Oecologia (1991) 88:233–237

Oecologia

Why vines have narrow stems: Histological trends in *Bauhinia* (Fabaceae)

Frank W. Ewers[1] **and Jack B. Fisher**[2,3]

[1] Department of Botany and Plant Pathology, Michigan State University, East Lansing, MI 48824, USA
[2] Fairchild Tropical Garden, 11935 Old Cutler Road, Miami, FL 33156, USA
[3] Department of Biological Sciences, Florida International University, Miami, FL 33199, USA

Received October 17, 1990 / Accepted in revised form May 23, 1991

Summary. Xylem (wood) tissue in plants functions both for mechanical support and water transport. Since vines are mechanical parasites, they allocate less biomass for xylem tissue than do free-standing trees or shrubs. Within the genus *Bauhinia*, stems of vine species were found to have not only less xylem per distal leaf area, but also less phloem and cortical tissue when compared to tree and shrub species. The phloem and cortical reductions are interpreted as an indirect effect of the developmental/geometric constraints imposed by the evolution of a reduced mechanical system. Apparently vines overcame these constraints with the evolution of wider vessels and wider sieve tubes and with many types of variant (anomalous) secondary growth. The long and wide vessels of vines, which compensate hydraulically for the reduced xylem areas, may help limit the distribution of vine species in nature.

Key words: Anomalous growth – Huber value – Lianas – Sieve tubes – Translocation – Vessels – Xylem transport

Although vines are an enormously important growth form in temperate and especially tropical ecosystems, their biology has been relatively little studied. The vine habit appears to have evolved independently in many different families of non-flowering and especially flowering plants (Putz 1984; Stevens 1987; Gentry 1991). By definition, vines are plants that are rooted in the ground but dependent upon external plants or objects for mechanical support. Vines may thus be interpreted as mechanical parasites that are in competition with their host plants for light, water, and mineral resources (Putz 1984; Stevens 1987). Since xylem (wood) is the tissue most responsible for both mechanical support and water transport in stems of vascular plants, evolutionary adjustments might be expected to have occurred in this tissue.

Stems of vines have been reported to have a small transverse area relative to the amount of foliage they bear (Schenck 1893; Putz 1983; Ter Welle 1985; Ewers 1985). Huber values (ratio of xylem transverse area to distal leaf weight or area; Huber 1928) have been reported for some taxa, but the various stem tissue regions (xylem, phloem, cortex) have not been compared in these studies. Preliminary data suggested that within the genus *Bauhinia*, vine (liana) species had greater maximum vessel lengths and vessel diameters than do tree or shrub species (Ewers et al. 1990). In the present paper we survey stem tissue areas and cell dimensions in transverse section as a function of the leaf area distal to a particular stem segment. The distal leaf area reflects the leaf area that a stem must supply with water and minerals. The purpose is to determine what tissue modifications, if any, have occurred with the evolution of the vine habit in *Bauhinia*.

Materials and methods

Tree, shrub, and vine species of *Bauhinia* were cultivated at Fairchild Tropical Garden in Miami, FL. One to three genotypes were used for each of six species including the trees *Bauhinia blakeana* Dunn. and *B. variegata* L., the shrubs *B. aculeata* L. and *B. galpinii* N.E. Br., and the vines *B. fassoglensis* Kotschy ex Schweinf. and *B. vahlii* Wight & Arn.

The total area of all leaves distal to a stem segment was measured directly with a Li-Cor leaf area meter. Stem segments were transversely sectioned at 15 to 30 μm with a sliding microtome, dehydrated in an ethanol series and mounted in permount. Transverse tissue areas and the circumference of the vascular cambium were determined from stereomicroscope camera lucida drawings (Fig. 1). The perivascular fibers were used to demarcate the innermost cortex. The periderm and/or epidermal tissue was included with the cortex since none of the stems had thick periderms or multiple periderms; the periderm and epidermal layers were too thin to be accurately measured as a separate tissue region with our techniques.

Cell measurements and counts were made with an ocular micrometer on a compound microscope. Maximum vessel diameter and maximum sieve tube diameter were determined by measuring

---

Offprint requests to: F. Ewers

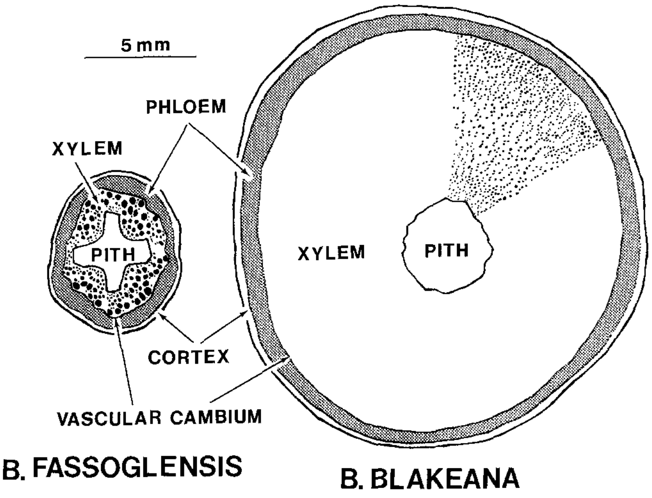

Fig. 1. Camera-lucida drawings of stem transverse sections of a vine *Bauhinia fassoglensis* and a tree *B. blakeana*, each at the same magnification. Each stem bore the same distal leaf area of about 2.45 m^2. In the xylem tissue regions the vessel lumen areas are indicated in solid black for all but the narrowest vessels. The tree stem had greater tissue areas, especially for the xylem, and a greater vascular cambium circumference, but maximum vessel diameter was greater in the vine

the lumen of the widest vessel and widest sieve tube in a section. Sieve tube measurements were made only on cells with a clearly visible sieve plate and/or a clearly associated companion cell. Since vessels and sieve tubes were generally elliptic in transverse outline, two diameter measurements were averaged for a cell, the maximum lumen diameter and the diameter of the bisecting line perpendicular to the maximum dimension.

