-m tall stem of the self-supporting *Trimenia neocaledonica* had vessels 65 μm in mean diameter. (e) A stem 1.6 cm diameter and 18 m long of lianescent *T. moorei* had vessels 93 μm in mean diameter. Scale bar = 50 μm .

2000). But because conduction in a pipe increases with radius to the fourth power (Cruziat *et al.* 2002), small increases in vessel diameter are predicted to be sufficient to offset drops in conductivity with increase in conductive path length (Becker & Gribben 2001). Selection is therefore expected to favour vessels that widen from the narrow apical vessels found in leaves and twigs to the wide ones found at stem bases, buffering path length-imposed resistance. HO models thus give reason to expect a predictable relationship between average vessel diameter and plant height, and that the relation should be similar across angiosperm lineages, habits and habitats (Enquist 2003; Anfodillo *et al.* 2006; Savage *et al.* 2010; Hölttä *et al.* 2011; Petit & Anfodillo 2011).

Identifying whether climate or height is the main factor driving vessel diameter variation across communities and species would contribute to constructing explanations of plant hydraulic evolution. Finding that climate is a better predictor of average vessel diameter than stem length would mean that selection favouring embolism resistance via narrow vessels in dry and cold areas overcomes that favouring the maintenance of constant hydrodynamic resistance. Because HO models posit that selection favouring constant resistance is stronger, finding that climate is a better predictor would suggest that these models require modification. Finding, instead, that stem length is a stronger predictor of average vessel diameter than climate would mandate explicitly factoring conductive path length into virtually all studies of hydraulic architecture across habits, habitats and plant sizes. The approach we propose

here represents the first quantitative integration of stem size into studies of mean vessel diameter variation across angiosperm lineages, habits and habitats. To achieve this integration, we first examine HO predictions regarding the relationship between size and average vessel diameter. The resulting information then allows us to turn to the vessel diameter–climate relationship.

The two main HO predictions that we test are *scaling as such* and *specific exponent* predictions. Scaling as such refers to the expectation of a predictable relationship of specified sign between average vessel diameter and stem length across clades, habits and habitats. Specific exponent predictions refer to the value of the slope of this scaling relationship. Although the former is implicit in the latter, it is important to separate them here. This is because, whatever the exact exponent, finding a predictable relationship across species means that the vessel diameter–stem length relationship can be used to ‘factor out’ stem size when examining vessel diameter–climate hypotheses. A universal vessel–stem relationship across the flowering plants has never been posited by any conceptual framework other than HO models, and all current HO models predict a positive vessel diameter–stem length relationship. As a result, finding a scaling-as-such relationship would provide strong support for current HO models.

With regard to specific exponent predictions, although all agree that vessel diameter should scale with a positive slope against stem length, different HO models often generate different predictions regarding the specific values of scaling

exponents. Comparing the observed vessel diameter–stem length exponent with model predictions illuminates the different aspects of plant hydraulic biology that HO models depict. We examined the prediction, based on West *et al.* (1999; see also Anfodillo *et al.* 2006; Petit & Anfodillo 2009; Enquist *et al.* 2009; West *et al.* 2009; Savage *et al.* 2010), that across a broad sampling of plants, the vessel diameter–stem length scaling exponent should converge on a minimum value of about 0.2 (Fig. S1). This exponent expresses how fast or slow vessels become wider with distance from the stem tip. Lower exponents denote very narrow vessels basally, high hydrodynamic resistance and low photosynthetic productivity. Higher exponents lead to wider conduits basally. More rapidly widening vessels lower resistance, but lead to distribution networks with very large fluid volumes per body mass. Excessive fluid volumes likely lead to high network construction and transport costs, so selection is expected to minimise fluid volume to the extent possible (Banavar *et al.* 1999). In addition, wider vessels are in general more vulnerable to embolism (Carlquist 1985, 2012; Hargrave *et al.* 1994; Wheeler *et al.* 2005; Hacke *et al.* 2006; Cai & Tyree 2010). A vessel widening exponent approaching 0.2 is predicted to maintain whole-tree hydraulic resistance and leaf-specific conductivity constant as a tree grows in height, while minimising embolism risk and network fluid volume (see Fig. S1; West *et al.* 1999; Enquist 2003; Anfodillo *et al.* 2006; Savage *et al.* 2010; Petit & Anfodillo 2011).

After documenting the vessel diameter–stem length relationship, we then examined to what extent variation in vessel diameter was accounted for by climate. Using temperature, precipitation and evapotranspiration data, we tested the often repeated prediction (Baas & Carlquist 1985; Lens *et al.* 2004; Wheeler *et al.* 2007; De Micco *et al.* 2008; Bosio *et al.* 2010; Boura *et al.* 2011; Carlquist 2012 etc.) that plants of dry or cold areas should have narrower vessels than plants from warm, moist habitats, e.g. '[conduit dimensions]... are related to plant size, but populations in cooler locations have narrower [conduits] than one would expect on the basis of plant size and age, and smaller [conduits] are believed to be of selective value in these environments because of their resistance to embolisms' (Carlquist 1989, p. 257).

