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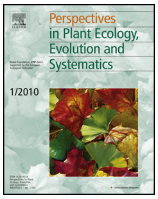

Research article

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.

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

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Abbreviations: SL, stem length; *SD*, stem diameter; *Dh*, hydraulically weighted vessel diameter; *VD*, vessel diameter; Vmm^{-2}, vessel density.

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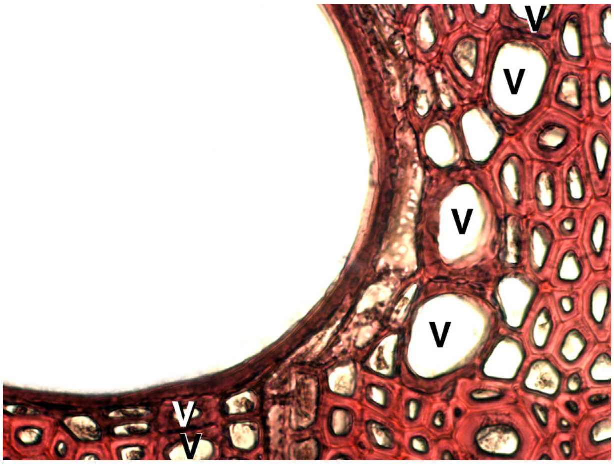

Fig. 1. Anatomical phenomena in lianas. Lianas are universally cited as having very wide vessels. However, lianas also often have narrow (V) vessels surrounding the wide ones, as in this stem of *Pandorea pandorana* (Bignoniaceae).

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 rappeling 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.