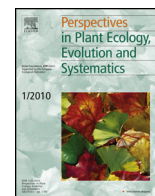




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Research article

Do lianas really have wide vessels? Vessel diameter–stem length scaling in non-self-supporting plants



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ABSTRACT

Lianas and other climbing plants are known for their extraordinarily wide vessels. Wide vessels are thought to contribute to the extreme hydraulic efficiency of lianas and to play a part in their ability to dominate many tropical habitats, and even their globally increasing abundance with anthropic disturbance. However, recent hydraulic optimality models suggest that the average vessel diameter of plants generally is the result of tip-to-base vessel widening reflecting the effects of selection buffering conductive path length-imposed hydraulic resistance. These models state that mean vessel diameter should be predicted by stem length, by implication even in lianas. We explore vessel–stem relations with 1409 samples from 424 species in 159 families of both self- and non-self-supporting plants. We show that, far from being exceptional in their vessel diameter, lianas have average natural (not hydraulically weighted) vessel diameters that are indistinguishable for a given stem length from those in self-supporting plants. Lianas do, however, have wider variance in vessel diameter. They have a small number of vessels that are wider than those in self-supporting plants of similar stem lengths, and also narrower vessels. This slightly greater variance is sufficient to make hydraulically weighted vessel diameters in lianas higher than those of self-supporting counterparts of similar stem lengths. Moreover, lianas have significantly more vessels per unit of wood transection than self-supporting plants do. This subtle combination of slightly higher vessel diameter variance and higher vessel density for a given stem length is likely what makes lianas hydraulically distinctive, rather than their having vessels that are truly exceptionally wide.

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Introduction

In his 1682 *Anatomy of Plants*, Nehemiah Grew discussed the vessels of a rattan, a lianescent palm, noting that the vessels “are so wide, that. . . your Breath will immediately pass, through the *Aer-Vessels*, the length of the *Cane*” (p. 116). In the subsequent centuries, one of the most often-repeated observations in comparative plant morphology is that lianas have unusually wide vessels given their stem diameters as compared to self-supporting plants (Carlquist, 1985a and cites therein; de Bary, 1884; Ewers et al., 1990; Ewers and Fisher, 1991; Haberlandt, 1914; Westermaier and Ambronn, 1881, etc.; Fig. 1). The distinctive hydraulics of lianas is even cited

as explaining their dominance in seasonal tropical forests (Jiménez-Castillo and Lusk, 2013; van der Sande et al., 2013) and why lianas appear to be increasing in abundance as a result of anthropic disturbance globally (Schnitzer and Bongers, 2011).

Despite a very long tradition of regarding lianas as having unusually wide vessels, recent work suggests that their average vessel diameter might be more or less what would be expected given their stem length. Hydraulic optimality models lead to the expectation that vessels should be wider on average at the bases of large plants than of small ones. This pattern is thought to be due to selection favoring the maintenance of constant hydraulic resistance as plants grow larger (Anfodillo et al., 2006; Bettiati et al., 2012; Enquist, 2003; Tyree and Ewers, 1991; West et al., 1999; Zwieniecki et al., 2001). A relation known as Poiseuille's Law suggests that, without compensatory changes elsewhere in the system, increases in conductive path length will lead to a drop in flow rate (Vogel, 2003). Small increases in conduit diameter lead to substantial increases in flow rate, meaning that flow rate can be maintained constant as length increases. Narrow conduits are favored at stem

Abbreviations: SL, stem length; SD, stem diameter; Dh, hydraulically weighted vessel diameter; VD, vessel diameter; Vmm⁻², vessel density.

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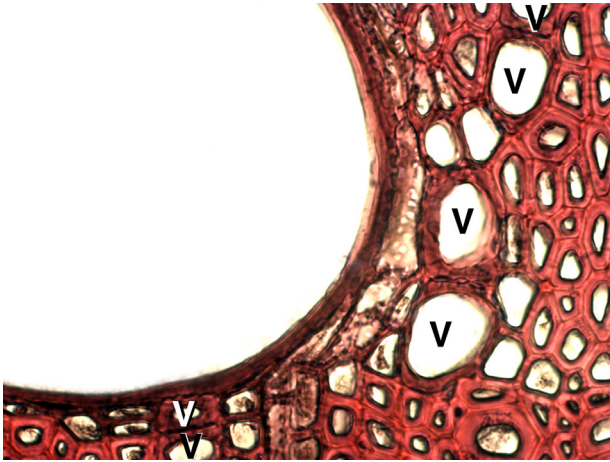


Fig. 1. Anatomical phenomena in lianas. Lianas are universally cited as having very wide vessels. However, lianas also often have narrow (V) vessels surrounding the wide ones, as in this stem of *Pandorea pandorana* (Bignoniaceae).

tips and leaves, likely for several reasons. One reason is that, as in animal capillaries, diffusion is most efficient out of very narrow conduits. In self-supporting plants, vessels become predictably wider farther and farther from the tip down the stem (Anfodillo et al., 2006, 2013). The notion that liana vessel diameter could be explained as the result of selection favoring lowered resistance is a longstanding one, e.g. “In [lianas] the construction of the conducting system is governed. . . by two factors, namely the great length of the conducting region and the relatively small cross-sectional area available for the disposition of the conducting elements. These conditions render it highly necessary that all features which tend to lower the rate of conduction should be eliminated; in the case of water-conducting vessels the most serious obstacle to rapid flow arises from the adhesion of the water to the walls of the tube. This difficulty can be most readily overcome by an increase in the diameter of the tube, since in the case of a cylinder of a given height the area of the wall is directly proportional to the radius, whereas the volume varies as the square of the radius.” (Haberlandt, 1914, pp. 324–325, citing Westermaier and Ambronn, 1881)