We also examined the roles of vessel density and the climbing vs. self-supporting habit in explaining mean vessel diameter variation. There is a marked negative relationship between vessel diameter and density across the angiosperms generally, with few large vessels or many small vessels trading off for stem transectional space (Sperry *et al.* 2008). Given that the trade-off is pervasive, variation in average vessel diameter for a given stem length seems likely associated with differences in vessel density. Moreover, habit is often cited as being strongly associated with differences in mean vessel diameter (Carlquist 1985, 2012; Ewers *et al.* 1990; Lens *et al.* 2004; Wheeler *et al.* 2007; Olson & Rosell 2013). Most notably, lianas and other non self-supporting plants have been known for centuries to have vessels that are much wider for a given stem diameter than in self-supporting counterparts (Fig. 1d, e). We test the prediction that liana vessels are wide for a given stem diameter because their stems are disproportionately long.

We show that across the woody angiosperms, stem length is by far the most important driver of variation in mean vessel

diameter. Despite vast differences in habitat, stem construction, stem length–diameter proportions and vessel diameter–stem diameter relations across habits, when average hydraulically weighted vessel diameter is plotted against stem length, a global scaling-as-such proportionality emerges. Our results agree to a remarkable degree with predictions regarding the specific values of vessel diameter–stem length scaling exponents. We comment on testable causal scenarios suggested by our data, and in the context of global vessel–stem scaling show that climate and habit have only minor explanatory roles.

METHODS

Sampling and anatomical measurements

To test the prediction of 'universal' vessel diameter–stem length scaling, it is necessary to examine the widest possible array of habitats, habits and xylem constructions across a maximal phylogenetic span. With 609 samples from 257 species (Appendix S1), our sampling covered virtually all the vessel bearing angiosperm orders (Appendix S2). With regard to habit, we sampled self-supporting plants ranging from shrubs 0.5 m tall to trees 60 m tall, including succulents, parasites and monocots (Appendix S2). Plants that could not maintain their tips above ground level when the base of the sampled stem was held erect there were classed as non self-supporting and included scramblers and climbers from 0.5 to over 50 m long. The self-/non self- distinction was reflected in a binary 'habit' variable (Appendix S1). With regard to habitats, most samples came from wild plants, and covered an alpine-to-lowland, tropical-to-temperate and wet-to-dry range spanning the majority of woody plant biomes.

We collected one sample per individual from the outer basal wood, usually from three individuals per species, and processed them using standard anatomical technique for light microscopy (vouchers at MEXU). Given a constant rate of vessel widening across species, if some have wider apical conduits, then they will also have wider basal conduits. To take apical vessel diameter into account, we sectioned samples from distalmost twigs. We measured stem diameter or circumference at the height at which samples were taken using a tape, and height with a Tru-Pulse 200B laser rangefinder (Laser Technology Inc., Centennial, CO, USA), or with a tape, using rappelling gear when necessary. Mean vessel diameters were based on 25 vessels per sample drawn at random from the outer xylem layers, traversing growth rings when present. We converted natural vessel diameter to hydraulically weighted diameter per sample using the formula

$$Dh = \frac{\sum_{n=1}^N d_n^5}{\sum_{n=1}^N d_n^4}$$

where d_n is the natural vessel diameter in μm of vessel n (Kolb & Sperry 1999). Using these values per sample we then calculated species mean values of average vessel diameter at the stem base (Dh_0), at the stem apex (Dh_{N-1}) and stem diameter and length (Appendix S1). Vessel density at the base (Vmm_0) and at the apex (Vmm_{N-1}) was measured as the number of vessels per 25 fields, divided by the field diameter or the radial

subset thereof occupied by xylem, to calculate the number of vessels per square millimetre of xylem transection.

Linear models testing HO predictions

To examine the scaling relationship between stem length and diameter we fitted a model predicting stem length based on stem diameter, habit and a stem diameter · habit interaction term, using species mean values. A significant interaction would mean differing scaling slopes between self- and non-self-supporting plants. When this interaction was not significant, we refitted the model without it to test for differences in intercept between habits. Differing intercepts would suggest different mean values of stem length for a given stem diameter per habit.

Fitting similar models, we examined how well vessel diameter at the base of the plant was predicted by stem diameter, habit and stem diameter · habit, and by stem length, habit and stem length · habit. Likewise, for stem tips we fitted a model predicting vessel diameter based on stem length, habit and stem length · habit. Models predicting Dh_0 and Dh_{N-1} based on stem length (SL) allowed us to calculate the Widening Ratio (WR), given that if $Dh_0 \propto SL^a$, and $Dh_{N-1} \propto SL^b$, then $WR = SL^a/SL^b$.

