

Chapter 6

Lianas as Structural Parasites

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1 Introduction

Lianas, or woody vines, have been referred to as structural or mechanical parasites (Putz 1984; Stevens 1987). Although they are rooted in the soil, they depend upon host plants or other external objects for their mechanical support. Studies suggest that lianas may be detrimental to the host trees. They receive “free” mechanical support and increase static mechanical loading on the hosts and also increase “sail area” exposed to wind forces. They compete with the host, both above ground for light, and below ground for water and mineral nutrients (Stevens 1987; Schnitzer 2005; Schnitzer et al. 2005). When compared to free-standing species, lianas may be able to provide water and minerals to their leaves without investing as much biomass in stem mechanical tissues; they use wide vessels to apparent hydraulic advantage (Fig. 6.1). They certainly have long stems; their tissue allocation strategy allows for greater stem extension per unit carbon invested in stems than can self-supporting plants (Gartner 1991a, b, c). Another feature of liana stems is they often have cambial variants such as successive cambia or multiple vascular cylinders (Fig. 6.2), which may allow for greater flexibility and effective wound healing following tree fall events (Fisher and Ewers 1989, 1992).

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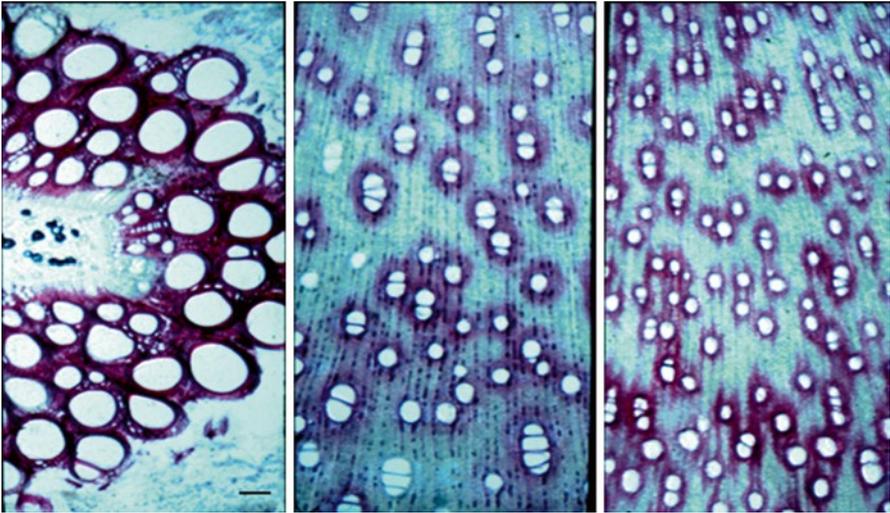


Fig. 6.1 Comparison of basal stem transverse sections of three growth forms within the genus *Bauhinia*. From left to right, the liana *B. fassoglensis*, the tree *B. blakeana*, and the shrub *B. galpinii*. The stems were each supplying about 3.5 m² of leaf area, but the liana was accomplishing this with much less xylem area and much greater maximum vessel diameter. All three at the same magnification, with the scale bar 200 μm. From Ewers et al. (1991)

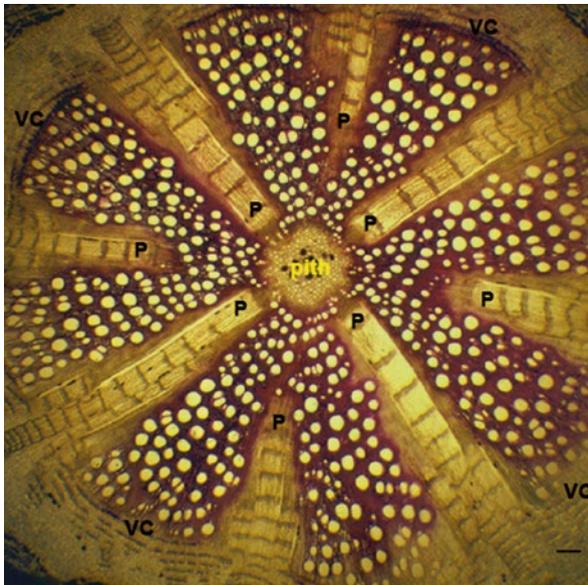


Fig. 6.2 Lianas often have variant secondary growth, as shown in this transverse section of *Macfadyena unguis-cati* of the Bignoniaceae. The “cross vine” morphology with phloem wedges within the xylem is typical for lianas in this family. Very early in secondary growth (see area close to the pith) four phloem wedges were produced (P); the vascular cambium in those areas produced abundant phloem but very little xylem. Later four additional phloem wedges were produced. Normal portions of the vascular cambium (VC) produced much xylem to the inside (red staining here) and relatively little phloem to the outside of the stem. Such stems are flexible and effective at wound healing. Scale bar is 500 μm

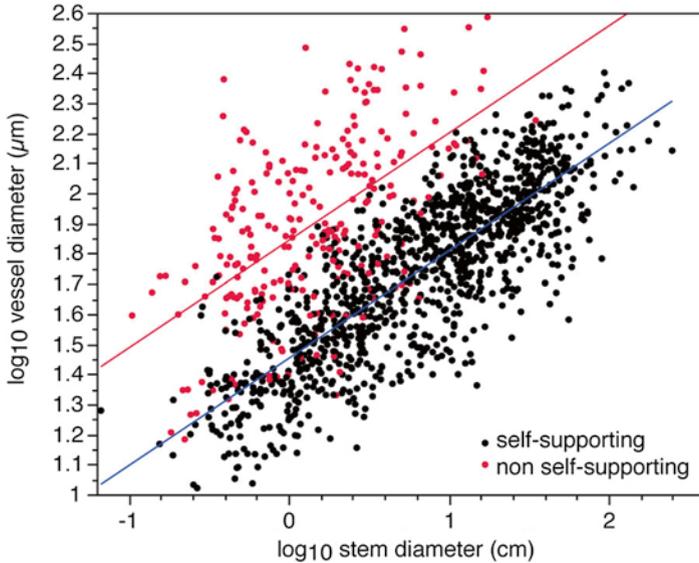


Fig. 6.3 Controlling for stem diameter, non-self-supporting species (mostly lianas), on average have wider vessels than in self-supporting species such as shrubs and trees. Data from 1,047 samples from 528 species from Olson and Rosell (2013), Olson et al. (2014), and Rosell and Olson (2014). $R^2=0.62$, slope 0.36

Most of the discussion in this chapter will be on the hydraulics of liana stems, which are better known than the roots and leaves of lianas. Lianas consistently have very narrow stems in relation to the leaf area they supply (Schenck 1893; Putz 1983; Ewers et al. 1991). Liana stems have exceptionally wide vessels for a given stem diameter as compared to self-supporting plants, often 500 μm or more in maximum diameter in stems less than 20 cm in diameter. We have found examples of individual liana vessels that were as wide as 700 μm (in large specimens of *Cissus hypoglauca* and *Entada phaseoloides*). Similarly, the monocotyledonous “woody” vine *Smilax panamensis* has vessels as wide as 700 μm (Tyree and Ewers 1996). In addition, for a given stem diameter liana vessels are exceptionally long, up to many meters in maximum length. They have much less xylem transverse area and many fewer fibers per unit stem transection than in trees or shrubs supplying similar leaf areas (Ewers et al. 1989, 1991; Ewers and Fisher 1991). Although liana stems have wider vessels than in similar diameter stems of trees and shrubs (Fig. 6.3), much of this can be explained by the relationship between stem length and vessel diameter. Hydraulic optimality models suggest that, for plants in general, longer stems should have wider vessels near the base (West et al. 1999; Petit and Anfodillo 2009; Savage et al. 2010; Sperry et al. 2012). Lianas may be most exceptional in having some of the longest stems in the plant kingdom, up to 200 m or more (Burkill 1966). Lianas are most common and abundant in the tropics and most of the examples in this chapter involve tropical lianas. Grapevines are perhaps the most important and well studied of the temperate lianas, and it serves for a case study in the chapter on “Grapevine xylem development, architecture, and function.”