Although it has been in the literature for over 100 years, the notion that average vessel diameter should in some way be predicted by stem length in lianas has only been examined very recently. Anfodillo et al. (2006) included a single non-self-supporting plant, *Hedera helix*, in their comparative study of hydraulic vessel diameter–stem length relations. They found that average hydraulic vessel diameter at the stem base was predicted well by stem length across species, with *Hedera* not appearing as an outlier when plotted with self-supporting plants. Other authors have found that vessel diameter in lianas was broadly predictable based on stem diameter, which should be related to stem length (Ewers et al., 1990; Jacobsen et al., 2010; see also Gehring et al., 2004 on stem diameter–biomass allometry; Niklas, 1994a). Lianas had higher vessel diameter–stem diameter intercepts, meaning that for a given stem diameter, lianas had wider vessels than self-supporting plants (Olson et al., 2013; Olson and Rosell, 2013). However, much remains to be explored regarding the pervasiveness and causes of this pattern.

Here, we used a dataset of over 1400 samples to explore in detail the differences in average vessel diameter between self- and non-self-supporting plants. With a broad phylogenetic and morphological sampling, our first aim was to examine how lianas and self-supporting plants, despite their very different biomechanical constructions, differ or resemble one another in their stem length–diameter relations. Second, we tested the prediction, in

accordance with hydraulic optimality models (Petit and Anfodillo, 2009; Savage et al., 2010; Sperry et al., 2012; West et al., 1999), that vessel diameter–stem length scaling should be similar in self- and non-self-supporting plants. Finally, we compared vessel abundance between self- and non-self-supporting plants. Some authors have reported that lianas have more abundant vessels than conventional plants (e.g. Carlquist, 1985a, and references therein) whereas others report that they are less abundant (e.g. Angyalossy et al., 2012; Baas and Schweingruber, 1987; Crivellaro et al., 2012). This approach allowed us to examine the common impression that lianas have stem lengths that are not predictable for a given stem diameter, and vessels that are exceptionally wide and abundant as compared to self-supporting plants.

Materials and methods

We use the shorter term “lianas” interchangeably with “non-self-supporting plants”; our non-self-supporting category included prostrate plants, scramblers, and many sorts of climbers, e.g. via tendrils, roots, twining, hooks, etc. as well as climbing monocots, herbaceous climbers, and species with successive cambia or multiple vascular cylinders, in an attempt to include all the major types of non-self-supporting plants (Isnard and Silk, 2009; Rowe et al., 2004). We measured 1409 samples (267 non-self-supporting and 1142 self-) from 424 species (84 non-self-supporting, 340 self-supporting), in 331 genera and 159 families, representing 58 orders or major clades of angiosperms (sensu APG, 2009, see Appendix A). We selected species, most collected in the wild, from across the angiosperm phylogeny and thereby included non-self-supporting species from all orders that include lianas. We usually collected three or more individuals per species (80% of species), but in some cases two (10%) or only one (10%). We collected individuals of the same general size of each species, emphasizing the larger individuals in a population. We excluded plants with dead terminal portions, but otherwise made no effort to select undamaged individuals.

We classed each species as self- or non-self-supporting. If, when the base was held erect at ground level, a stem could not support its own weight such that the tip rested on the ground, we classified it as non-self-supporting. We attempted to cover the span of stem length–diameter relations in non-self-supporting plants, and one species (*Palmeria scandens*) had representatives in both categories. To measure the lengths of lianas, we measured the length of the stem from the base to the first branch, using rappelling gear when necessary. We then measured the lengths of the major branches to determine which was the longest. We repeated this procedure on the successively more terminal orders of branching to determine the longest base-to-tip distance, and used the sum of these lengths as stem length. For self-supporting plants, we measured height either with a tape measure or a Tru-Pulse 200B laser rangefinder (Laser Technology Inc., Colorado, USA). Some data were available for all collections, whereas others, such as vessel density and stem length, were measured on a subset of the species. Tables 1–3 give the sample sizes, which varied from 264 to 423 species, used in each model we fit. We collected samples of xylem at the stem base, above the roots and above any basal swelling or area of buttresses. When plant size permitted, we collected wedges of outer xylem in an effort to minimize the impact of sampling, but it was necessary to collect entire stem segments from small plants. We measured stem diameter at the site of sample collection.

To gather the requisite data on vessel diameter and abundance, we prepared thin sections for light microscopy using standard wood anatomical methods. We measured 25 vessels per sample from the outer xylem, spanning growth rings when present.

Table 1
Linear models based on species means to examine bivariate relationships between stem diameter (*SD*), stem length (*SL*), raw (*VD*) and hydraulically weighed vessel diameters (*Dh*), and how these relationships varied between habits (self- and non-self-supporting).

