

Vessel diameter–stem diameter scaling across woody angiosperms and the ecological causes of xylem vessel diameter variation

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Summary

- Variation in angiosperm vessel diameter is of major functional significance. In the light of recent models predicting optimal vessel taper given resistance imposed by conductive path length, we tested the prediction that plant size should predict vessel diameter, with dryland plants having narrower vessels for their stem sizes.
- We assembled a comparative dataset including vessel and stem diameter measurements from 237 species from over 40 angiosperm orders across a wide range of habits and habitats.
- Stem diameter predicted vessel diameter across self-supporting plants (slope 0.36, 95% CI 0.32–0.39). Samples from 142 species from five communities of differing water availability showed no tendency for dryland plants to have narrower vessels. Predictable relationships between vessel diameter and stem diameter mirrored predictable relationships between stem length and diameter across self-supporting species.
- That vessels are proportional to stem diameter and stem diameter is proportional to stem length suggests that taper in relation to conductive path length gives rise to the vessel diameter–stem diameter relationship. In turn, plant size is related to climate, leading indirectly to the vessel–climate relationship: vessels are likely narrower in drier communities because dryland plants are on average smaller, not because they have narrow vessels for their stem sizes.

Introduction

Variation in the diameters of vessels, the tubes that transport water in most woody plants, is thought to be of central adaptive importance (Sperry *et al.*, 2006). Wider vessels conduct water more efficiently (Pfeffer, 1900; Ewart, 1906; Stopes, 1907; Dimond, 1966), but also seem likely to be more vulnerable to breaking of the conductive stream and blockage by gas embolism (Wheeler *et al.*, 2005; Hacke *et al.*, 2006; Christman *et al.*, 2009). Because different combinations of habit and habitat are expected to allow different balances of efficiency vs vulnerability, selection should favor different mean vessel diameters in different selective contexts (Carlquist, 1966, 2001; Tyree & Zimmermann, 2002). Despite the importance of understanding the role of variation in vessel diameter in plant function, it is still unclear whether selection favors a given mean vessel diameter as a function of environmental conditions, stem size, or both.

On one hand, there are compelling reasons to expect that mean vessel diameter between individuals should vary as a function of plant size. Studies of plant hydraulics have long incorporated principles from fluid mechanics theory to build these explanations; for example, ‘The flow of water through open

vessels filled with sap takes place in accordance with Poiseuille’s formula for the flow through rigid cylindrical tubes... [h]ence the velocity of flow is directly proportional to the pressure and to the square of the radius of the tube, inversely proportional to the length of the tube and to the viscosity of the liquid’ (Ewart, 1904–1905, p. 554; Jost, 1907; Farmer, 1918b; Woodhouse, 1933). Building on Poiseuille’s law, explicit quantitative models have been constructed to describe plant conductive systems (Levitt, 1956; Bonner, 1959; Cowan, 1965; Byrne *et al.*, 1977). Recent years have seen a flowering of hydraulic models, all of which share their inclusion of both vessel diameter and Poiseuille’s law as central considerations (recent examples include West *et al.*, 1999; Becker *et al.*, 2000; Comstock & Sperry, 2000; Mencuccini, 2002; Enquist, 2003; McCulloh *et al.*, 2003; Hacke *et al.*, 2006; Sperry *et al.*, 2008; Savage *et al.*, 2010; Hölttä *et al.*, 2011; Bettiati *et al.*, 2012).

Poiseuille’s law suggests how, for a conduit of uniform diameter, increased length will lead to predictable increases in resistance to flow. These increases can be ameliorated if vessels widen basipetally (‘taper’; Farmer, 1918b; Becker & Gribben, 2001; James *et al.*, 2003; Fan *et al.*, 2009; Bettiati *et al.*, 2012). Hydraulic scaling models predict ways that vessels should widen as path length increases. Based on anatomical studies, mean

conduit diameter clearly seems wider in larger stems (Grew, 1682; Carlquist, 1969, 1984, 1985b, 1989; Baas *et al.*, 1988; Butterfield *et al.*, 1993; Lens *et al.*, 2004; Olson & Rosell, 2006; Wheeler *et al.*, 2007; Christensen-Dalsgaard *et al.*, 2008; Vázquez-Sánchez & Terrazas, 2011). Moreover, conduits in a limited sampling of conifers and angiosperms do appear to widen from the stem tip toward the base (Sanio, 1872; De Bary, 1884; Ewers & Zimmermann, 1984; Ewers *et al.*, 2004; Anfodillo *et al.*, 2005; McCulloh & Sperry, 2005; Hacke *et al.*, 2006; Weitz *et al.*, 2006; Coomes *et al.*, 2007; Mencuccini *et al.*, 2007, 2011; Olson, 2007; Nygren & Pallardy, 2008; Sperry *et al.*, 2008; Terrazas *et al.*, 2008; Fan *et al.*, 2009; Petit *et al.*, 2010; Petit & Anfodillo, 2011). Thus, both theoretical predictions and empirical evidence seem to support the dependence of vessel diameter on stem size.