2 Root Systems of Lianas, Root Pressures

There are biomechanical and carbon investment reasons to expect lianas to have different root systems as compared to self-supporting plants. The root systems of self-supporting plants contribute in resisting mechanical loads (e.g., Niklas et al. 2002 and citations therein). Many large trees have deep bayonet, sinker, or tap roots which help anchor the plants and presumably resist the forces resulting from loads such as wind pushing the plants to one side (Fig. 6.4). Moreover, trees usually have multiple laterally spreading roots close to the surface that also likely act in transmitting lateral mechanical loads to the substrate. Many trees, especially tropical trees, also have root buttresses. Given that lianas are supported by the host plant along their lengths, and often trail on the ground before ascending into the canopy (Fig. 6.4), in most cases the mechanical loads transmitted to the root system are negligible. In lianas, freedom from mechanical selection pressures on stems and roots could make large amounts of carbon available for diversion to other structures. One possibility is that with greater carbon available for investment in roots, lianas could have deeper root systems on average than self-supporting plants of similar crown area, and thus proportionally greater access to water. It has also been observed that liana roots tend

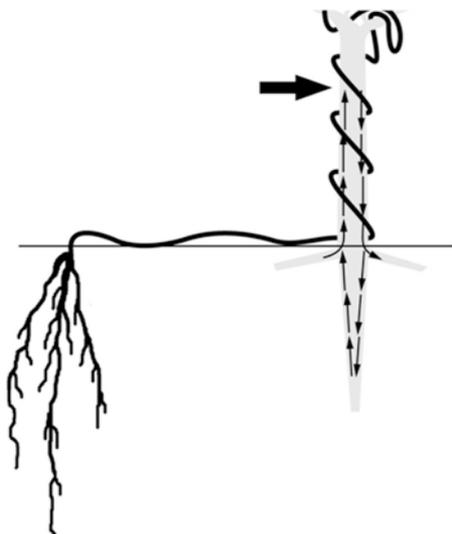


Fig. 6.4 Mechanical loading and potential rooting depths of trees versus lianas. The root system of a tree (gray) includes lateral support roots and vertical bayonet, sinker, or tap roots (tree drawing follows Niklas et al. 2002). These roots help resist mechanical loads, such as wind (*large horizontal arrow*). Tension and compression forces (*small black arrows*) are transmitted to the roots and through them to the ground (*black horizontal line* is ground level). In contrast, in lianas (*black*), essentially no mechanical loads are transmitted from the stem to the roots. Carbon that would otherwise be allocated to support roots can be deployed as resource acquiring roots. The drawing here uses the same number of pixels (carbon) to draw the belowground parts of the tree and the liana. Using a similar amount of “carbon” as the tree, the liana can potentially reach deeper water sources

Table 6.1 Root versus stem vessel diameters, with a comparison of 8 liana species and 11 free-standing species (trees and shrubs) of the Fabaceae

Vessel diameter	Roots \pm SE	Stems \pm SE
Mean, liana species	121 \pm 9	164 \pm 22 ^a
Mean, free standing	120 \pm 9	101 \pm 11 ^a
Maximum, liana species	240 \pm 20	304 \pm 42 ^a
Maximum, free standing	197 \pm 23	164 \pm 16 ^a

For liana species, vessels were significantly wider (in μm) in woody stems than woody roots. In contrast, for free-standing species, vessels were significantly wider in roots. Liana stems differed from stems of free-standing growth forms, but the root vessel diameters were not different between growth forms. From Ewers et al. (1997b)

^aSignificant difference between stems and roots based upon Wilcoxon's Signed-Rank test at $p < 0.05$

to have larger rays, more axial parenchyma, and more parenchyma in contact with vessels than what occurs in trees (Carlquist 1985a, 1991).

It has been suggested that lianas may have exceptionally deep roots compared to trees (Putz 1984; Schnitzer 2005; Chen et al. 2015), but this is not a consistent trait. Both shallow and deep rooted liana species can be found at a site (Tyree and Ewers 1996), and some lianas have very large basal tubers developed from the hypocotyl or from the root (Brenan 1967; Mooney and Gartner 1991; Hearn 2006). Based upon stable isotope composition of the xylem sap versus soil water at various depths, lianas may obtain their water from deeper soils than the trees they climb upon. However, this varies with the site and the season. In one study, liana species appeared to obtain water from similar depths as did co-occurring trees in both the wet and dry season (Andrade et al. 2005). In another study, at two sites with severe seasonal soil water deficit, lianas used a significantly higher proportion of "deep soil water" during the dry season (from 151 to 250 cm depth) than did co-occurring trees. However, the same study showed that at a third site, which had moist soils even in the dry season, lianas and trees appeared to obtain water from similar depths (Chen et al. 2015).

In terms of vessel diameter, a study of 51 liana species and 11 nonclimbing species (trees and shrubs) showed there was no significant difference between growth forms in the root vessel diameters (sampled woody roots were about 9 mm diameter for both growth forms). This same study showed consistently wider vessels in the stems of lianas than in similar diameter stems of trees and shrubs (Ewers et al. 1997b). A subset of those results, for eight liana species and 11 free-standing species all of the Fabaceae, are summarized in Table 6.1. Unfortunately, vessel lengths in roots of lianas have been little studied due to the general difficulty of sampling long roots of woody plants.