In addition to stem length, we examined the role of vessel density in the prediction of vessel diameter. It was not possible simply to add vessel density to the model predicting vessel diameter based on stem length and habit because of collinearity. Accordingly, we generated residuals of the model predicting vessel diameter based on stem length and habit. We then fitted another model to examine how well the residual variation in vessel diameter (not explained by stem length and habit) was accounted for by vessel density. We also examined the scaling of vessel density with length by fitting models predicting vessel density at the base and tip based on stem length (i.e. tree height or liana length, not distance from the tip from which the tip sample was collected), habit and stem length · habit.

To test for differences between monocots and ‘dicots’ (angiosperms minus monocots), we fitted models predicting vessel diameter at the base and at the tip of the stem based on stem length (again, tree height or liana length), a monocot-dicot binary variable (Appendix S1) and a stem length · monocot-dicot interaction. We \log_{10} transformed all continuous data and fitted models using R v.2.14.1. (www.R-project.org). Given a constant rate of vessel widening, the ‘cause’ of a given average vessel diameter is stem length. Moreover, the error in measurement of stem length was likely much less than that in anatomical measurements. Given both causal hypothesis and error considerations, we used ordinary least squares regression (Smith 2009). We also analysed data in a phylogenetic context. Based on a supertree of the sampled species, we estimated phylogenetic signal in the data and fit linear models taking into account phylogenetic relationships (methods and results in Appendix S2).

Environmental variables and vessel diameter–climate associations

Climate is often thought to predict mean vessel diameter, with narrow vessels favoured in dry or cold embolism-prone areas,

and wide vessels in moist, warm ones (Baas & Carlquist 1985; Carlquist 1989, 2012). Using ArcGis 9.3 (ESRI, Redlands, CA, USA), we tested these expectations by extracting 19 temperature, precipitation and seasonality variables from WorldClim (Hijmans *et al.* 2005) and yearly potential evapotranspiration from the CGIAR-CSI Global Soil-Water Balance Database (www.cgiar-csi.org). WorldClim variables formed groups of strongly correlated variables. These groupings were reduced into four environmental indices using principal component analyses (PCA): two indices reflecting the precipitation of the moist and dry portions of the year, an index of mean temperature and another reflecting temperature seasonality. All variables, except for those in the mean temperature index, were \log_{10} transformed before PCA, given that their distributions were skewed and included only positive values. The first principal components of each PCA explained a very large percentage of the variation (66–90%, Table S2) and were used as indices. We calculated Pearson correlations between $\log_{10} Dh_0$ and the yearly potential evapotranspiration and between $\log_{10} Dh_0$ and the four environmental indices. We calculated partial correlations between these variables controlling for \log_{10} stem length.

RESULTS

In species mean values, our sampling spanned a range in stem length from 0.50 to 49.2 m, stem diameter from 0.13 cm to 1.5 m, and hydraulically weighted vessel diameter at the base of the plant (Dh_0) of 13.47–423.94 μm and at the stem tip (Dh_{N-1}) of 6.69–178.8 μm .

Linear models testing HO predictions: scaling as such

Stem length–diameter allometry had a slope of 0.71 (95% CI 0.66, 0.75) across both self- and non self-supporting plants (albeit nearly significantly differently, with the stem diameter · habit (self-/non self-) interaction term $P = 0.061$; Table 1). As expected, non self-supporting plants had a much higher stem length–diameter intercept than self-supporting plants (Fig. 2a). The relationship between hydraulically weighted vessel diameter at the stem base (Dh_0) and stem diameter paralleled the stem length–diameter relationship (slope 0.34; Table 1). For a given stem diameter non self-supporting plants had significantly wider vessels (Fig. 2b).

The conspicuous differences in Dh_0 -stem diameter scaling between self- and non self-supporting plants nearly collapsed when Dh_0 was plotted against stem length (Fig. 2c). The stem length · habit interaction term was not significant ($P = 0.176$, Table 1), and the difference in intercepts between self- (1.50) and non self-supporting plants (1.67) was minimal (even less at the apex, Dh_{N-1} , Fig. 3a). This means that lianas and other non self-supporting plants do have wider hydraulic diameters than self-supporting plants for a given stem length, but that this difference is slight. By the same token, monocots and ‘dicots’ had identical slopes, despite their very different constructions and ontogenies, and differed slightly in intercepts (Table 1). Monocots have slightly wider vessel diameters than dicots at the base (Fig. 3b), likely associated with their wide apical vessels (Fig. 3c). Models taking into account phylogenetic relationships were very similar to those based on

Table 1 Linear allometric models fitted, with all continuous variables \log_{10} transformed