	<i>SL</i> ~ <i>SD</i> · self-/non	<i>VD</i> ~ <i>SD</i> + self-/non	<i>VD</i> ~ <i>SL</i>	<i>Dh</i> ~ <i>SL</i> · self-/non	<i>Dh</i> ~ <i>SL</i> · self-/non without outliers ^a
<i>n</i>	283	423	285	285	283
<i>R</i> _{adj} ²	0.83	0.65	0.69	0.69	0.68
Model ANOVA	$F_{(3,279)} = 454.7, P < 0.001$	$F_{(2,420)} = 391.4, P < 0.001$	$F_{(1,283)} = 644.2, P < 0.001$	$F_{(3,281)} = 215.7, P < 0.001$	$F_{(2,280)} = 300.2, P < 0.001$
Equality of slopes test	$P = 0.01$	$P = 0.65$	$P = 0.25$	$P = 0.04$	$P = 0.07$
Equality of intercepts test	–	–	$P = 0.14$	–	$P < 0.001$
Non-self-supporting intercept	0.83 (0.77, 0.88)	1.87 (1.83, 1.91)	1.47 (1.43, 1.50)	1.57 (1.48, 1.66)	1.64 (1.58, 1.70)
Non-self-supporting slope	0.88 (0.76, 0.99)	0.37 (0.35, 0.40)	0.49 (0.45, 0.53)	0.56 (0.47, 0.65)	0.48 (0.44, 0.52)
Self-supporting intercept	–0.003 (–0.07, 0.07)	1.45 (1.40, 1.49)	Common intercept, see non-self-	1.56 (1.46, 1.66)	1.55 (1.49, 1.60)
Self-supporting slope	0.72 (0.60, 0.85)	Common slope, see non-self-	Common slope, see non-self-	0.46 (0.36, 0.56)	Common slope, see non-self-
Figure	2(a)	–	2(b)	2(c)	–

Note. *P*-values for the interaction terms correspond to the initial model when non-significant, and the rest of the terms correspond to the final model.

^a Outlier species in this model were single samples of *Entada phaseoloides* and *Merremia peltata*.

Table 2
Linear models of species mean vessel diameter based on the five narrowest and five widest vessels per sample to explore differences in vessel diameter distributions between self- and non-self-supporting plants.

	<i>VD</i> ~ <i>SL</i> + self-/non	<i>VD</i> ~ <i>SL</i> + self-/non
Bias in vessel diameter	Five widest	Five narrowest
<i>n</i>	285	285
<i>R</i> _{adj} ²	0.69	0.63
Model ANOVA	$F_{(2,282)} = 320.8, P < 0.001$	$F_{(2,282)} = 245.3, P < 0.001$
Equality of slopes test	$P = 0.06$	$P = 0.38$
Equality of intercepts test	$P < 0.001$	$P < 0.001$
Non-self-supporting intercept	1.68 (1.62, 1.73)	1.22 (1.16, 1.27)
Self-supporting intercept	1.59 (1.53, 1.64)	1.30 (1.25, 1.36)
Common slope	0.48 (0.44, 0.52)	0.45 (0.41, 0.49)
Figure	3(a)	3(b)

Note. Mean vessel diameters were calculated by selecting the five widest or five narrowest vessels for each sample, and then calculating species averages using these vessels; *P*-values for the interaction terms correspond to the initial model when non-significant, and the rest of the terms correspond to the final model.

Table 3
Linear models based on species means to examine bivariate relationships between vessel density (*Vmm*^{–2}), stem length (*SL*), stem diameter (*VD*), and vessel diameter (*VD*), and how these relationships varied between habits (self- versus non-self-supporting).

	<i>Vmm</i> ^{–2} ~ <i>SL</i> + self-/non	<i>Vmm</i> ^{–2} ~ <i>VD</i> + self-/non
<i>n</i>	264	375
<i>R</i> _{adj} ²	0.41	0.74
Model ANOVA	$F_{(2,261)} = 93.4, P < 0.001$	$F_{(2,372)} = 544.3, P < 0.001$
Equality of slopes test	$P = 0.97$	$P = 0.05$
Equality of intercepts test	$P < 0.001$	$P < 0.001$
Non-self-supporting intercept	2.25 (2.11, 2.39)	4.76 (4.56, 4.96)
Non-self-supporting slope	–0.72 (–0.83, –0.62)	–1.65 (–1.75, –1.55)
Self-supporting intercept	1.98 (1.83, 2.13)	4.40 (4.20, 4.59)
Self-supporting slope	Common slope, see non-self-	Common slope, see non-self-
Figure	4(a)	4(b)

Note. *P*-values for the interaction terms correspond to the initial model when non-significant, and the rest of the terms correspond to the final model.