Root pressures are reported to be much more common in climbing plants than in trees (Fisher et al. 1997; Ewers et al. 1997a; Jiménez-Castillo and Lusk 2013). Some of the classic reports of root pressure involved lianas (Hales 1727; White 1938). Root pressures, caused by osmotic water uptake following solute taken into the root stele, are generally greatest during rainy seasons and when transpiration is minimal such as

at night, during rainstorms, or just prior to leaf emergence in the case of deciduous lianas (Sperry et al. 1987; Cochard et al. 1994; Fisher et al. 1997; Tibbetts and Ewers 2000). Reported root pressures in lianas (e.g., maximum of 148 kPa near the stem base in *Cissus*, Vitaceae; Fisher et al. 1997) are usually modest, mostly well under 100 kPa, and probably not sufficient to reverse embolism in the upper stems in a forest canopy. Even without leakage or absorption, the gravity gradient would indicate a loss of 10 kPa per m of height. However, root pressures in lianas may be significant in reversing possible embolism in roots and in the lower stems. They may also reflect a high starch storage capacity in roots of lianas, given the high amounts of parenchyma in the roots and the common occurrence of storage tubers (Mooney and Gartner 1991). When the starch is broken down and mobilized, it could contribute to root pressures. However, the common occurrence of root pressures in lianas may also be due to lower capacitance in liana stems relative to trees. In trees, root pressures may be quickly dissipated with height as there is absorption of water under positive pressure into the various tissues of the wide stems. It may be that shallow rooted liana species are more likely to exhibit root pressures than deep rooted species. Root pressures may dissipate along an extended xylem pathway from deep soils.

3 Leaves of Lianas

The leaves of lianas, although highly variable, appear to differ from those of trees, especially in dry tropical forests. Compared to the host trees on which the stems climb, liana leaves can have lower leaf mass per area, they often have greater maximum photosynthetic capacity, they are shorter lived, and they have higher nitrogen and phosphorous content (Cai et al. 2009; Zhu and Cao 2009; Tang et al. 2012). One study showed that leaves of two liana species were more prone to embolism than the tree species that they were climbing upon (Johnson et al. 2013). However, in two studies liana leaves gave very similar results as tree leaves for many physical and physiological parameters (Santiago 2010; van der Sande et al. 2013). And when gas exchange measurements were made the day after a rainstorm in the canopy of a moist tropical forest, sun leaves of lianas underperformed compared to host trees, with lower rates of stomatal conductance and lower rates of carbon assimilation (Santiago and Wright 2007). Another study showed that liana leaves had greater photosynthetic capacity than the host trees at seasonally dry sites, but there was no apparent liana advantage at moist sites (Chen et al. 2015).

4 Stem Xylem Conductivity

Unlike free-standing growth forms, liana stems have both wide vessels and relatively high vessel frequency per mm² (Carlquist 1991; Baas et al. 2004). Since the mechanical requirements are much less for liana stems than for free-standing species, it follows that lianas tend to have lower wood density, lower percent fiber area,

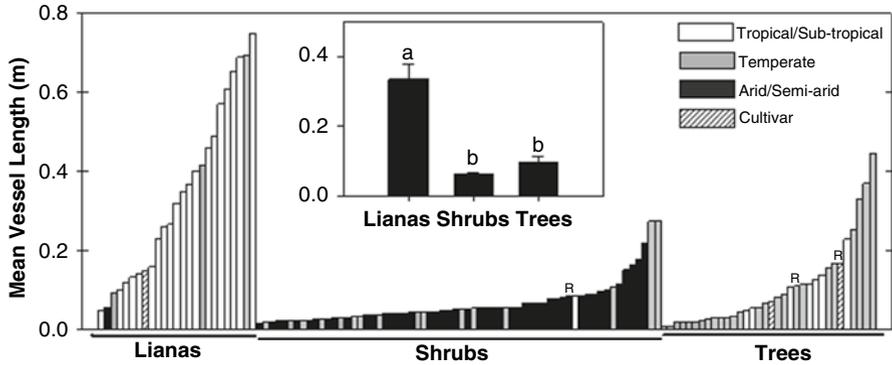


Fig. 6.5 Based upon a meta-analysis, lianas are shown to have long vessels when compared to self-supporting growth forms (shrubs and trees). Each bar represents a different species. From Jacobsen et al. (2012)

and vessel diameters and frequencies that are closer to the theoretical “packing limit” (Crivellaro et al. 2012).

Liana stems are well known to have wider vessels and higher specific conductivity (hydraulic conductivity per xylem transverse area, K_s) than in trees and shrubs of similar stem diameters (Ewers et al. 1989, 1991; Gartner et al. 1990; Chiu and Ewers 1992; Feild and Balun 2008; Zhu and Cao 2009; Jiménez-Castillo and Lusk 2013). Similarly, sap flow gauges have shown lianas to have much higher sap flux density (J_s in $\text{g m}^{-2} \text{s}^{-1}$) than trees, at least when soil water availability is high (Chen et al. 2015). Lianas also have greater average vessel lengths (Fig. 6.5) and greater maximum vessel lengths than in free-standing growth forms of similar stem diameters (Ewers and Fisher 1989a, b; Ewers et al. 1990). Given the wide vessel diameters, the high K_s and J_s values in liana stems can be explained by Poiseuille’s Law for ideal capillaries. Conductivity should be proportional to vessel diameter to the fourth power. As an illustrative example, in a study of five liana species and nine tree species which served as hosts, mean vessel diameter was 2.2 times higher in the lianas, and the mean K_s was 18.3 times higher (Jiménez-Castillo and Lusk 2013). For perfect capillaries, a 2.2-fold increase in diameter would correspond to a 23-fold increase in conductivity, roughly similar to the 18.3-fold increase observed. As another example, in a common garden study, comparisons of lianas versus free-standing growth forms within the genus *Bauhinia* showed the liana species to have about six times greater K_s , but the free-standing species had about five times greater Huber values. The leaf-specific conductivity, LSC, was similar in the different growth forms (Table 6.2).

Although Poiseuille’s Law provides a good first approximation, vessels do not behave as ideal capillaries, of course. For one thing, conductivity appears to be colimited by vessel length as well as vessel diameter; measured conductivity is typically about 50 % of that predicted by Poiseuille’s Law. Vessel length is much less measured than vessel diameter, but lianas have among the longest vessels reported in the plant kingdom (Fig. 6.5).

Table 6.2 Xylem transport parameters: comparison of lianas versus free-standing growth forms (trees and shrubs) within the genus *Bauhinia* (Fabaceae), including Huber value (transverse xylem area per leaf area distal to the stem segment), sapwood-specific conductivity (K_s), leaf-specific conductivity (LSC), maximum transpiration rates, and maximum predicted pressure stem xylem pressure gradients (max dp/dx)

Growth form, species	Huber value in 10^{-5} m/m	Specific gravity of xylem	K_s in $\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$	LSC in $10^{-4} \text{ kg MPa}^{-1} \text{ s}^{-1} \text{m}^{-1}$	E max in $\text{mmol m}^{-2} \text{ s}^{-1}$	Max dp/dx in MPa m^{-1}
Liana						
<i>B. fassoglensis</i>	1.4±0.3	0.18±0.3	171.1±29.7	11.0±0.7	6.10±0.38	0.101
<i>B. vahlii</i>	2.4±0.6	0.40±0.1	35.3±3.7	6.8±0.7	4.45±0.38	0.119
Free standing						
<i>B. aculeate</i>	15.8±6.9	0.65±0.09	6.7±0.7	6.2±0.5	3.41±0.49	0.100
<i>B. blakeana</i>	11.8±3.1	0.33±0.08	14.1±1.9	11.2±1.4	3.24±0.33	0.053
<i>B. galpini</i>	6.0±0.8	0.49±0.01	11.0±1.9	5.8±0.8	2.64±0.55	0.083
<i>B. variegata</i>	9.4±1.0	0.42±0.03	15.6±1.7	12.3±1.2	5.71±0.60	0.085

N > 12 shoots per species. From Ewers et al. (1989, 1991)

It has been well established for lianas that within a stem are a wide range of vessel diameters and lengths, with more short and narrow conduits than long and wide ones (Carlquist 1985a; Ewers and Fisher 1989a, b; Ewers et al. 1990). The same may apply, but to a lesser extent, to plants in general (Zimmermann and Jeje 1981; Zimmennann and Potter 1982; Tyree and Zimmermann 2002).