However, average vessel diameter appears just as clearly predicted by water availability across habitats. By far the most frequently cited result from studies of variation in wood anatomy across habitats is that vessels are narrower in dryland plants (Carlquist, 1966, 1975; Carlquist & Hoekman, 1985; Baas & Schweingruber, 1987; Lens *et al.*, 2007; Wheeler *et al.*, 2007; Sonsin *et al.*, 2012). Positive association between vessel diameter and climate is usually interpreted as reflecting a response to environmental conditions. Conductively efficient, wide vessels are seen as adaptations to moist conditions, with more cavitation-resistant narrow vessels expected to be favored in drier areas (Carlquist, 2001; Tyree & Zimmermann, 2002).

The perspective that environment should dictate vessel diameter would seem to contradict the notion that stem size should predict vessel diameter. For environment to predict vessel diameter would require independence of vessel diameter from stem size. Independence of vessel size from stem size is the only way that the vessels of dryland plants could be narrower than those of counterparts of identical stem dimensions in moist areas. By the same token, the prediction that stem size should predict vessel diameter requires the assumption that vessel diameter is insensitive to environment. From this point of view, because hydrodynamic resistance should accumulate by the same amount per increase in conductive path length irrespective of environmental situation, similar-sized stems should have similar-sized vessels independent of water availability. Here, we attempt to reconcile these conflicting perspectives.

We compared these divergent predictions regarding the importance of stem size and environment on vessel diameter with a sampling of over 200 species spanning most orders of woody vessel-bearing angiosperms. We tested the expectation that vessel diameter should scale predictably with stem size across self-supporting species in the light of a recent scaling model (Savage *et al.*, 2010). This model provides reasoning regarding the value of the optimal proportionality between vessel and stem diameter. It gives reason to suspect that, for self-supporting plants, above a vessel diameter–stem diameter proportionality of *c.* 0.33, the increase in cavitation risk fast outstrips any gain in carbon fixation rate. By the same token, below 0.33, the drops in conductive rate are so severe as to offset any gains in persistence via greater embolism resistance.

Our wide sampling provides a test of the prediction of Savage *et al.* (2010) that the vessel diameter–stem diameter relationship should converge on a scaling exponent of 0.33 regardless of environment or phylogenetic ancestry.

Conductive path length is a central part of this interpretation, because basal vessel diameter should reflect taper in the context of a given conductive path length. Therefore, we tested the participation of conductive path length in producing the vessel–stem diameter relationship in two ways. First, we compared vessel–stem diameter relations across the self-supporting species with 33 non self-supporting species. In general, the stems of non self-supporting plants are much longer for their diameters than in self-supporting plants (Ewers *et al.*, 1990). If basal vessel diameter reflects the effects of selection favoring basipetal vessel widening moderating path length imposed hydrodynamic resistance, then non self-supporting plants, with their longer stems and therefore path lengths, should generally have wider vessels for their diameters than self-supporting plants. That lianas have markedly wide vessels for their stem diameters has long been known (e.g. Grew's 1682 descriptions of *Calamus* vessels; Carlquist, 1985a). We expected non self-supporting plants to describe a vessel diameter–stem diameter relationship with a higher *Y*-intercept than self-supporting species (Ewers *et al.*, 1990). Moreover, variation about the *Y*-axis of the vessel–stem diameter relationship should be higher in non self-supporting plants. Self-supporting plants are expected to have broadly predictable stem length–diameter proportions (Niklas & Spatz, 2004). By contrast, non self-supporting plants seem to span a very wide range of stem length–diameter proportionalities. This heterogeneous 'non self-supporting' category includes, at one extreme, species that arch, scramble, or are decumbent (e.g. *Acanthocereus*, *Mirabilis*). Such species would be expected to have stems only slightly longer for their diameters than in self-supporting plants. At the other extreme are climbing lianas, which are extremely long for their diameters (e.g. *Entada*, *Nissolia*). If taper related to conductive path length determines basal vessel proportions, then heterogeneity in stem proportions should predict heterogeneity in the vessel–stem diameter relationship across non self-supporting plants. Finally, the notion that vessel diameter should scale predictably with stem diameter is predicated on the assumption that stem diameter scales with conductive path length, and that path length is approximated by stem length (Savage *et al.*, 2010). We therefore tested the expectation that stem length should be predicted by stem diameter across 75 of the self-supporting species we studied anatomically.