	$SL \sim SD + \text{Habit}$	$Dh_0 \sim SD + \text{Habit}$	$Dh_0 \sim SL + \text{Habit}$	$Dh_{N-1} \sim SL + \text{Habit}$	$Dh_0 \sim SL + \text{Mono/Dico}$	$Dh_{N-1} \sim SL + \text{Mono/Dico}$	Residuals $Dh_0 \sim SL + \text{Habit} \sim Vmm_0$
R²_{adj}	0.80	0.56	0.63	0.26	0.60	0.35	0.33
Model fit	PGLS: 0.82 $F_{(2, 251)} = 517.1$, $P < 0.001$	PGLS: 0.60 $F_{(2, 251)} = 159.7$, $P < 0.001$	PGLS: 0.68 $F_{(2, 254)} = 218.4$, $P < 0.001$	PGLS: 0.35 $F_{(2, 254)} = 45.52$, $P < 0.001$	PGLS: 0.66 $F_{(2, 254)} = 195.3$, $P < 0.001$	PGLS: 0.43 $F_{(2, 254)} = 70.15$, $P < 0.001$	PGLS: 0.41 $F_{(1, 209)} = 104.8$, $P < 0.001$
Equality of slopes	$P = 0.061$	$P = 0.654$	$P = 0.176$	$P = 0.386$	$P = 0.562$	$P = 0.352$	–
Equality of intercepts	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.021$	$P < 0.001$	$P < 0.001$	–
Slope	0.71 (0.66, 0.75)	0.34 (0.30, 0.38)	0.46 (0.41, 0.51)	0.24 (0.18, 0.30)	0.52 (0.47, 0.57)	0.29 (0.24, 0.34)	–0.17 (–0.211, –0.14)
Non self-supporting intercept	PGLS: 0.71	PGLS: 0.35	PGLS: 0.48	PGLS: 0.24	PGLS: 0.52	PGLS: 0.30	PGLS: –0.19
Self-supporting intercept	0.85 (0.80, 0.91)	2.06 (2.01, 2.11)	1.67 (1.60, 1.73)	1.33 (1.26, 1.41)	–	–	0.27 (0.22, 0.33)
Dicot intercept	PGLS: 0.79	PGLS: 2.04	PGLS: 1.67	PGLS: 1.39	–	–	PGLS: 0.30*
Monocot intercept	0.05 (–0.03, 0.12)	1.52 (1.45, 1.59)	1.50 (1.43, 1.57)	1.257 (1.18, 1.33)	–	–	–
	PGLS: 0.003	PGLS: 1.53	PGLS: 1.55	PGLS: 1.28	1.50 (1.45, 1.54)	1.22 (1.17, 1.27)	–
Monocot intercept	–	–	–	–	PGLS: 1.51	PGLS: 1.18	–
K of residuals	0.157	0.177	0.202	0.232	1.68 (1.57, 1.80)	1.59 (1.47, 1.70)	–
Phylogenetic signal test	$P = 0.414$	$P = 0.113$	$P < 0.01$	$P < 0.001$	PGLS: 1.72	PGLS: 1.57	0.173
Figure	Fig. 2a	Fig. 2b	Fig. 2c	Fig. 3a	Fig. 3b	Fig. 3c	Fig. 4c

*This model does not have a self–non self-variable as a predictor because habit was taken into account in the model used to generate vessel diameter–stem length residuals; the global model intercept is given here.

SL, stem length; *SD*, stem diameter; *Habit*, a self- vs. non self-supporting binary variable; *Dh₀*, average hydraulically weighted vessel diameter at the stem base; *Dh_{N-1}*, hydraulically weighted vessel diameter at the stem apex; *Mono/Dico*, a monocot vs. ‘dicot’ (angiosperms minus the monocots) binary variable; *Vmm₀*, vessel density at the base; PGLS, results from phylogenetic generalised least squares models, see Appendix S2; K, the K phylogenetic statistic, see Appendix S2.