Mean vessel diameter provides only very simplified prediction of the conductivity. The hydraulically weighted vessel diameter (Kolb and Sperry 1999) is a much better predictor, but that is also a simplification since stems also vary in vessel frequency per transverse area. Vessel frequency is generally inversely proportional to mean vessel diameter in plants (Zanne et al. 2010). However, in addition to greater vessel diameter, lianas are sometimes reported to have greater vessel frequency than in related trees and shrubs (Carlquist 1975, 1985a, 1991; Ewers and Fisher 1991; Gasson and Dobbins 1991). All of these sources of variation affect measures of hydraulic performance in lianas.

The K_s values correct for xylem transverse area whereas leaf-specific conductivity, LSC, controls for the leaf area supplied by a stem. Although K_s are consistently high in lianas, the LSC values have been reported as similar or lower in lianas than in trees and shrubs (Ewers et al. 1991; Gartner 1991a; Tyree and Ewers 1996; Feild and Balun 2008; Zhu and Cao 2009). In those studies the only consistent advantage that liana stems had is a low Huber value, that is, low xylem transverse area per leaf area supplied. However, K_s , LSC, and Huber value do not correct for the length of the pathway. If we consider the greater internode elongation for lianas, and the long and rambling pathways that liana stems often take along the ground and through the canopy, the hydraulic advantage for liana stems may disappear. Liana stems can be up to 200 m in length (Burkill 1966), much longer than the pathways that water travels in the host tree. Given the low Huber values there would appear to be little redundancy per leaf area supplied in the liana stem compared to the host trees on which they climb. When liana vessels become embolized the alternate routes for water transport may be severely diminished, unless narrow vessels and tracheids, mentioned below, can partially compensate. In addition, the greater lengths of liana stems can mask the total biomass allocation. In a study comparing lianas with free-standing shrub forms of the same species, the lianas had greater stem lengths but that same above ground biomass (Gartner 1991b, c).

It has been argued that the evolution of the vessel may have been essential to the widespread evolution of the liana habit in angiosperms (Feild et al 2012). Among gymnosperms the most prominent lianas are among the Gnetales, which have vessels that are functionally very similar to those of angiosperms (Fisher and Ewers 1995). Conifers do not include lianas in the usual sense, although there are some prostrate or scrambling conifers. The limitation of tracheids as conduits may be related to the fact that, in a tracheid-based transport system, the tracheid provides mechanical support as well as transport (see chapter on “The hydraulic architecture of conifers”). The mechanical function of tracheids may limit the hydraulic potential of tracheid systems (Pittermann et al. 2006). In contrast, vessel systems depend on fibers for mechanical reinforcement. Xylem fibers are important for stem support for plants in general, but perhaps also for the prevention of implosion of vessels

when the water columns are under tension (Carlquist 1975; Hacke et al. 2001; Jacobsen et al. 2005). This is not mainstream thinking, but in lianas fiber presence and distribution may be mostly favored in the prevention of vessel implosion, since the stem support needs are largely provided by the host plant.

5 Stem Length and Vessel Diameter in Lianas

From Nehemiah Grew (1682) to the present day (e.g., Schenck 1893; Ewers et al. 1990; Fisher and Ewers 1995; Fisher et al. 2002; Baas et al. 2004; Gartner et al. 1990; Carlquist 1991; Gartner 1991b; Cai et al. 2009; Isnard and Silk 2009; Zhu and Cao 2009; Angyalossy et al. 2012; Jiménez-Castillo and Lusk 2013; van der Sande et al. 2013; Wyka et al. 2013), virtually every published work on liana anatomy or hydraulics remarks that lianas have exceptionally wide vessels. These studies usually take stem diameter as their basis for comparison, and it is clear that lianas have much wider mean vessel diameters for a given stem diameter than self-supporting plants do. What is not clear is whether stem diameter is always the appropriate metric for making these comparisons.

There are reasons to expect mean vessel diameter to be predicted by stem length across plant habits. The biological significance of Poiseuille's law, published in the mid-1800s, was not lost on plant biologists, who soon invoked notions of hydraulic resistance to explain the wide vessels of lianas (e.g., Westermaier and Ambronn 1881; Haberlandt 1914). Lengthening of a vessel of constant diameter adds fluid-wall friction and therefore hydraulic resistance. As a consequence, with no vessel diameter increase, flow rate would drop as the stem and therefore the conductive path becomes longer. Vessels tend to be narrow closer to stem apices, and even narrower in terminal leaf veins. The average diameter of vessels widens with distance from the stem tip. The phenomenon is readily seen in transverse view as a radial increase in vessel diameter in going from the pith out to the vascular cambium. Narrow vessels near the stem center correspond to when the stem was short (see Mencuccini et al. 2007). Although often attributed to Sanio (1872), the pattern of conduit increase with growth was first described by Grew (1682). Although the idea that conductive path length should be related to vessel diameter has been present in the literature for a long time (Westermaier and Ambronn 1881; Haberlandt 1914; Ewart 1904–1905; Jost 1907; Cowan 1965), it was not modeled until fairly recently.

The vessel diameter–stem length relationship has been modeled thoroughly by West et al. (1999), Becker and Gribben (2001), McCulloh et al. (2003), Mencuccini (2002), Enquist (2003), Mencuccini et al. (2007), Coomes et al. (2007), Petit and Anfodillo (2009), Petit and Anfodillo (2011), Savage et al. (2010), Sperry et al. (2012), and von Allmen et al. (2012). Recent data seem congruent with the expectation that conductive path length, as reflected by stem length, predicts average basal vessel diameter in both self-supporting and non-self-supporting plants. In their comparative study of mean vessel diameter–stem length relations, Anfodillo et al. (2006) included one non-self-supporting plant, *Hedera helix*. They plotted the average hydraulically weighted conduit diameter against stem length across 31 species.