Finally, to test the prediction that vessel diameter should reflect moisture availability, we focused on samples from 142 species from five communities of highly contrasting environments, including two lowland rainforests, one seasonally dry tropical deciduous forest, a temperate woodland and a tropical dry savanna. We tested the prediction that plants of moist areas should have wider vessel diameters for a given stem diameter than similarly-sized counterparts in dry areas. We conclude this article by discussing ways to reconcile the apparently contradictory observations that vessel diameter is predicted by both stem size and environment.

Materials and Methods

Sampling and anatomical measurements

The prediction of Savage *et al.* (2010) is that vessel diameter \propto stem diameter^{1/3} in self-supporting plants. In other words, given a stem diameter X , we predict a given vessel diameter Y regardless of phylogenetic affinity. Because this involves a prediction of convergent evolution, the most stringent test for this hypothesis would include the widest phylogenetic divergence possible, maximizing the opportunities for departing from the expected pattern. For this reason, we collected data from a wide phylogenetic, ecological, and morphological range. We included species from most of the 50 or so orders or major clades (Stevens, 2001 onwards) of vessel-bearing nonmonocot angiosperms (plus two palms and a *Pandanus*) from a very wide range of habitats, including freezing-prone temperate highland forest at 3400 m to tropical lowland forests, mangroves, temperate forest and shrubland, deserts, etc. (Table 1; see the Supporting Information Table S1, with climate data from the WordClim database of Hijmans *et al.* (2005)). Moreover, we have made every effort to sample from the entire span of wood constructions (e.g. from dense, fibrous wood to parenchymatized succulents; from species with a single vascular cambium to species with hundreds of successive cambia and monocots; growth ring types, etc.) and woody plant habits, including trees, shrubs, succulents, lianas and a limited number of arborescent monocots.

We collected one sample per individual from the outer basal wood, usually from three or more individuals per species (200 species; 20 were represented by two individuals and 17 species by one, see Table S1) and processed them using standard anatomical technique for light microscopy. We measured the vessel lumen as a chord that was intermediate between the major and minor diameters from 25 vessels per sample drawn at random from the outer xylem layers (Carlquist & Hoekman, 1985; Lens *et al.*, 2007). In cases in which narrow vessels were scattered among

abundant vascentric tracheids (e.g. *Prostanthera*), we preferentially measured cells in which perforation plates were visible. For all samples in the vessel–stem diameter dataset (Table S1), we measured in the field the stem diameter or circumference at the height at which samples were taken. We also measured stem height directly or extracted this information from the literature for 75 species (Table S2).

From these measurements we constructed four datasets: (1) 204 self-supporting species (the species designated ‘self’ in the self/nonself column in Table S1); (2) 142 species drawn from dataset 1 from five communities with contrasting climate (Table 1; the species designated by codes in the ‘community’ column in Table S1); (3) 33 non self-supporting species (the species designated ‘nonself’ in the self/nonself column in Table S1); and finally, (4) stem length–diameter data from 75 of the species in dataset 2 (Table S2).

Vessel diameter–stem diameter scaling across orders

To test the expectation of predictable vessel diameter–stem diameter scaling, and in particular the hypothesis of an exponent of 0.33 of Savage *et al.* (2010), we fitted a linear model predicting vessel diameter based on stem diameter across the 204 self-supporting species (dataset 1). Stem and vessel diameters were log₁₀ transformed to linearize relationships between variables and to meet regression assumptions. These and subsequent statistical analyses were performed in R v. 2.14.1 (R Development Core Team, 2011).

Environmental influence on the vessel diameter–stem diameter relationship

We then examined the expectation that dryland species should have narrower vessels than those in moist areas. We took this prediction to mean that, while larger plants do have larger vessels, samples from communities in areas of lower water availability

Table 1 Locations and climates of the 142 species in five communities varying in moisture availability used to test the hypothesis that dryland species should have narrower vessels for their stem diameters than plants in moist areas

Locality	Coordinates	Vegetation	Mean annual precipitation (mm)	Mean annual temperature (°C)	Precipitation of wettest month (mm)	Precipitation of driest month (mm)	Cold month temperature (°C)	Precipitation of warm quarter (mm)
Chamela, Jalisco, Mexico	19°29'58"N, 105°2'8"W	Tropical dry forest	794	26	216	1	16.0	406
Yengo, NSW, Australia	32°46'44"S, 150°55'38"E	Temperate sclerophyll forest	807	16	109	35	2.9	296
Howard Springs, NT, Australia	12°29'58"S, 131°6'0"E	Tropical savanna	1513	27	373	1	17.2	409
Daintree, QLD, Australia	16°6'12"S, 145°27'9"E	Tropical rainforest	2091	26	462	26	18.2	1035
Los Tuxtlas, Veracruz, Mexico	18°34'51"N, 95°4'26"W	Tropical rainforest	3454	25	590	62	17.1	947

Species designated by codes in the ‘community’ column in the Supporting Information, Table S1. Climate data for the additional 94 species studied from other localities are given in Supporting Information Table S1

should have narrower vessels for a given stem size than those in areas of greater water availability. To test this prediction, we analysed a subset of our dataset consisting of 142 self-supporting species belonging to five communities varying markedly in water availability and vegetation (Table 1, dataset 2).