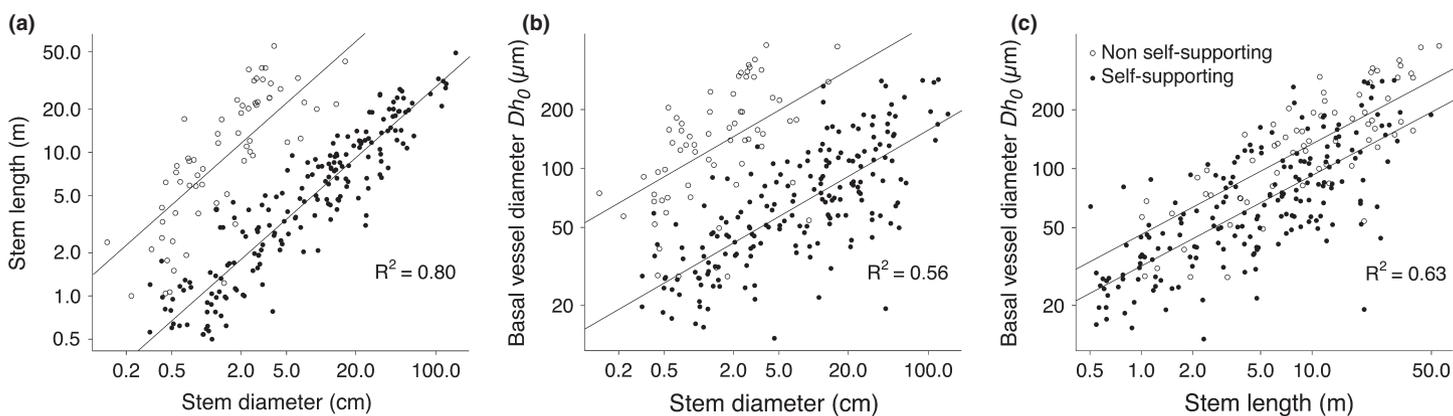


Figure 2 The universal relationship between vessel diameter and stem length. (a) The predictable stem length–diameter relation across the flowering plants. Non self-supporting plants have much longer stems for a given diameter than self-supporting plants. (b) The relationship between hydraulic vessel diameter at the base of the plant (Dh_0) and stem diameter parallels the stem length–diameter relationship: lianas have markedly wider vessels for a given stem diameter than self-supporting plants. (c) Virtually all differences between self- and non self-supporting plants disappear when Dh_0 is plotted against stem length. Non self-supporting plants have very slightly higher hydraulic vessel diameter for a given stem length than self-supporting plants, but the degree of tip-to-base vessel widening is identical (see Table 1).

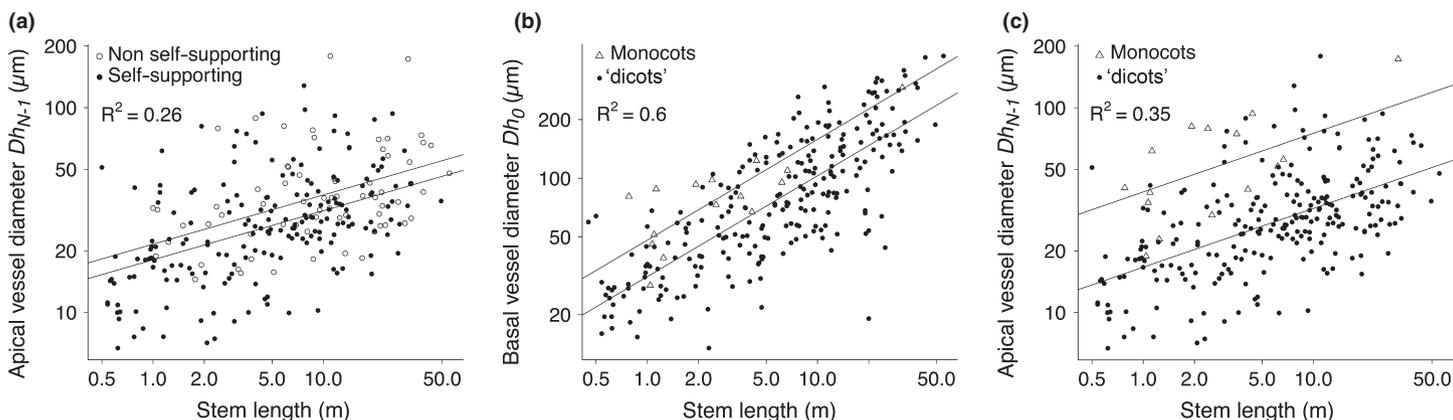


Figure 3 Vessel diameter scaling at the stem tip between self- and non self-supporting plants, and base and tip scaling between monocots and ‘dicots’ (a) Hydraulically weighted vessel diameter at the stem tip Dh_{N-1} scales with total stem length (tree height or liana length) with a similar exponent between self- and non self-supporting plants, with plants with longer stems having wider vessels apically. Underscoring the ‘universal’ nature of the relationship, vessel-stem length scaling is similar between monocots and ‘dicots’ (angiosperms minus the monocots) both at the stem base (b) as well as at the stem apex (c), despite their very different ontogenies and anatomical configurations.

standard statistics (see Table 1), as expected given the low phylogenetic signal detected in our data (see Appendix S2).

Linear models testing HO predictions: specific exponent predictions

Stem length predicted average vessel diameter well, both at the base of the plant as well as the tip (Fig. 2c, 3a). Average hydraulic vessel diameter at the base of the plant (Dh_0) scaled with stem length (SL) with an exponent of 0.46 (95% confidence interval 0.41–0.51; $Dh_0 \propto SL^{0.46}$). Average vessel diameter at the tip of the plant (Dh_{N-1}) scaled with stem length with an exponent of 0.24 (95% CI 0.18–0.30; $Dh_{N-1} \propto SL^{0.24}$), suggesting that taller plants on average bear wider vessels at the base and at the apex (Fig. 2c, 3a; Table 1). If tip-to-base vessel widening occurs at a similar rate across angiosperms, but vessels are wider at the stem apex of some species, then vessels will be wider at the stem base of these species. The relative

rate of widening in vessel diameter across angiosperms is represented by the Widening Ratio (WR). Given the scaling relationships between Dh_0 , Dh_{N-1} and stem length SL that we recovered in models that distinguish between habits (Table 1), then $WR = SL^{0.46}/SL^{0.24} = SL^{0.22}$ across species. A scaling exponent of 0.22 is in agreement with HO expectations (Petit & Anfodillo 2011), given that it is slightly larger than the predicted minimum value of 0.2. The models predicting Dh_0 and Dh_{N-1} based on stem length and the dicot vs. monocot variable gave nearly identical results, with $WR = SL^{0.52}/SL^{0.29} = SL^{0.23}$.