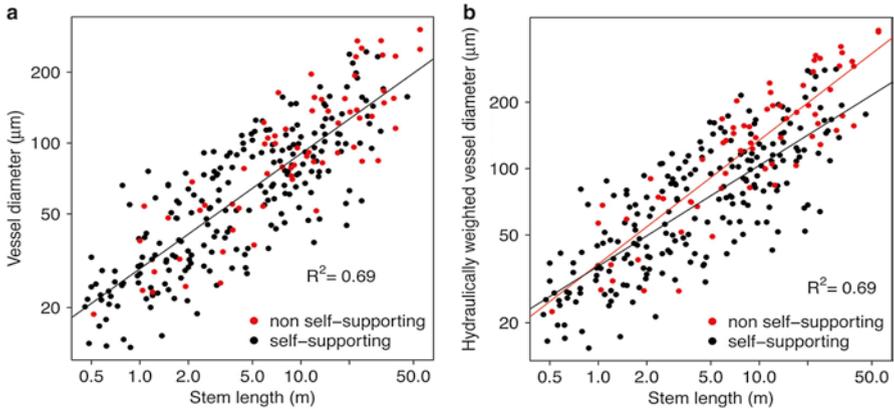


Fig. 6.6 The relationship between mean vessel diameter and stem length. Lianas are traditionally regarded as having wide vessels, but they have the same mean natural (nonhydraulically weighted) vessel diameter that self-supporting plants do for a given stem length (a). Because lianas tend to have greater maximum and minimum vessel diameters (greater extremes within a stem), their hydraulic vessel diameter tends to be very slightly greater than in self-supporting plants when stem length is controlled for (b). After Rosell and Olson (2014)

They found that mean vessel diameter was predictable given stem length, with taller plants having predictably wider vessels basally. *Hedera* fell where it would be expected to given its stem length. Rosell and Olson found that the slope of the vessel diameter–stem length relationship was the same in both lianas and self-supporting plants (Fig. 6.6a). Moreover, for a given stem length, lianas had slightly greater average hydraulically weighted diameters as compared to self-supporting plants. This appears to be achieved by a widening of the vessel diameter variance in lianas. That is, lianas have more extremes in vessel diameter within a stem. The occurrence of just a few wider vessels is sufficient to make the mean hydraulically weighted vessel diameter of lianas slightly wider than those of similar length self-supporting plants. In contrast to the common perception, when standardized by stem length, the difference in mean vessel diameter between lianas and self-supporting plants is very subtle (Fig. 6.6b). This comparison underscores the need to standardize by stem length in morphological and physiological studies of the xylem (see Sect. 6.11). In addition, this result highlights an often overlooked aspect of lianas, mentioned earlier, their abundance of narrow vessels.

6 The Importance of Narrow Vessels and Tracheids in Lianas

One of the interesting/complicating things about liana stems is that they tend to have an exceptionally high number of narrow vessels in addition to their wide vessels (Carlquist 1985a; Ewers and Fisher 1989a, b; Ewers et al. 1990), as illustrated by an example in Fig. 6.7. In addition, conductive imperforate cells (various types of tracheids) are common in liana stems.

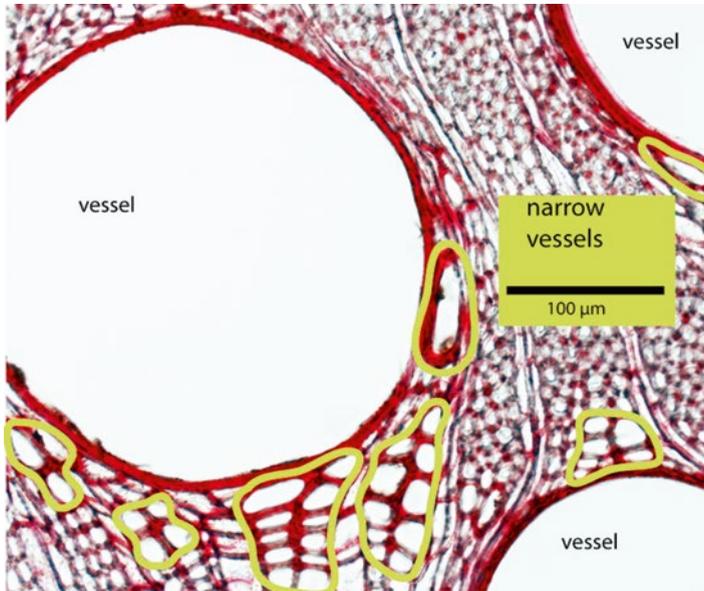


Fig. 6.7 In addition to wide vessels (portions of three are shown here), lianas tend to have a large number of narrow vessels, as in this stem of *Gouania lupuloides* (Rhamnaceae). The narrow vessels (circled in yellow) may be important for redundancy of the hydraulic pathway. The narrow vessels and fibers may also function in mechanical support of the transport system, preventing implosion under water stress

The narrowest vessels in a stem can be difficult to detect without corroborative observations with longitudinal sections or macerations. Narrow vessels may be confused with tracheids or even fibers in some cases. Figure 6.8a, b shows different tissue allocations in a liana and tree stem, and the impact of narrow vessels on measurements of mean, median, and hydraulically weighed mean vessel diameters in a tree and a liana. Narrow vessels of lianas can lead to a misleading value for mean vessel diameter; hydraulic means should be used if the interest is in conductive potential. However, as noted by Carlquist (1985a, b) the narrow vessels may be important for hydraulic redundancy and alternate pathways in the event of vessel dysfunction. Narrow vessels may also have a mechanical role, along with the fibers, in helping to prevent vessel implosion by the wide vessels.

Conductive imperforate tracheary elements have been classified as true tracheids, vasicentric tracheids, and vascular tracheids (Carlquist 1985b; Rosell et al. 2007). Vasicentric tracheids (see also the chapter on “Integrative xylem analysis of chaparral shrubs”) are particularly common in lianas and are found in vessel groupings, often large ones, apparently serving as maximally safe conductive cells that both connect vessels laterally as well as maintain a minimal conductive stream in case of embolization of the wide vessels. In contrast to the large groups of vessels and vasicentric tracheids in lianas, when true tracheids are present, vessels are solitary as seen in transverse view.

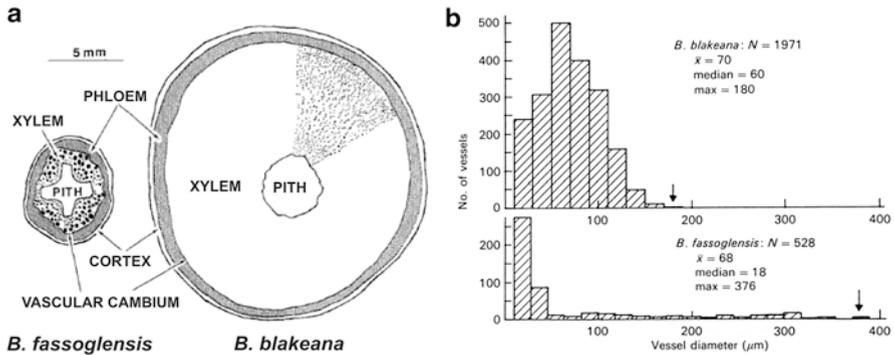


Fig. 6.8 Stem cross sections of a stem of a liana (*Bauhinia fassoglensis*) and a tree (*B. blakeana*) each supplying the same leaf area. (a) Comparison of tissue distributions of stems, arrow indicates maximum vessel diameter. (b) Comparison of vessel diameter frequency distributions from same stems. Note that in this case the mean vessel diameter was essentially the same, but the maximum vessel diameter was much greater in the liana. The hydraulic mean vessel diameter was 112 μm for the tree versus 286 μm for the liana. (a) is From Ewers and Fisher (1991), (b) is from Ewers et al. (1991)

7 Hormonal Mechanisms of Vascular Differentiation and Hydraulic Adaptation

The global pattern of tip-to-base vessel widening that occurs across the flowering plants is consistent with what is known about the hormonal control of vascular development. Vessels appear to develop in the context of an auxin gradient along the length of stems. Auxin is apparently produced in abundance in developing leaves (Uggla et al. 1998; Scarpella and Meijer 2004), and directional movement of auxin along the sites of differentiating secondary xylem cells establishes a high–low concentration gradient leaf to root (Aloni and Zimmermann 1983; Aloni 1987; Lovisolo et al. 2002). In the case of basipetal vessel widening, lower concentrations of auxin correlate with the developmental outcome of wider vessels. Wider conduits appear to develop because of a longer time of development rather than an accelerated widening rate (Anfodillo et al. 2012, 2013).