To test the prediction that communities in moist environments should have higher vessel diameter–stem diameter Y -intercepts (i.e. wider vessels for a given stem diameter), we fit a linear model predicting \log_{10} vessel diameter based on \log_{10} stem diameter and the nominal variable ‘site’, which was represented by four dummy variables. The driest community (the dry forest at Chamela, Mexico) was chosen as the reference category against which to perform statistical comparisons. We included a \log_{10} stem diameter–site interaction term, which, if significant, would indicate differences in the slope of the relationship (scaling) between vessel diameter and stem size in different environments. After finding that the interaction was nonsignificant ($P=0.84$, see the Results section) and that all communities described the same scaling slope, we tested for differences in the intercept. Significant differences in intercept values would mean that mean vessel diameter changed across environments while controlling for stem diameter. In this way, we tested the prediction that the plants of moister sites would have wider vessels for a given stem diameter than the plants in drier sites.

Vessel diameter, stem diameter, and conductive path length

The vessel diameter–stem diameter relationship is thought to be an indirect one, via stem length and the associated rate of basipetal vessel widening. Accordingly, we examined the role of stem length–diameter relations in two ways. First, we added 33 species of non self-supporting plants (dataset 3 in the initial Materials and Methods paragraph) to our dataset with 204 self-supporting species (dataset 1). Species with stems longer for a given diameter, as in lianas compared with self-supporting plants (Ewers *et al.*, 1990), should have wider vessels for a given stem diameter (Carlquist, 1985a). We fitted a model predicting \log_{10} vessel diameter based on \log_{10} stem diameter and the nominal variable ‘habit’, which took the values ‘self-supporting’ and ‘non self-supporting’ and was represented by a dummy variable. Non self-supporting plants were taken as the reference category against which intercept comparisons were performed. We tested for differences in the scaling of vessel diameter on stem size between the two habits by examining the statistical significance of an interaction term between habit and stem diameter. After finding that scaling did not differ between habits (interaction was nonsignificant with $P=0.59$), we tested for differences between the intercepts of the fitted lines for self-supporting and non self-supporting plants. Differences in intercepts would reflect differences in the mean value of vessel diameter between habits.

In addition, we tested the expectation that a predictable vessel diameter–stem diameter relationship across species implies broadly predictable stem length–diameter relationships across species. We assembled a dataset with direct measurements and

literature values for stem height and diameter from 75 self-supporting species (Table S2). To test the expectation of similar scaling patterns across species, we fitted a linear model predicting \log_{10} height based on \log_{10} diameter.

Diagnosing phylogenetic signal

To explore the need for phylogenetically informed analyses, we constructed a phylogeny for the 204 species of self-supporting plants that are the core of hypotheses testing (the species designated ‘self’ in the self/nonself column in Table S1). This phylogeny (Fig. S1; key to taxon codes given in Table S3) was based on Stevens (2001 onwards) and the pertinent literature for particular groups. We set branch lengths to one, except for polytomies, which we resolved with 0.001 branch lengths. We tested for the presence of phylogenetic signal in the residuals of a regression of vessel diameter on stem diameter through a randomization procedure based on phylogenetically independent contrasts (PICs; Felsenstein, 1985; Revell, 2010) and the K statistic of Blomberg *et al.* (2003) using the R package Picante (Kembel *et al.*, 2010). Phylogenetic signal was detected in residuals (see the Results section), so we recalculated correlations and refit linear models based on PICs.

Results

Across self-supporting species, mean vessel diameter ranged from 15.8 to 218.8 μm , and stems varied from 3.1 mm to 1.1 m in diameter. For non self-supporting species, vessel diameter varied from 31.7 to 383.2 μm , and stem diameter from 4.4 mm to 15.8 cm (Table S1).

Vessel diameter–stem diameter scaling across orders

The model predicting \log_{10} vessel diameter based on \log_{10} stem diameter across self-supporting species is included in Table 2. The model predicted the data well, explaining 65% of the variation in vessel diameter (Fig. 1). The 95% confidence interval for the slope of this relationship included the exponent of 0.33 predicted by Savage *et al.* (2010).