Linear models testing HO predictions: Role of vessel density

We explored the role of vessel density using the residuals of the model predicting Dh_0 based on stem length and habit (Fig. 4a, b). The model predicting these residuals based on

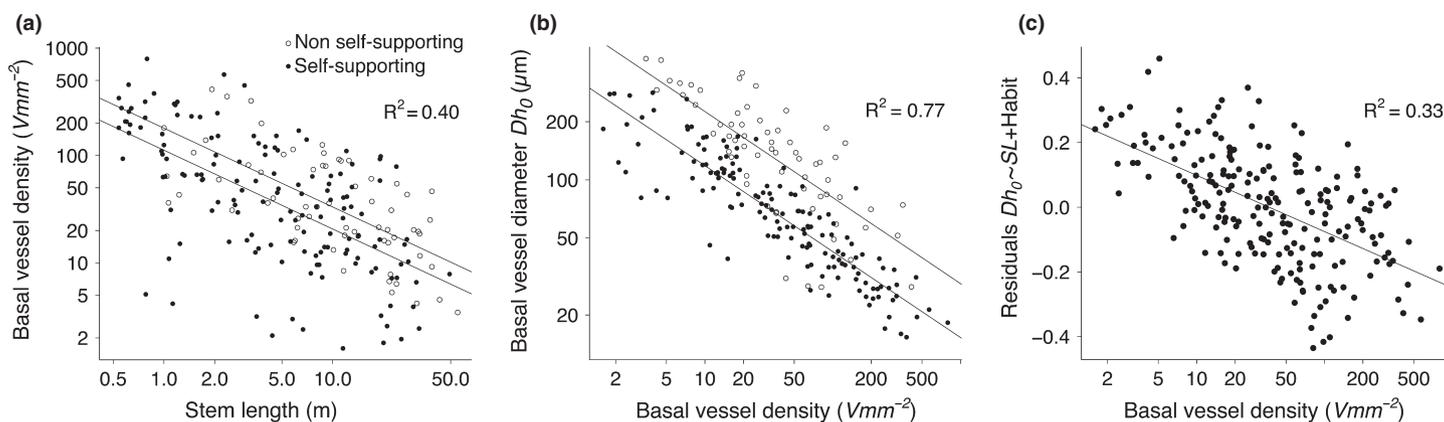


Figure 4 ‘Universal’ elements of angiosperm hydraulic architecture and the interplay between vessel density, stem length and vessel diameter. (a) Vessel density decreases with increasing stem length, while vessel diameter increases (Fig. 2c). (b) Decrease in vessel density with an increase in diameter reflects a space trade-off between few wide vs. many narrow vessels, manifest in the negative relation here. (c) Of the residual variation in basal vessel diameter (Dh_0) regressed on stem length (SL) plus habit, 33% is explained by variation in vessel density. Together, stem length, vessel density and the self- vs. non self-supporting habit explain the bulk of variation in mean vessel diameter globally. Other factors, such as climate, explain very little of the residual variation.

vessel density explained 33% of the variation in vessel diameter. In other words, a third of the total variance in vessel diameter not explained by stem length and habit was explained by vessel density (Table S1, Fig. 4c). Vessel density was predicted well by stem length and habit at the base of the plant (Fig. 4a), and more loosely at the tips (Table S1). Again, no difference in vessel density–stem length scaling was detected between habits ($P = 0.577$). The vessel diameter–vessel density trade-off (in our data set represented by a correlation of -0.84 , Fig. 4b; Sperry *et al.* 2008), in tandem with basipetal vessel widening, led to basal vessel density decreasing with stem length with a slope of -0.73 independently of habit (95% C.I. -0.86 , -0.61 ; Fig. 4).

Environmental variables and vessel–climate associations

Although traditionally Dh_0 is regarded as a clear reflection of water availability and temperature, climate variables explained only a limited amount of variation in vessel diameter, especially when stem length was taken into account. Yearly potential evapotranspiration and mean temperature respectively accounted for 15 and 20% of the variation in non-stem size-standardised vessel diameter (Table 2). However, both percentages decreased to just 6% when stem length was taken into account (Table 2). Precipitation of the moist portion of

the year and temperature seasonality explained around 9% of variation in Dh_0 , but this percentage was not significantly different from zero when stem length was taken into account (Table 2). Precipitation of the dry portion of the year was not significantly associated with Dh_0 .