Models of vascular differentiation highlight missing developmental information vital to testing hypotheses of the adaptive causes of tip-to-base vessel widening. It is clear that there must be *some* developmental mechanism controlling vessel diameter, but the particulars are hardly important when trying to elucidate *why* the patterns are observed. Even if every species of plant on the planet had a completely different developmental mechanism, the adaptive prediction of West et al. (1999) would remain valid, as would efforts to test it with anatomical data. In fact, the majority of studies examining vessel-stem size scaling, such as West et al. (1999), Becker and Gribben (2001), McCulloh et al. (2003), Mencuccini (2002), Mencuccini et al. (2007), Coomes et al. (2007), Savage et al. (2010), Gleason et al. (2012), Sperry et al. (2012), and von Allmen et al. (2012) cite no developmental information

at all and require none. This is because developmental mechanisms do not predict *why* a global vessel diameter–stem diameter relationship should be observed across the angiosperms, much less that a specific exponent should be observed. Natural selection acts on heritable variation between individuals. Establishing the adaptive basis of vessel widening therefore involves understanding the degree to which heritable variation in vessel widening exponents is possible, and to study directly how these different exponents vary in their hydraulic performance (cf. Olson 2012).

8 Liability Between Self-Supporting and Climbing Habits

Depending upon their climbing mode, lianas can be characterized as shoot twiners, tendril climbers, root climbers, and scramblers, the latter of which tend to fall upon their host plants (Reddy and Parthasarathy 2006; Campanello et al. 2007). Lianas may have thorns, spines, or hooks to latch onto the host. The scrambler mode would seem to require the fewest evolutionary steps.

The tendency for mechanically supported stems to become liana like in xylem properties may be inherent to all woody plants, as can be observed by well-known “thigmotropic” responses. Within a species, or even within a clone, when plants are provided mechanical support by staking the stems, the stems become liana like compared to stems that are either self-supporting or stems subjected to mechanical perturbation. In a wide range of gymnosperms and angiosperms, it has been shown that staked stems are longer and narrower than free-standing stems, with larger leaves (Neel and Harris 1971; Pruyne et al. 2000; Kern et al. 2005). The xylem properties of unperturbed staked stems also become more liana like, with greater K_s , greater mean, maximum and hydraulic vessel diameters, and greater vessel lumen area per xylem area. It is of particular interest that in staked plants, although the vessel diameters increase, the vessel frequency per transverse area remains the same (Gartner 1991a; Kern et al. 2005). Selection for a mechanically weaker stem would be concomitant with a longer, narrower axis with wider vessels near the base.

An interesting case study involved a species, *Toxicodendron diversilobum*, which grows as a liana when provided external mechanical support but grows as a shrub when free standing (Gartner 1991a, b, c). Supported stems had lower Huber values, greater K_s , greater vessel diameters, and greater vessel lumen areas than free-standing stems (Gartner 1991a, b). However, the leaf biomass, leaf number, and stem biomass were not different between growth forms. Supported stems were longer and had a more gradual taper. They had greater internode elongation than free-standing stems (Gartner 1991b, c). Apparently the liana habit mostly involved “stretching out” the stem. As discussed in Sect. 6.5, with greater stem lengths, the wider vessels in supported stems would be as expected.

Plastic variation between self- and non-self-supporting forms within species is paralleled by extreme evolutionary liability between self- and non-self-supporting plants. The liana habit has arisen many times in the flowering plants (Fig. 6.9). For example, *Trimenia moorei* is closely related to self-supporting *Trimenia* species, and *Bursera instabilis*, an unusual tree with lianescent branches, is found within an

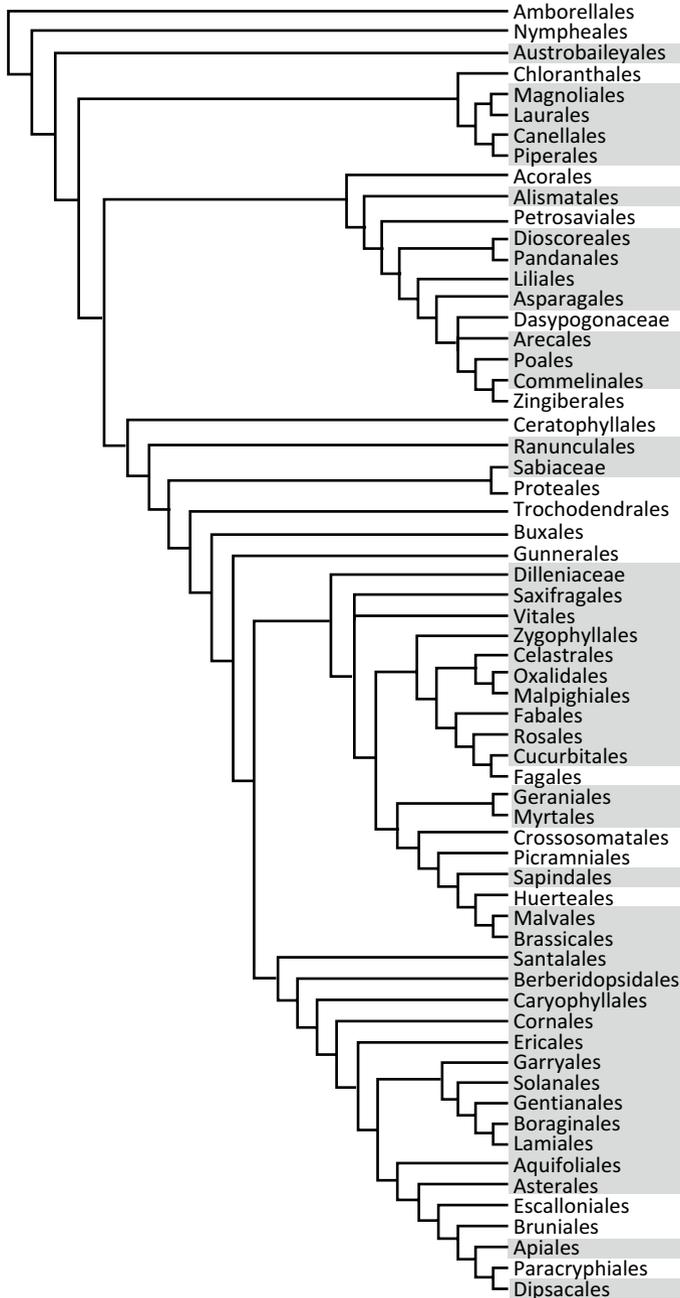


Fig. 6.9 Ordinal distribution of lianas, following Stevens (2001). Orders that include climbing plants are boxed in *gray* to show that they are present in almost all orders of angiosperms. Within orders, it seems that there have been very frequent independent derivations of the liana habit from self-supporting ancestors. Some orders, such as Cucurbitales, Malpighiales, Solanales, and Vitales include self-supporting species that have apparently evolved from liana ancestors