Many lianas have abundant very small vessels intermingled with wide ones (Fig. 1). Because the wide vessels are so conspicuous, it is easy for measurements to be biased toward the wide ones. To avoid this tendency and ensure a random sampling of vessel diameters, for liana and all other samples, we selected vessels by scanning across each section and selecting for measurement vessels whose approximate centerpoint was passed through by a designated point on the ocular micrometer. This procedure ensured that vessel selection was not biased by vessel diameter and resulted in measuring narrow, intermediate, and wide vessels. Lianas also often have conductive imperforate tracheary elements, especially vascentric and true tracheids (Carlquist, 1985a; terminology follows Carlquist, 1985b and Rosell et al., 2007). Distinguishing these cells from narrow vessels is often difficult in transection, so for narrow cells we preferentially measured ones with visible perforation plates. In species with vascentric or true tracheids, we excluded from measurement cells with bordered pits that were of similar diameter as the ground tissue tracheary cells when perforation plates were not visible. We also counted the number of vessels per unit transection, averaging counts from 25 fields. We calculated mean values per sample (Appendix A) of natural (i.e. non-hydraulically transformed) vessel diameter as well as vessels per unit transection, and calculated hydraulically weighted vessel diameter as $Dh = \frac{\sum_{n=1}^N d_n^5}{\sum_{n=1}^N d_n^4}$, with d_n representing the natural (non-hydraulically transformed) vessel diameter in μm of vessel n (Kolb and Sperry, 1999). We calculated mean values per species of average vessel diameter at the stem base (*VD*), hydraulically weighted vessel diameter (*Dh*), stem diameter (*SD*) and length (*SL*), and vessel density (*Vmm*^{–2}). We used these species means in the following analyses, log₁₀ transforming continuous variables and fitting models in R v.2.14.1 (www.R-project.org).

Statistical analyses

The predictable relationship between stem length *SL* and diameter *SD* in self-supporting plants has been extensively explored (Niklas, 1994b; Niklas et al., 2006). For plants of moderate size, the *SL*–*SD* relationship is predictable across angiosperm orders and even across land plant classes ($SL \propto SD^{2/3}$). In contrast, the relationship between stem length and diameter is generally regarded as more or less idiosyncratic in lianas, with any given diameter having a very wide range of possible lengths. With stem length–diameter data from both non-self-supporting plants, from scramblers to lianas, and self-supporting trees, shrubs, succulents, etc. we fit a

linear model predicting SL based on SD , a “self-/non-self-” categorical variable, and a $SD \cdot \text{self-/non-self-}$ interaction term. This approach allowed us to detect a linear relationship between stem length and diameter across non-self-supporting plants, and to compare the liana SL – SD scaling slope with that in self-supporting plants. We also fit analogous VD – SD models.

If vessels widen at a similar rate from the stem tip toward the base across plants generally, then SL should predict VD regardless of habit or the SL – SD slope. To test this prediction, we fit a linear model predicting VD based on SL , the self-/non-self-categorical variable, and a $SL \cdot \text{self-/non-self-}$ interaction term. After finding that the interaction term was nonsignificant, we refit the model without it. The self-/non-self-term then lost significance, making the final model VD predicted only by SL . We then fit models of analogous structure predicting Dh , finding that the Dh – SL slope was significantly steeper in non-self-supporting species.

We then explored the causes of the differing Dh – SL relationship between lianas and self-supporting plants as compared to their identical VD – SL intercepts and slopes. The only way for mean VD and Dh values to differ for a given stem length between lianas and self-supporting plants is if the underlying VD distributions differ between lianas and self-supporting plants. For example, the entire VD distribution could be shifted toward higher values in lianas, with the attendant higher mean VD , but so slightly that the difference is too small to detect based on VD and is only revealed via the amplifying effect of Dh transformation. Alternatively, the mean VD variance could be altered, leaving mean vessel diameter identical between lianas and self-supporting plants. In a situation of higher liana VD variance, because it weights wide vessels disproportionately, Dh transformation would lead to a higher mean Dh in lianas as compared to VD .

We tested these ideas regarding differences in the VD distributions between self- and non-self-supporting plants in two steps. First, we compared the variance between these two groups. To do so, we calculated the per-sample VD variance and based on these values generated a per-species average variance. We then carried out a t -test on the average variance values between non-self- and self-supporting species after testing whether the non-self- and self-supporting groups were homoscedastic. Finding evidence for higher variance in lianas, we then fit linear models to examine which tail of the distribution caused the higher liana VD variance. In addition to the models described above, fit based on species means from 25 vessels measured randomly per sample, we fit additional models based on species means calculated with the five largest or the five smallest vessels in each sample. These two models predicted VD based on SL , the self-/non-self-variable, and an $SL \cdot \text{self-/non-self-}$ interaction. If both self- and non-self-supporting plants have similar variances in their distributions of vessel diameters, then this means that lianas necessarily achieve their higher Dh via a shift in mean vessel diameter. In this case, the models based on the narrowest and widest vessels should show the same relative differences in intercepts β_0 , i.e. $\beta_0^{\text{non-self-widest}} > \beta_0^{\text{self-widest}}$ and $\beta_0^{\text{non-self-narrowest}} > \beta_0^{\text{self-narrowest}}$. Alternatively, if $\beta_0^{\text{non-self-widest}} > \beta_0^{\text{self-widest}}$ but $\beta_0^{\text{non-self-narrowest}} = \beta_0^{\text{self-narrowest}}$, then this would mean that lianas achieve their wider mean vessel diameters by a widening of the upper tail of the distribution. Likewise if $\beta_0^{\text{non-self-narrowest}} < \beta_0^{\text{self-narrowest}}$, then a widening of the lower tail of the distribution of liana vessel diameters would be inferred. In addition to allowing us to identify which tail of the distribution is involved in the wider variance of lianas, these models allowed us to examine whether the slopes of self- and non-self-supporting plants differed when based on the widest and narrowest conduits. Different slopes in these models would suggest different scaling for the widest and/or narrowest conduits between lianas and self-supporting plants. Larger plants,

which have greater access to water, might be expected to have fewer small vessels and so slopes could differ when considering only the largest or smallest vessels. Given that lianas are thought to have deeper roots than self-supporting plants, slopes might differ between these two habit types.