Environmental influence on the vessel diameter–stem diameter relationship

The model predicting \log_{10} vessel diameter based on \log_{10} stem diameter and ‘site’ predicted the data well, explaining 72% of the variation in vessel size (Fig. 2, Table 2). The stem diameter \times site interaction term was nonsignificant ($P=0.84$), implying that all communities showed the same vessel size–stem size scaling slope regardless of environmental conditions. Again, the predicted value of 0.33 was included in the 95% confidence interval for the slope of the model (Table 2). The comparison of mean vessel diameter values through the intercept of the fitted lines per site indicated that all communities had mean vessel diameters that were statistically indistinguishable from one another, except for the dry savanna site (Howard Springs, Table 2), which had

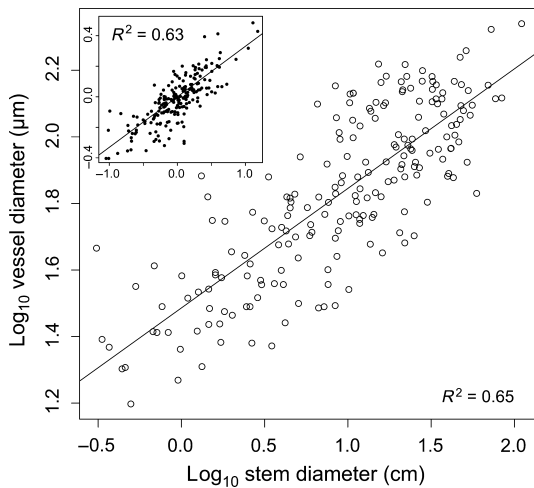


Fig. 1 Vessel diameter is strongly predicted by stem diameter across 204 self-supporting woody species from > 40 orders of angiosperms. Points are species means and the line is a fit of a linear model with $R^2 = 0.65$ and a slope of 0.36 (95% confidence interval 0.32–0.39). Inset shows fit based on phylogenetically independent contrasts (PICs: slope = 0.33, 95% CI 0.29–0.36).

slightly larger vessels. Howard Springs is a dry savanna of rainfall much lower than Los Tuxtlas or Daintree (the rainforests included in the comparison of five communities), with a prolonged hot dry season. These results revealed no tendency for water availability to predict vessel diameter when stem size was taken into account.

Vessel diameter, stem diameter, and conductive path length

The model predicting \log_{10} vessel diameter based on \log_{10} stem diameter and 'habit' predicted the data well, explaining 64% of the variation in vessel size. In contrast with the prediction of

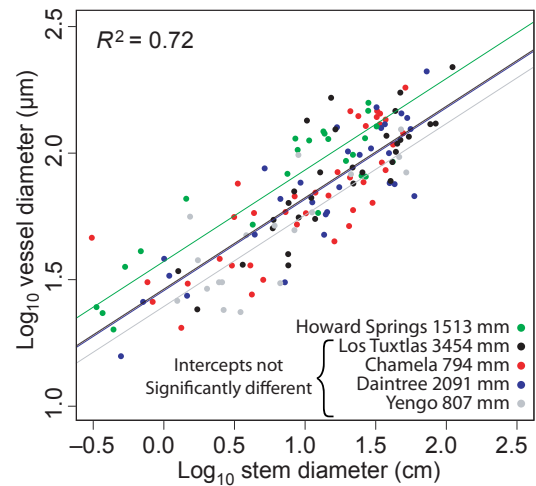


Fig. 2 The fit of a linear model predicting \log_{10} vessel diameter based on \log_{10} stem diameter plus site across five communities ($R^2 = 0.72$) revealed no tendency for plants of drylands to have narrower vessels for their stem diameters than plants from moist areas (full model in Table 2). The communities are listed at lower right according to their position in the graph from top to bottom (their Y-intercepts). Only Howard Springs (green points and line) had a Y-intercept significantly higher than the other communities. However, Howard Springs is one of the drier and more seasonal habitats we sampled, with moderate rainfall falling in a short wet season punctuating a prolonged dry season (see climate data in Table 1). These results contradict the traditional expectation that vessel diameter is greater in areas of greater moisture availability. The figures in the legend refer to mean annual precipitation.

differences in scaling among self-supporting and non self-supporting plants, the model indicated that both habits have the same slope, that is, the same vessel–stem diameter scaling relationship (the stem diameter \times habit term was nonsignificant, $P = 0.59$), and that the 95% confidence interval included the predicted value of 0.33 (Table 2, Fig. 3). Congruent with expectations, non self-supporting plants had a higher intercept than