otherwise self-supporting genus (Rosell et al. 2012). Every time lianescence arises, it is accompanied by the attendant shifts in vessel diameter–stem diameter proportions. By the same token, the shift from liana to self-supporting plant seems to have occurred numerous times (e.g., Lahaye et al. 2005). One route to the evolution of self-supporting plants from lianas likely is the cooption of the very abundant storage parenchyma (Carlquist 1985a) to form self-supporting water storing trees, often with twining or tendril-bearing branches (e.g., *Dendrosicyos*, some tree *Ipomoea*, *Adenia karibaensis*, etc., see Olson 2003; Hearn 2009).

9 Problems of Sampling Vessels in Long Stems

In most cases, stem diameter has been used as a basis for comparison between growth forms. Comparisons based upon supplied leaf area have also been done. However, as noted above, lianas have much longer stems for a given diameter than do self-supporting plants. If mean vessel diameter is a reflection of stem length, then comparisons that are standardized by stem diameter will reflect very different conductive path lengths. Given a constant rate of basipetal vessel widening, then the lianas, with their very long stems, will inevitably have much wider vessels and therefore higher mean vessel diameters, higher conductivities, greater embolism vulnerabilities, and probably longer vessels as well.

Standardizing comparisons by stem length and by leaf area supplied would seem more appropriate, especially for main trunk comparisons. Comparing a 60 m long liana and a 60 m long self-supporting tree shows that these both have similar mean vessel basal diameters (Rosell and Olson 2014). Use of the residuals of mean vessel diameter regressed on stem length is one way of “factoring out” stem length (Olson et al. 2014).

Studies of plant hydraulics need to take conductive path length into account. To the extent that vessel diameter is related to vulnerability to cavitation and embolism, comparing stem segments drawn from different distances to the stem tip certainly introduces a confounding factor. The wider vessels of the stem taken from a greater distance to the tip will have many wider vessels and therefore higher flow rates and vulnerabilities to embolism (Petit and Anfodillo 2009, 2011). Vessels are expected to become longer with increasing distance from the stem tip (Comstock and Sperry 2000).

The exponential form of tip-to-base vessel widening must be taken into account. Vessel widening follows a power law in which the slope of the mean vessel diameter–stem length curve becomes less pronounced with distance from the tip. As a result, variation in vessel diameter per unit stem length increment will be much more pronounced when sampling terminal twigs as compared to main trunks. The best strategy for standardizing in these cases is not entirely clear, mostly due to the potential role of leaf size and its influence on terminal twig vessel diameter. Larger leaves have longer conductive paths within the lamina and so we would predict them to have wider vessels in their petiole bases.

Following that logic, plants with larger leaves should have wider terminal twig vessels. Some work remains to be done to identify ways of generating truly comparable measurements of hydraulic performance in twigs (Petit and Anfodillo 2011). Moreover, recent results suggest that terminal twig vessel diameters scale positively with tree height and liana stem length (Olson et al. 2014). This would mean that stem length could potentially be a confounding factor not only in comparisons between liana and self-supporting plant twigs but leaves as well. This is because wide terminal twig vessels might indicate wider vessels entering into petioles. If plants of many different lengths were sampled in these comparisons, then the results might reflect the variation introduced by stem length rather than inherent liana/self-supporting differences. As a result, studies that standardize by stem length are needed.

Studies of hydraulic performance on lianas also face the challenge of taking into account the changing stem proportionalities that lianas undergo tip to base. The terminal parts of liana stems are often mostly self-supporting. These “searcher” stem segments help lianas make their way across open spaces between host branches. The stem length–diameter relations in self-supporting plants and lianas less than 1 m long are quite similar (Fig. 6.10). Therefore, studies of liana hydraulics based only on slender terminal stems may not accurately reveal the differences between lianas and self-supporting plants.

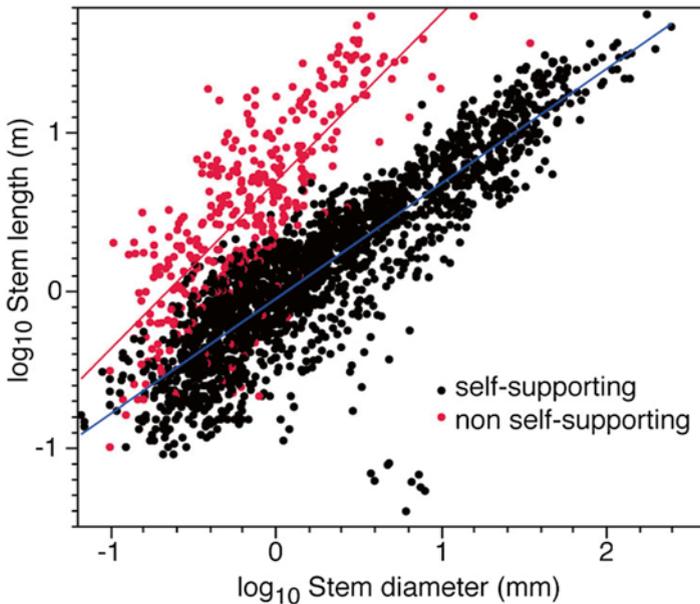


Fig. 6.10 Self- versus non-self-supporting plant stem length–diameter allometry, based on data from 2,388 samples from 472 species. From Olson et al. 2014, Rosell and Olson 2014 and unpublished data. $R^2=0.76$, self-supporting slope 0.90, non-self-supporting slope 1.065. There is extensive overlap at short stem lengths, but as stem length becomes longer, there are fewer and fewer individuals occupying the space between the main liana and self-supporting scaling lines

10 Xylem Dysfunction in Lianas

Since LSCs are not exceptional in lianas, the predicted stem pressure gradients in lianas are similar to those for trees and shrubs with similar transpiration rates (Table 6.2). Thus, lianas with very long stems could actually be at a hydraulic disadvantage in a mature forest.

Considering the great lengths that liana stems typically have, the few long and wide vessels in the basal parts of liana stems may represent low-cost high-risk investments. Such conduits should be more vulnerable to embolism caused by freeze–thaw, water stress, bending stress, pathogens, and herbivores. An additional level of risk is the low level of redundancy in liana conduits (Carlquist 1975; Ewers et al. 2007). Low Huber values in liana stems indicate there are fewer alternate pathways when some vessels become air blocked—this adds to the risk in the liana transport system, which may or may not be sufficiently ameliorated by abundant narrow vessels and tracheids in the xylem.