Finally, because there are conflicting reports in the literature, some asserting that lianas have higher and others suggesting that they have lower vessel densities (Vmm^{-2}) as compared to self-supporting plants, we fit two models, one against SL and the other against VD , to determine whether Vmm^{-2} is higher, lower, or indistinguishable between self- and non-self-supporting plants.

Results

Mean vessel diameter across species, with maximum and minimum per-sample values given in parentheses, varied from 13.6 to 244.3 μm in self-supporting species (4.2–348.3 μm), and from 18.8 to 349.9 μm in non-self-supporting plants (6.6–736.1 μm). Mean stem diameters for lianas ranged from 0.22 to 15.8 cm in stem diameter (0.11–35.0 cm) and from 52 cm to 55 m in stem length (26 cm to 55 m). For self-supporting plants, mean diameter ranged from 0.31 cm to more than 2 m in mean stem diameter (0.07 cm to 2.5 m), and from 47 cm to 45.8 m in mean length (13 cm to 56.4 m).

In the model predicting SL based on SD plus self-/non-self- and a self-/non-self- $\cdot SD$ interaction term, the interaction was significant ($P=0.01$), meaning that self- and non-self-supporting plants had different SL – SD allometries (Table 1). The fit of the final model was high, with an R_{adj}^2 of 0.83 (Fig. 2a).

Models predicting natural (non-hydraulically weighted) vessel diameter VD based on SL showed that VD – SL scaling was identical, regardless of self-/non-self-supporting status (cf. also VD – SD , Table 1). The $VD \cdot SL$ interaction term was nonsignificant ($P=0.25$), indicating that VD scales with SL with a similar slope in both self- and non-self-supporting plants (Table 1). We refit the model without the $VD \cdot SL$ interaction and found that the coefficient associated with the self-/non-self-binary variable was also non-significant ($P=0.14$), that is, the VD – SL intercept was statistically indistinguishable between self- and non-self-supporting plants. This means that for a given stem length, there was no significant difference in mean VD between lianas and self-supporting plants (Fig. 2b).

However, there was a significant difference in slope between self- and non-self-supporting plants in our model predicting hydraulically weighted vessel diameter Dh based on SL and the self-/non-self-binary variable (Fig. 2c, Table 1). Note that the difference in slope was caused by the two samples of the lianas *Entada phaseoloides* and *Merremia peltata* (upper right points in Fig. 2c); without these samples the slopes are identical but the intercept was higher in non-self-supporting plants (see model fit without them in Table 1). The Dh conversion weights wider vessels more than narrow ones, to reflect the increase in conductivity with vessel diameter to the fourth power predicted by Poiseuille’s law (Vogel, 2003). That VD should show no significant difference in scaling against stem length, but that the Dh – SL relationship is significantly steeper, suggests that the difference is due to differences in the variance of lianas, in particular due to a few slightly wider vessels in lianas. The difference would necessarily be so slight as to be undetectable based on VD , but would be revealed by the amplifying effect of weighting the wider vessels under the Dh conversion.

To test this idea, we compared the variance of self- and non-self-supporting species. Lianas had significantly higher variance (43.3) than non-self-supporting plants (18.0, $t_{89.9} = 7.16$, $P < 0.001$). To examine whether this higher variance was due to the right tail of liana distribution only (i.e. VD distributions similar to those in

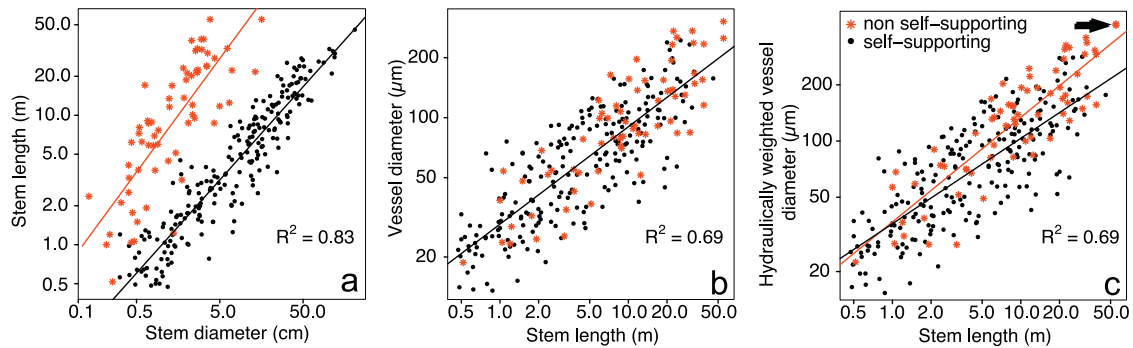


Fig. 2. Stem length–diameter and vessel diameter–stem length relations. (a) Lianas have much longer stems for a given diameter than self-supporting plants, and scale with a slightly higher stem length–stem diameter slope. (b) Natural (non hydraulically weighted) vessel diameter in non-self-supporting plants scales with stem length indistinguishably from self-supporting plants in both intercept and slope. (c) In contrast, the slope of hydraulically weighted vessel diameter versus stem length is slightly higher in non-self-supporting plants than self-supporting ones. The difference is caused by the amplifying effect of hydraulic transformation on a very few slightly larger vessels per stem length in non-self-supporting plants (see Fig. 3). The two outliers causing the difference in slope are indicated with arrows. Points are species mean values.