Table 2 Linear models predicting \log_{10} vessel diameter based on \log_{10} stem diameter of the self-supporting species only, the self-supporting species in five communities with differing water availability, and of both self-supporting and non self-supporting species, as well as the linear model predicting stem length based on stem diameter in self-supporting species

	$\log_{10}VD - \log_{10}SD$	$\log_{10}VD - \log_{10}SD + \text{Site}$	$\log_{10}VD - \log_{10}SD + \text{Habit}$	$\log_{10}SL - \log_{10}SD$
<i>n</i>	204	142	237	75
R^2	0.65	0.72	0.64	0.78
Model ANOVA	$F_{(1,202)} = 376.3^{***}$	$F_{(5,136)} = 74.7^{***}$	$F_{(2,234)} = 208.0^{***}$	$F_{(1,73)} = 269.6^{***}$
$\log_{10}SD$ (95% CI)	0.36 (0.32–0.39) ^{***}	0.36 (0.32–0.40) ^{***}	0.36 (0.32–0.40) ^{***}	0.63 (0.55–0.71) ^{***}
Intercept	1.49 (1.45–1.53) ^{***}	1.46 (1.40–1.52) ^{***}	1.87 (1.82–1.93) ^{***}	0.19 (0.09–0.30) ^{***}
Chamela	–	See intercept	–	–
Daintree	–	–0.01 (–0.07–0.06) ^{ns}	–	–
Howard Springs	–	0.11 (0.04–0.18) ^{**}	–	–
Los Tuxtlas	–	0.001 (–0.06, 0.07) ^{ns}	–	–
Yengo	–	–0.07 (–0.14, 0.01) ^{ns}	–	–
Non self-supporting	–	–	See intercept	–
Self-supporting	–	–	–0.39 (–0.45 to –0.33) ^{***}	–

CI, confidence interval; VD, vessel diameter (μm); SD, stem diameter (cm); ^{***}, $P < 0.001$; ^{**}, $P < 0.01$; ^{ns}, not significant.

self-supporting species (Table 2, Fig. 3). As would be expected given the wide range of non self-supporting stem proportionalities, there was pronounced scatter in the relationship between vessel diameter and stem diameter across the non self-supporting species studied (Fig. 3).

If basal vessel diameter is a reflection of conductive path length, then predictable vessel diameter–stem diameter scaling across self-supporting plants (Fig. 1) suggests that we should observe a predictable stem length–diameter relationship across these species. Bearing out this prediction, height in self-supporting plants was strongly predicted by stem diameter (Fig. 4).

Diagnosing phylogenetic signal

Significant phylogenetic signal was detected in residuals of the regression of \log_{10} vessel size on \log_{10} stem diameter based on self-supporting species ($K=0.19$, $P<0.001$). Significant signal is often taken as indicating that species traits are more similar than expected by chance given the tree topology, branch lengths and the model of evolution the method implies. However, the K statistic was well below 1, suggesting relatively little phylogenetic structuring (to be expected given the lability of size and habit across the clades studied). In any event, recalculation of the correlation between these two variables based on PICs ($r=0.79$, $P<0.001$) was almost identical to that based on raw data ($r=0.81$, $P<0.001$). The model fit with PICs had a slope of 0.33 (95% CI 0.29–0.36, see inset in Fig. 1), congruent with the prediction of Savage *et al.* (2010).

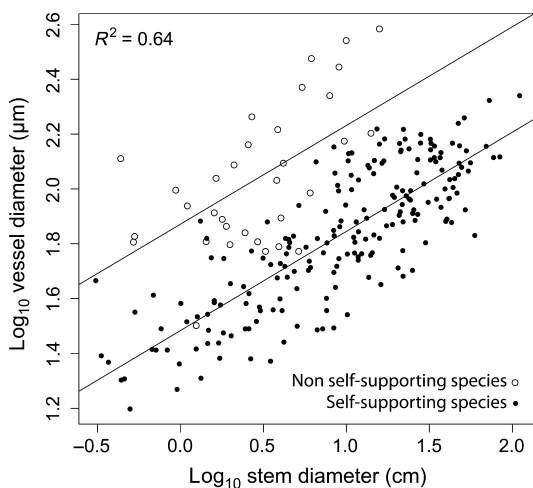


Fig. 3 The vessel diameter–stem diameter relationship reflects the stem length–diameter relationship. Stems that are longer for a given diameter, as in lianas and other non self-supporting species, have vessels that are wider for their stem diameter than in self-supporting species. This result is expected if basal vessel diameter reflects taper as a function of conductive path length, because species with stems that are longer for a given diameter have longer conductive path lengths and as a result wider vessels. Lines are from a linear model predicting vessel diameter based on stem diameter and self-/non self-supporting habits ($R^2=0.64$, slope = 0.36, 95% CI 0.32–0.40).