DISCUSSION

Across the flowering plants, the abundant variation in features such as vessel element morphology, imperforate tracheary element type and parenchyma distribution is overlain on what can be thought of as universal elements of angiosperm hydraulic architecture. Within this architecture, a very large proportion of variation in vessel diameter is explained by stem length (63%). Of the residual variation, over a third is explained by differences in vessel density (Table 1, Fig. 4c), leaving little variation available for explanation by other factors. Possible additional factors affecting hydrodynamic resistance include features such as pit membrane characteristics, perforation plate type and vessel length distribution (e.g. Comstock & Sperry 2000; Christman & Sperry 2010; Jacobsen *et al.* 2012). Given the relatively small amount of variation not accounted for by stem length and vessel density (Fig. 4), it seems possible that additional factors either contribute little to explaining variation in basal vessel diameter,

Table 2 Variation in hydraulically weighted vessel diameter ($\log_{10} Dh_0$) explained by environmental indices (see Table S2)

Environmental variable	Explained variation of Dh_0 , not taking stem length into account		Explained variation of Dh_0 taking stem length into account (Dh_0 -stem length + habit residuals)	
	R^2	P -value	R^2	P -value
Yearly potential evapotranspiration*	0.15 (+)	< 0.001	0.06 (+)	< 0.001
Precipitation of the moist portion of the year	0.09 (+)	< 0.001	<0.01 (+)	0.53
Precipitation of the dry portion of the year	<0.01 (–)	0.23	0.01 (–)	0.14
Mean temperature index	0.20 (+)	< 0.001	0.06 (+)	< 0.001
Temperature seasonality index	0.08 (–)	< 0.001	<0.01 (–)	0.23

* log transformed. Correlations significant at $\alpha = 0.05$ in bold. (+) or (–) gives the sign of the corresponding correlation coefficient.

or scale with stem length in ways that are proportional with vessel diameter.

Compared with climate, stem length is by far the main driver of global variation in mean vessel diameter. Direct correlations between vessel diameter and environmental variables revealed several significant associations ($R^2 \leq 0.2$, Table 2), albeit weak in comparison with stem length. If climate were the principal selective agent on vessel diameter independently of stem length, then climate–vessel correlation would be high even factoring out stem length. However, once stem length was taken into account, vessel–climate correlations lost significance or became very low ($R^2 \leq 0.06$, Table 2). HO models along with our data suggest that within populations any heritable variants with vessel diameter–stem length exponents < 0.2 (high hydraulic resistance) or $>> 0.2$ (risk of embolism and redundant network fluid volume) will tend to be selected against, leading to large samples converging on the 0.2 exponent (Fig. 2c, Fig. S1).

Given these results, it seems necessary to incorporate vessel widening in the context of stem length into explanations of variation in average vessel diameter. Given a constant vessel diameter–stem length slope, our data also suggest that, congruent with the hypothesis of Carlquist (1989) quoted above, there is slight room for higher or lower vessel diameter–stem length intercepts across climates. Higher intercepts imply slightly wider vessels for a given stem length. Analyses using stem length-corrected vessel diameter suggested that plants of warmer locales with higher potential evapotranspiration have very slightly wider vessels for a given stem size (Table 2). The approach taken here thus offers a means of taking stem size into account when testing predictions regarding the causes of variation in average vessel diameter.

Vessel diameter and the climbing habit

One of these predictions, tested here, is that vessel widening should be similar across habits, even lianas. Lianas are universally highlighted as having unusually wide vessels (Carlquist 1985; Ewers *et al.* 1990; Fig. 1d, e). We show that their mean hydraulically weighted vessel diameters are only slightly wider given stem length than those of self-supporting plants (Table 1). Liana vessel diameters widen with stem length at the same rate as their self-supporting counterparts irrespective of vastly different tissue mechanical properties and stem length–diameter proportions (Figs 2 and 4). Given such pervasive patterns of scaling, selection minimising hydraulic resistance via vessel widening as a function of stem length plausibly appears to be a major factor shaping hydraulic architecture globally, even across habits as diverse as trees, succulents and lianas. The patterns recovered also suggest the role of vessel widening in plant carbon economy.