self-supporting plants with the addition of a few wide vessels), we fit a pair of models based on the mean of the five widest and five narrowest VD per sample based on SL . In neither of the models was the $SL \cdot \text{self-/non-self-}$ interaction term significant, meaning that lianas and self-supporting plants scaled with similar VD – SL slopes with respect to their narrowest or widest conduits (Table 2). The VD_{widest} model showed that non-self-supporting plants have significantly wider vessels for a given stem size than self-supporting plants do at the wide end of the vessel diameter distribution curve, $\beta_0^{\text{non-self-}} > \beta_0^{\text{self-}}$ (Fig. 3a). We recovered an opposite result with regard to $VD_{\text{narrowest}}$. The $VD_{\text{narrowest}}$ model showed that non-self-supporting plants have significantly narrower vessels for a given stem size than self-supporting plants do at the narrow end of the vessel diameter distribution curve, $\beta_0^{\text{non-self-}} < \beta_0^{\text{self-}}$ (Fig. 3b, Table 2), indicating that lianas have wider, but also narrower conduits than their self-supporting counterparts.

In neither of the models predicting vessel density (Vmm^{-2}) based on SL or VD (Table 3) were interaction terms significant, indicating identical scaling slopes between self- and non-self-supporting plants. The self-/non-self-binary variable was significant in both models, indicating significantly different intercepts. The model predicting Vmm^{-2} based on SL revealed

lianas to have significantly more abundant vessels per unit stem transection than self-supporting plants (intercepts of 1.98 versus 2.25; Fig. 4a). Similarly, the model predicting Vmm^{-2} based on VD also suggested that lianas have more vessels per unit stem transectional area for a given stem length (Fig. 4b).

Discussion

We show that, in contrast to a centuries-long tradition of considering them to have very wide vessels, lianas have vessel diameters very much in line with their stem lengths as compared to self-supporting plants. For a given stem length, our data suggest that lianas do not achieve their higher hydraulically weighted diameters as compared to self-supporting plants with a shift in mean natural (non-hydraulically weighted) vessel diameter, but instead an expansion of vessel diameter variance as well as an increase in vessel density. Their distinctiveness therefore lies in that, for a given mean vessel diameter, lianas have only a few wider vessels than do self-supporting plants of similar length, but they also have narrower and more vessels as well. We turn to these considerations in more detail now.

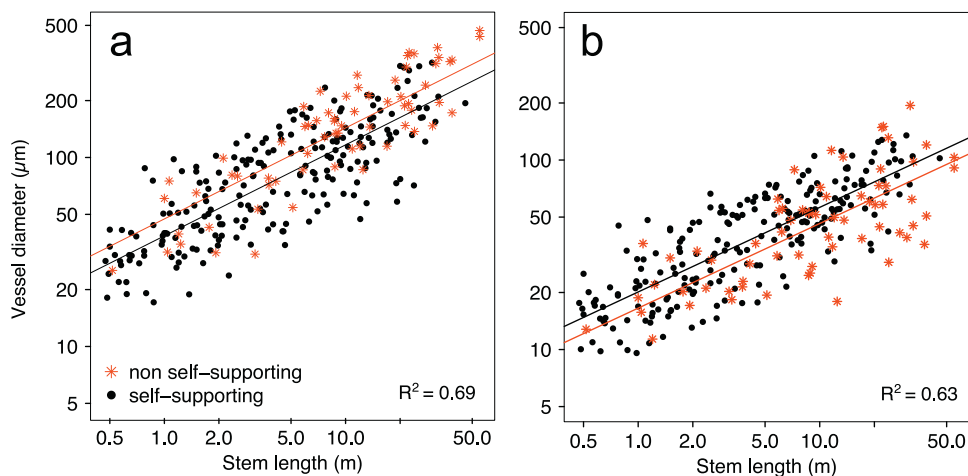


Fig. 3. Models predicting mean natural diameters of the five widest and five narrowest vessels. (a) Together with our previous models (Fig. 2), the model predicting VD_{widest} , the mean vessel diameter of the five widest vessels per sample, revealed that for a given stem length, lianas have a few significantly wider vessels. (b) By the same token, the model predicting $VD_{\text{narrowest}}$ showed that the narrowest vessels of lianas are, as compared to self-supporting plants of a similar stem size, significantly narrower. Points are species mean values.