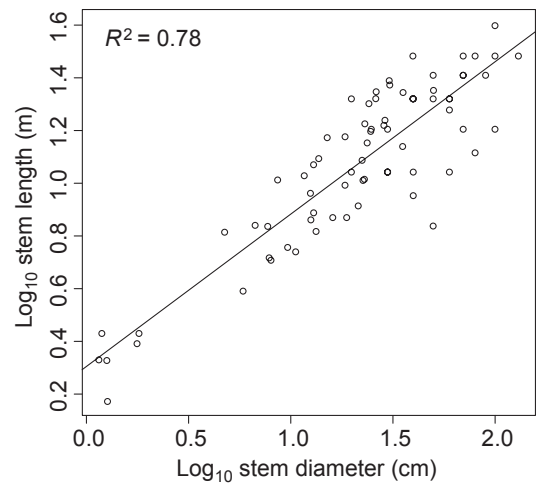


Fig. 4 Stem length–diameter allometry across 75 self-supporting species from the five communities in Fig. 2. If basal vessel diameter reflects taper as a function of conductive path length, then the predictable pattern in Fig. 2 predicts a similar stem length–diameter relations across species, congruent with the pattern recovered here.

Discussion

Our results illustrate the intimate adaptive relationship between environment, stem size, and vessel diameter. If narrower vessels are more resistant to cavitation, then it seems reasonable to expect that selection would favor narrower vessels in dryland plants. However, we found no tendency for species in drier areas to have narrower vessels (Fig. 2, Table 2; nor did Lundgren, 2004; Coomes *et al.*, 2007). In fact, instead of the rainforest species having wider vessels, the only community that had a vessel diameter–stem diameter scaling Y -intercept significantly greater than the others was Howard Springs, a tropical Australian savanna with moderate rainfall (Table 1) and a prolonged, hot dry season. The distribution of points in Fig. 2 suggests that further sampling could eliminate even the difference between Howard Springs and the rest of the communities (see green points in Fig. 2). In any event, these results are sufficient to show that water availability, however judged, did not predict vessel diameter across the communities studied when stem diameter was taken into account. This result points to the likely importance of basipetal widening of conduits in mitigating the increase in resistance as stems, and therefore total conductive path, increase in length (Petit *et al.*, 2008, 2010).

If vessel taper reflects stem length, then the nature of the vessel diameter–stem diameter relationship should at least coarsely predict the stem length–stem diameter relationship. Our results supported this expectation. First, we found a predictable vessel diameter–stem diameter relationship across self-supporting plants (Fig. 1), closely corresponding to the prediction of 0.33 of Savage *et al.* (2010). If this relationship is driven by selection favoring convergence on similar vessel–stem proportionalities as a function of path length-imposed resistance, then this implies that conductive path lengths should be similar for a given stem diameter (cf. Petit & Anfodillo, 2011). We would therefore expect similar patterns of stem length–diameter allometry across

self-supporting species. Across the 75 species for which data were available, this was the case (Fig. 4). We also compared vessel–stem diameter proportionalities between self-supporting plants and non self-supporting plants from a wide array of orders (Table S1). These plants had stems that were markedly longer for their diameters than self-supporting plants. If a given average basal vessel diameter is favored by selection as a function of conductive path length-imposed resistance, and if stem length adequately reflects path length, then individuals with stem lengths markedly longer for their diameters should have vessels that are wider basally (Ewers *et al.*, 1990; Petit & Anfodillo, 2011). Lianas have long been known for having very wide vessels (Carlquist, 1985a; Ewers & Fisher, 1991). However, the presence of wide vessels in lianas has traditionally been ascribed to the need to transport large volumes of water through stems that are much narrower than those that support a similar quantity of crown in self-supporting plants. Path length-induced hydrodynamic resistance is typically not cited in these explanations as a selective factor favoring wider vessels (though see Stopes, 1907; Ewers *et al.*, 1990; McCulloh *et al.*, 2003). Our results suggest that selection favoring optimal taper as a function of stem length could play a central role in driving the vessel diameter–stem diameter relation in lianas as well as in self-supporting plants.