Terminal vessel widening, basipetal variation in vessel density and plant carbon economy

Our data suggest that twig vessels in taller plants are wider than those in shorter ones (Fig. 3a, c), offering a potential element for exploration in HO models (e.g. West *et al.* 1999 and Savage *et al.* 2010). One testable explanation for increase in terminal

twig vessel diameter with height can be constructed by asking what conditions would, as plant size increases, permit an invariant amount of carbon to be invested in the active conduit network per unit leaf area. Given variants in a population, those that minimise supply costs per leaf area would be expected to be favoured, driving plants towards the maintenance of a (per-leaf area) fixed volume of active vascular tissue. Within this fixed volume, the conduits in a small plant are numerous and narrow. However, in a tall plant, to reach from base to tip, this fixed volume must be ‘stretched.’ Because hydraulic resistance increases with conductive path length, and given the inescapable many narrow vs. few wide trade-off, supplying a given leaf area with a constant flow through a longer, transectionally narrower volume could require wider and therefore fewer twig conduits. Slight widening of apical conduits with height growth would lead to a marked increase in total path conductance, potentially counteracting any loss of conductivity with reduction in conduit number. Terminal widening with height growth would therefore seem to offer a mechanism by which a given leaf area can be supplied with water even over vast height increases without the need for ever-increasing sapwood volume per unit leaf area, and therefore without increasing carbon investment in active xylem per unit leaf area as a tree grows (Enquist *et al.* 1999; cf. Dybzinski *et al.* 2011; Stephenson *et al.* 2014). This notion predicts an isometric leaf area–sapwood volume (not area) relation over all size classes, a prediction borne out by the few data available (e.g. see data in Table 1 of Sillett *et al.* 2010). This scenario also suggests that testing the relationship between conduit number and leaf area is an important element in understanding plant carbon economy.

Another factor that may contribute to carbon economisation with height growth was suggested by basipetal vessel density changes (Table S1). Because wider vessels occupy more stem transectional area than narrow ones, variation in vessel diameter (Dh) along the stem would inevitably cause variation in vessel density (Vmm). Assuming constant conductive area along the stem, Vmm would be expected to scale as $Vmm \propto Dh^{-2}$ given packing limit assumptions (Sperry *et al.* 2008). Given that we observed $Dh \propto SL^{0.46}$, we would expect $Vmm \propto SL^{-0.92}$. We observed a Vmm – SL scaling exponent of -0.73 with a confidence interval that is close ($-0.86, -0.61$), but does not include the expected value of -0.92 (see also Bettiati *et al.* 2012). A less negative exponent can be explained if conductive area increases towards the base of the plant. The observed relationship $Vmm \propto SL^{-0.73}$ would imply $Vmm \propto Dh^{-1.59}$. This divergence from the expected $Vmm \propto Dh^{-2}$ suggests that the vessel diameter–density trade-off could alter slightly base to tip, presumably via the diversion of additional space and likely carbon from neighbouring cell types to vessels. Methodological decisions, such as the inclusion of interfascicular areas in twig vessel density measurements, could affect comparisons of apical and basal vessel density. The pattern of increase implicated here therefore awaits confirmation, e.g. via measurements of conductive area along the lengths of stems. But taken together with apical vessel widening, slight increase in conductive area basipetally would plausibly contribute to maintaining the carbon costs of supplying a given leaf area constant even over vast increases in height.

CONCLUSION

Our data clearly suggest that the main driver in average vessel diameter variation is conductive path, as reflected by stem length. Factors such as climate, habit, or the monocot–dicot distinction (Table 1, Fig. 3c) had only limited roles in explaining mean vessel diameter variation. The vessel diameter–stem length scaling value found here is entirely in agreement with the model of West *et al.* (1999) as interpreted by Petit & Anfodillo (2009; also that of Savage *et al.* 2010 and Sperry *et al.* 2012; see also Becker & Gribben 2001), with the Widening Ratio = 0.22, very close to the predicted minimum of 0.2. Such strong coincidence of specific optimality model predictions with data from nature is very unlikely to be artefactual. Convergence on predicted exponent values strongly suggests that current HO models succeed to a remarkable degree in capturing important aspects of plant hydraulic biology. Our results therefore provide compelling evidence in favour of the interpretation that natural selection favours optimal rates of vessel widening compensating resistance with increase in conductive path. It is this selective process that leads to a universal degree of xylem vessel widening with respect to stem length across lineages, habits and habitats (Fig. 2). Derivative testable predictions regarding the plant–environment relation include that vessel diameter–stem length scaling variants (whether natural or produced via mutants or artificial selection) should have differing performance as predicted by Fig. S1, and that selection on plant stature should alter vessel diameter and vice versa. With regard to carbon economy, predictions include constant carbon investment in active xylem per unit leaf area, as reflected by leaf area–sapwood volume isometry, and the deviation of carbon from support to conductive tissue basipetally. The phenomenon of universal vessel diameter–stem length scaling therefore seems to offer a means of generating predictions regarding the ontogeny of plant hydraulics, the action of selection on heritable variation and plant evolutionary response to environmental differences across biomes.

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AUTHORSHIP STATEMENT

MO, TA and JR performed fieldwork, collected data, conducted analyses and wrote the manuscript; GP and AC contributed data, participated in analyses and in the writing of

the manuscript; SI coordinated NC fieldwork and contributed to various drafts; CL-G, LA-C and MC participated in field and laboratory work and contributed to the preparation of the manuscript.

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