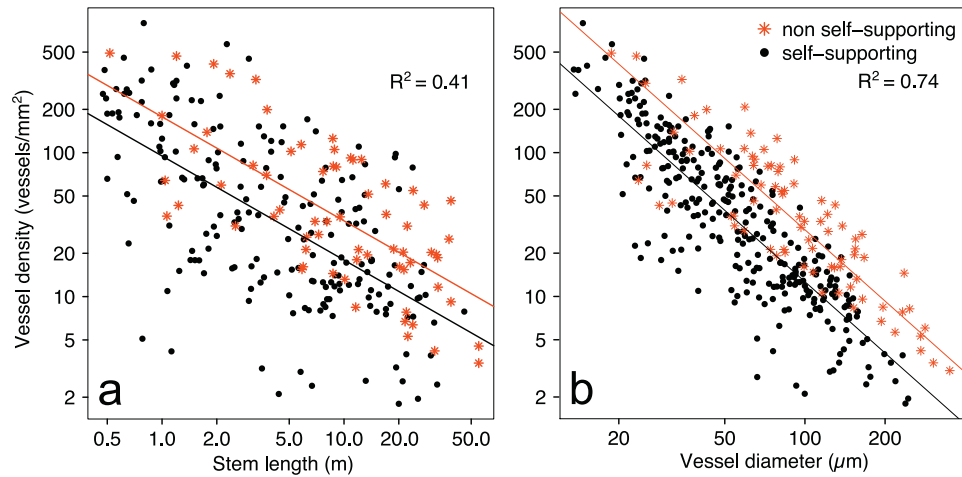


Fig. 4. Vessel density against stem length and vessel diameter. (a) Vessel density versus vessel diameter (\log_{10} natural vessel diameters) in self- and non-self-supporting plants, showing that non-self-supporting plants, even if they do not have significantly wider natural vessel diameters, do have significantly more vessels per mm^2 than self-supporting plants. Points are species mean values.

Lianas do not have exceptionally wide vessels

Our results show that from the point of view of the vessel diameter–stem length relationship, lianas do not have extraordinarily wide vessels. In fact, mean natural (non-hydraulically transformed) vessel diameter–stem length scaling, and mean diameter for a given length, are statistically indistinguishable between self- and non-self-supporting plants (Fig. 2b). Even mean hydraulically weighted diameter is only slightly wider in non-self-supporting plants as compared to self-supporting ones (Fig. 2c, Table 1). If natural selection favors the buffering of hydraulic resistance via tip-to-base widening of vessels, then the longer a stem is, whether self-supporting or not, it will have predictably wider vessels. Lianas therefore have wide vessels because their stems are long. They only appear exceptional because their stems are so narrow for a given length (Fig. 2a).

Instead, lianas have (a few) slightly wider vessels, as well as significantly narrower ones

To explore the causes of differences in vessel–stem allometry between natural and hydraulically transformed diameter (Fig. 2b versus c), we fit models using stem length to predict the species average vessel diameter of the five widest and five narrowest vessels per sample. These models showed that the widest vessels in lianas are indeed slightly wider than those of self-supporting plants (Fig. 3a, Table 2). However, the intercept of the model predicting the mean diameter of the five narrowest vessels was lower rather than higher than the self-supporting intercept (Fig. 4b, Table 2). Together, our results suggest that not only do lianas in general have only a few slightly wider vessels than self-supporting species, but that they also have vessels that are narrower than the narrowest ones found in self-supporting plants of comparable stem lengths. This means that, rather than the mean VD being shifted toward higher values, and the entire vessel diameter distribution with it, lianas achieve their higher hydraulically weighted diameter by virtue of the few wide vessels at the upper extreme of their higher VD variance. Previous authors have suggested that lianas have wider vessel diameter variances than self-supporting plants (Carlquist, 1985a; Ewers and Fisher, 1989; Ewers et al., 1990; Jiménez-Castillo and Lusk, 2013). Our approach quantifies these qualitative comparisons and in doing so offers a means to standardize comparisons by stem length.

Lianas have more vessels per unit transection

Different studies have reported different patterns, with some authors reporting lower vessel densities in lianas as compared to self-supporting plants (e.g. Carlquist, 1985a; van Vliet, 1981) and others reporting higher densities (e.g. Angyalossy et al., 2012; Baas and Schweingruber, 1987; Crivellaro et al., 2012). As Carlquist (1985a) noted, these differences probably have to do with the way that vessels of different size classes were or not included. Many measurements of liana VD and $V\text{mm}^{-2}$ probably include only the widest and most conspicuous vessels and ignore the narrowest ones. This is understandable because so many lianas have conductive imperforate tracheary elements, and it is not always possible to differentiate them from vessels in transections. Different criteria regarding which cells are counted as vessels therefore can lead to different conclusions. Here we include the full range of vessel diameter, applying identical criteria to both lianas and self-supporting plants, and all measurements were made by the same person. This uniformity increased the chance that the patterns we found reflect biological signal relative to comparisons between studies, some of which include narrow vessels and others that measure only the wide ones. Our data showed a significant tendency for lianas to have more vessels per unit transection, both when plotted against SL and against VD, as compared to self-supporting plants (Baas et al., 2004). This suggests that the packing limit does not impose the upper limit observed in the $V\text{mm}^{-2}$ –VD relationship across self-supporting plants (Crivellaro et al., 2012). The higher intercept of the $V\text{mm}^{-2}$ –VD relation in non-self-supporting plants shows that higher vessel densities than those observed in self-supporting plants are developmentally possible. The $V\text{mm}^{-2}$ –VD relation in self-supporting plants is therefore almost certainly one that is maintained by selection rather than a constraint in the sense of the only developmentally possible trait combination (Olson, 2012).