As would be predicted from their wide vessels and low vessel redundancy, liana stems tend to have higher P_{50} values than the trees they climb upon, that is, they are more vulnerable to water stress-induced embolism (Zhu and Cao 2009; van der Sande et al. 2013). In addition, lianas are clearly more prone to freeze–thaw embolism than are trees in temperate areas (Zimmermann 1983; Sperry et al. 1987; Tibbetts and Ewers 2000; Jiménez-Castillo and Lusk 2013). In fact, vulnerability to freeze–thaw embolism may be the major reason that lianas are much more common in tropical than in temperate forests.

11 What Lianas Tell Us About Self-Supporting Plants

Here, we briefly explain how lianas might help to identify features that are likely adaptive, both in lianas as well as in self-supporting plants, as opposed to those due to “constraint,” that is, a lack of developmental alternatives (Olson 2012). The theoretical packing limit is a prime example. The packing limit refers to the limited range of values that the relationship between conduit number and conduit diameter must necessarily occupy. The proportion of a given trans-sectional area of stem that is occupied by vessels is maximally 1 and minimally 0. As a result, because of the inescapable space trade-off involved in packing many small or few large conduits into a given area, the conduit number and diameter relationship can be thought of as “constrained” (Zanne et al. 2010). This space trade-off is associated with the negative relationship between vessel diameter and vessel density across the flowering plants, as well as the decay in vessel density with distance from the stem tip (Zanne et al. 2010; Olson et al. 2014). Lianas have higher vessel densities for a given average vessel diameter than self-supporting plants do. This can be due both to the lack of need to pack in as many fibers in the liana stem, as well as the tendency for lianas

to have many narrow vessels in addition to wide ones. While variation is bounded by the packing limit, the exact position of the vessel density–diameter intercept in self-supporting plants should be determined by natural selection (Crivellaro et al. 2012; Rosell and Olson 2014).

For stems longer than 2 m, the slope of the liana length–diameter relationship is statistically indistinguishable from that in self-supporting plants, with a significantly higher intercept in lianas. At shorter stem lengths, especially 2 m or shorter, stem length–diameter relations between lianas and self-supporting plants are very similar. For stems of up to 4 m long or so, many plants can be found with stems that lean or rest on other plants, without twining or climbing. Such intermediate morphologies are never observed at long stem lengths, beyond 10 m long. Figure 6.10 illustrates this tendency. This pattern suggests that leaning or semi-self-supporting plants of very long stem lengths are not favored by selection. This pattern of selection then leads to the empty space shown on the right of Fig 6.10.

12 Global Distribution of Lianas and Liana Strategies

Lianas are most diverse and abundant in tropical forests, especially dry tropical forests (Schnitzer and Bongers 2002; Schnitzer 2005). In such areas freeze–thaw embolism is generally not a risk. It has also been suggested that the thriving of lianas in dry tropical forests may be due to an exceptionally deep rooting system that taps into water resources that are not available to trees (Chen et al. 2015). Lianas have high levels of native embolism in their stems—they may operate with a narrow hydraulic safety margin (Tibbetts and Ewers 2000; Jiménez-Castillo and Lusk 2013; Johnson et al. 2013). If stems are “expendable” and roots are conserved, then a high-risk strategy for the stems and leaves would be adaptive.

Although lianas can survive at the top of mature forest canopies, they are most competitive and abundant in secondary forests and, in mature forests, in tree fall gaps (Putz 1984; Schnitzer 2005; Schnitzer et al. 2005; Schnitzer and Bongers 2011; Jiménez-Castillo and Lusk 2013). Based upon liana exclusion studies, at tree fall gaps lianas dramatically decreased the biomass production of trees (Schnitzer et al. 2014). In an extensive study of Costa Rican forests, the number of liana stems declined significantly with age of the forest, while the number of self-supporting stems did not change. With advancing forest age, species richness and biomass increased significantly for self-supporting plants, while lianas held steady or sometimes declined in those parameters (Letcher and Chazdon 2009). The predicted xylem pressure gradients are similar in stems of lianas as in free-standing growth forms (Table 6.2), which could mean that extremely long stems of lianas would eventually be at a hydraulic disadvantage. However, the relationship between vessel diameter and stem length should adjust for that in large plants. Such predictions also do not account for possible foliar absorption of water during periods of mist or rain (Rundel 1982; Burgess and Dawson 2004; Breshears et al. 2008; Limm et al. 2009).

We are not aware of studies of foliar absorption of water by liana leaves, but that phenomenon would dampen the pressure gradients and otherwise mitigate water stress.

In addition to the well-known “mechanical parasite” strategy, lianas might be categorized as ruderal plants (*sensu* Grime 1977) considering that they thrive most in early successional situations. This may be surprising given their great stem lengths. The inexpensive stems (on a per unit stem length basis) with throw-away leaves may be central to the ruderal liana strategy. This is especially evident in dry tropical forests, tree fall gaps, and in secondary tropical forests, where lianas most thrive (Schnitzer and Bongers 2002; Schnitzer 2005). Although lianas appear to be exceptional for their long and wide vessels, the great vessel widths may be only commensurate with their remarkable stem lengths. The anomalous anatomical features of many liana stems, such as successive cambia surrounded by unlignified conjunctive tissue, wide unlignified vascular rays, multiple steles and sectoried xylem, all tend to increase stem flexibility and regeneration capacity in the event of tree falls and other disturbance events (Dobbins and Fisher 1986; Fisher and Ewers 1989; Ewers and Fisher 1991; Fisher and Ewers 1992; Carlquist 2007). Many lianas are very effective at sprouting from the basal parts of the shoot. For example, Putz (1984) reported that 90 % of lianas at a site in Panama sprouted within 12 months after their host trees fell. Some lianas also are capable of splitting along sectoried xylem to form new individuals (Caballe 1994). When mature liana stems touch ground, they are very capable of rooting and in some cases forming new individuals by vegetative spread (Fisher and Ewers 1991). The root systems of lianas may be long lasting, and as noted above, the root xylem has abundant storage parenchyma. In contrast, the shoots may be expendable.

13 Future Research Directions

Many questions remain to be addressed, making liana biology a fertile field for research. The distinctness of roots systems of lianas versus self-supporting plants is one. Foliar absorption could ameliorate the water relations of liana shoots, but this has not been studied. There is a need to establish methodologies for making conductive path length-standardized comparisons of vessel dimensions and hydraulic performance between lianas and self-supporting plants, including the need to take leaf size into account. For analysis of risk, structure and function studies need to take into account the total length of the xylem pathways. The relative level of hydraulic redundancy in lianas is at question given the low Huber values but abundant narrow vessels and frequent presence of vasicentric tracheids. A clear priority is also determining whether variation in the taper exponent is heritable and how this variation affects hydraulic performance. Lastly, if lianas are regarded as ruderal, then they are the world’s longest weeds. Although much remains to be studied, it is clear that when the proverbial “tree falls in the forest,” whether someone hears it or not, lianas have the hydraulic capacity to rapidly exploit the newly opened space.

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