The observation that vessel diameter scales with stem diameter can now be reconciled with the observation that moisture availability positively predicts vessel diameter across habitats. That vessels are proportional to stem diameter (Fig. 1) and stem diameter is proportional to stem (and presumably conductive path) length (Fig. 4) suggests that taper in relation to stem length likely gives rise to the vessel diameter–stem diameter relationship. Climate–vessel relations are probably so often recovered in ecological wood anatomical studies because the narrow vessels of short-statured dryland plants are compared with the wide vessels of plants from moist areas, which are on average larger (Moles *et al.*, 2009). By contrast, we took pains to select a similar range of stem diameters across habitats to avoid this bias. The apparent dependence of vessel dimensions on stem dimensions means that if selection acts to increase cavitation resistance via narrower vessels, it will likely do so via smaller trunks. Similarly, selection favoring increased stature will favor wider vessels. Stem length, diameter and vessel diameter are therefore intimately associated through the action of selection. A prediction emanating from this conclusion is that vessel–stem dimensions in ontogeny should parallel comparative patterns (Olson & Rosell, 2006). Some species, however, may differ from the typical ontogenetic increase in vessel diameter; for example some species have diminishing length-on-age curves (Carlquist, 1975). If our hypothesis is correct, then these curves should still reflect conductive demands. For example, some succulent-stemmed plants produce broad leaves when the stem is actively elongating, but soon lose the leaves and remain largely leafless in subsequent years. How the vessel diameter–stem diameter relation of such species resembles the comparative pattern observed here remains to be examined. Given its likely significance, perhaps the most important direction for future work emerging from the present study is the need to

understand the causes of variation in the vessel diameter–stem diameter relationship.

Our data on the vessel diameter–stem diameter relationship in self-supporting plants showed a marked degree of variation about the Y axis (Fig. 1). Rather than reflecting just measurement error, at least some of this variation is likely of biological significance. It might diagnose variation in stem length–diameter allometry, which is known to vary even between closely related species (Rosell *et al.*, 2012). Variation in any factor that affects flow rate could be expected to affect the vessel diameter–stem diameter relationship (Kocacinar & Sage, 2004). For example, vessels are likely functional for longer times in species with successive cambia. Active vessels deep in the stem mean that outer vessels do not need to be as wide as in species with single cambia, leading to narrower average vessel diameters and lowered vessel diameter–stem diameter Y -intercepts (Carlquist, 1975, 2007). Factors other than vessel diameter likely intervene in the ability of a given species to resist cavitation, such as vessel or imperforate tracheary cell wall thickness, primary membrane properties, lateral wall pit area, phenology and stomatal behavior (Tyree & Sperry, 1989; Tyree & Ewers 1991; Tyree *et al.* 1994). Presumably, any of these factors could affect vessel diameter–stem diameter relations. Different patterns of accumulation of resistance, for example scalariform perforation plates (Christman & Sperry, 2010) or shorter vessels, would seem likely to affect the intercept as well. All else being equal, a species with a greater frequency of endwalls would have greater path length-associated resistance (Handley, 1936; Peel, 1965; Hacke *et al.*, 2006; Sperry *et al.*, 2006) and selection would likely favor more marked basipetal vessel widening. Similarly, differences in vessel density, vessel grouping, or the presence of conductive imperforate tracheary elements might be associated with much of the variation about the Y -axis in the vessel diameter–stem diameter relationship (Fig. 1). We examined relatively few ring porous or alpine species; these might show tendencies to have relatively wider or narrower vessels, but it seems likely that they will describe trajectories within the limits documented here. Some authors suggest that conduit diameter is affected by growth rate (Petit & Anfodillo, 2011). In addition to vessel diameter, many other xylem structural features seem to vary predictably with size. Ray histology seems generally related to stem size, with upright cells being present in narrow stems and procumbent cells in large ones, the long axis of the cells being aligned with the principal direction of translocation (Carlquist, 2001). At the same time, it is unclear how other ray features vary with size, such as the factors that determine the density of rays per unit stem volume. It seems clear that much remains to be investigated regarding the role of size in the evolution of woody plant structure.

Conclusion

Vessel diameter appears to vary across species as an inseparable function of stem size, likely as the result of selection favoring vessels with an optimal balance between hydraulic conductivity and vulnerability to cavitation given conductive path length. At the same time, average vessel diameter often varies with habitat.

These views are compatible if selection, when it increases cavitation resistance via narrow vessels, also reduces stature. By the same token, any increase or decrease in stature will be associated with selection for proportional vessel diameters. This view suggests the need to standardize for stem size when comparing vessel diameters between individuals, and the need to explore the dependence on size of other stem structural attributes. How pervasive these patterns are for plants extinct (Wiemann *et al.*, 1999; Wheeler *et al.*, 2007) and living, and the causes and degree of any deviation from them, are avenues for further work.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Phylogeny of the 204 self-supporting species used for phylogenetic comparative analyses.

Table S1 Species, data, localities, communities, habits

Table S2 Stem height–diameter data

Table S3 Taxon codes for phylogeny

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