Liana stem allometry is predictable

Given the difficulty of following liana stems through the canopy, it is understandable that relatively little is known about liana stem length–diameter relations. Our dataset, the most extensive collected on liana stem length–diameter allometry, suggests instead that stem length not only appears to be predictable in lianas based on diameter but also, in lianas longer than 2 m or so, that this slope is parallel to the self-supporting scaling slope

(Table 1, Fig. 2a). Given that lianas are usually regarded as having very variable stem lengths for a given stem diameter, this general predictability suggests that the deployment of carbon per unit stem volume is similar in lianas and self-supporting plants.

The gap between self- and non-self-supporting plant stem length–diameter allometry

In addition to predictable liana stem length–diameter allometry, a second unexpected result was that, rather than a uniform continuum between self- and non-self-supporting plants, stem length–diameter allometry revealed what appeared to be two main areas where the *SL–SD* points fell densely (Fig. 2a). We made every effort to collect the entire range of stem length–diameter relations across species, including scramblers and semi self-supporting plants, and did not deliberately select the longest stems for a given diameter. Given this sampling strategy, we expected to find a continuum between self- and non-self-supporting plants. However, Fig. 2a seems to suggest an area of *SL–SD* space that is sparsely occupied between the self- and non-self-supporting scaling lines, especially at longer stem lengths (see also Niklas, 1994a). If real, this gap could suggest that the evolution of self- versus non-self-supporting stem proportions is usually an either-or one, with intermediate allometries generally maladaptive.

The need to standardize by stem length

The dependence of vessel diameter on stem size highlights the need for revising ways of studying and describing vessel diameter and related performance measures, not only of lianas but of plants in general. Virtually all authors who have written about lianas have asserted that they have wider vessels than those of self-supporting plants (e.g. Angyalossy et al., 2012; Wyka et al., 2013). Given the dependence of *VD* on *SL* that we describe here, when comparing vessel diameter between individuals, standardizing by stem length seems essential. Otherwise, saying that “species A has a wider mean vessel diameter than species B” may simply be a way of saying “species A has a longer stem than species B.”

By the same token, studies of plant hydraulics that standardize their samples by stem diameter rather than by stem length very likely introduce variation into their results. According to our *SL–SD* allometric equations in Table 1, comparing stems 1 cm in diameter would pit the hydraulics of a 1 m long self-supporting plant against those of a 6.7 m long non-self-supporting one. Based on the *Dh–SL* equations in Table 1 (last column), this would mean comparing a mean self-supporting *Dh* of 35.3 μm with a mean liana *Dh* of 109.2 μm . Standardizing by stem diameter, or not standardizing samples at all, would therefore not seem recommendable practice. Comparing the wider vessels of long stemmed liana samples with the narrow ones of short stemmed self-supporting plants is likely one reason that empirical studies consistently find much higher hydraulic conductivity in lianas as compared to self-supporting plants. These conclusions ideally should be reexamined with length-standardized samples.

Using stem diameter as a standard for comparison will also introduce variation because, even though in large samples plants generally scale with broadly similar stem length–diameter relations (Fig. 2a), *SL–SD* proportions vary between species and in ontogeny (e.g. Rosell et al., 2012). For example, the slope of the *SL–SD* relation was steeper in lianas in samples <2 m long; the slopes were parallel in samples >2 m (Fig. 2a; models not shown). Likewise, the spectrum of traits related to Corner’s Rules also probably affect the relationship between twig diameter and vessel

diameter and abundance. For a given diameter, species with large leaves or succulent stems usually have very short, stubby twigs whereas species with small leaves tend to have long, slender twigs (Olson et al., 2009). Given these sources of variation, from the 1 cm diameter point, distance to the stem tip will be much shorter in some species than others. In addition, tip-to-base vessel widening follows a power law, which means that widening is very rapid toward the stem tip, and becomes nearly constant along the bole of a tall tree (Petit et al., 2010). As a result, any variation in distance from the tip from which a given sample is collected will necessarily lead to marked variation in measurements such as vessel diameter, vessel density, and very likely functional parameters such as vulnerability to cavitation and sap flux density (see also Gleason et al., 2012 on xylem specific conductivity; Petit and Anfodillo, 2011; Anfodillo et al., 2013).

Conclusion

Carlquist (1985a, p. 153) noted that “we should do well to emphasize not merely the wide vessels of vines, but the abundance of narrow ones.” Our results bear out Carlquist’s admonition. Lianas do have wider vessels, but apparently only a very few for a given stem length as compared to self-supporting plants. An important pattern in our data is that not only do lianas have an abundance of narrow vessels, but they also appear to have vessels that are actually narrower than those found in self-supporting plants of similar stem lengths. This would mean that the higher hydraulic diameters of lianas are not due to a global shift in mean but to a shift in variance (compare Fig. 2b with Fig. 3a and b). Moreover, higher hydraulic conductivity in lianas is also likely due to a greater number of vessels, of all sizes, per unit transection. Our analyses therefore show that, far from having exceptionally wide vessel diameters, lianas differ in their vessel diameter and density–stem length relations from self-supporting plants only in subtle but predictable ways.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2014.08.001>.

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