Additional measurements on cambial cell size and counts of cell numbers were made in two taxa for which we had the most complete data set, the tree *B. blakeana* and the vine *B. fassoglensis*. In each stem section the tangential width of each of twelve vascular cambium initial cells was measured. These were sampled from four equidistant locations in the cambium. The total number of cambial initials in transverse view was calculated as the circumference of the vascular cambium divided by the mean initial width. Since we found no statistically significant correlation between mean initial width and leaf area supplied by a segment, a single overall mean tangential width of the cambial initial, 21.8 μm (SE = 0.32) for *B. fassoglensis*, and 15.2 μm (SE = 0.41) for *B. blakeana*, was used. In order to quantify rates of radial cell production in the xylem and phloem of these species we counted ray parenchyma cells, an easily identifiable cell type that occurs in both the xylem and phloem tissue. Uniseriate vascular rays that extended in transverse view throughout the secondary xylem and secondary phloem were identified. The number of xylem and phloem ray parenchyma cells were counted in three roughly equidistant rays in each stem section and averaged.

Results and discussion

More xylem, phloem, and cortical tissue was produced in stems of trees and shrubs than in vines with equivalent leaf areas (Figs. 1 and 2). This is the first report of phloem and cortical tissue areas being less in vines than in trees or shrubs. Previous studies have shown this trend in regard to xylem area or total stem area (Schenck 1893; Putz 1983; Ewers 1985; Gartner 1991).

The difference between growth forms was greatest for the xylem tissue region. Note the different scales used for the three tissue types in Fig. 2. The y-intercepts were similar in the different growth forms, but slopes of the regression lines indicate that, as the shoots grew, about 19 times more xylem was produced in trees + shrubs than in vine species, versus 9 times more cortical tissue and only 5 times more phloem.

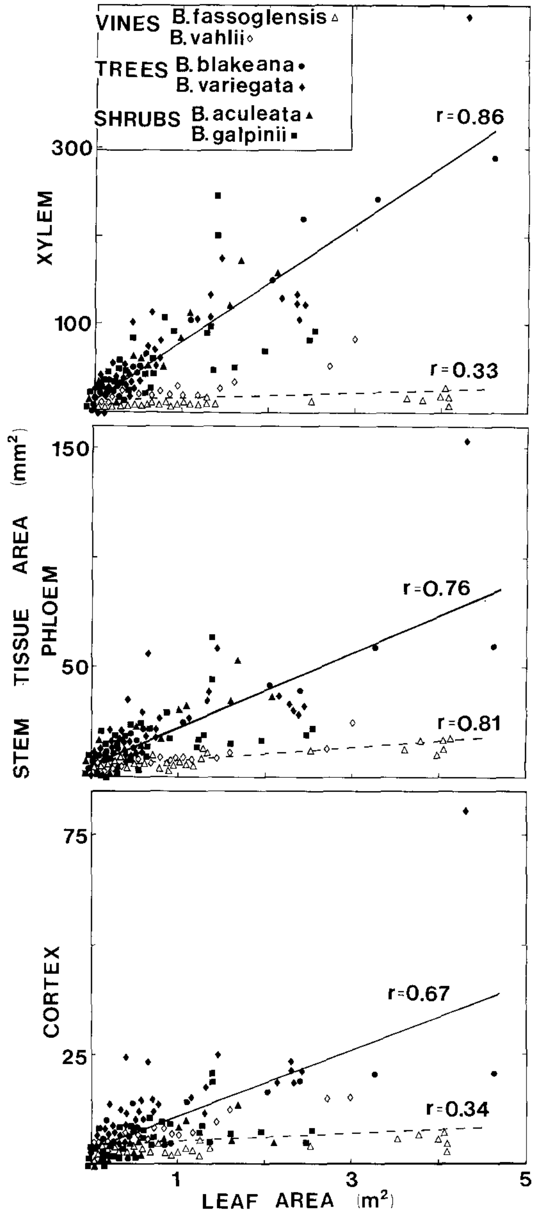

Fig. 2. Stem tissue areas as functions of the (one-sided) leaf area distal to the stem segment. Each point represents a single transverse section of one stem segment. The dashed regression lines and open symbols are for liana stems, the solid regression lines and closed symbols are for tree + shrub stems

Assuming vines are derived growth forms, the evolutionary reduction in the xylem is much more pronounced than that which occurred in the phloem. The xylem is both a mechanical support and a water transport tissue. The presumed selective advantage of reduced xylem area in vines is to minimize resource allocation to mechanical tissue. Heavy vine stems, in addition to being mechanically redundant, would have the deleterious effect of

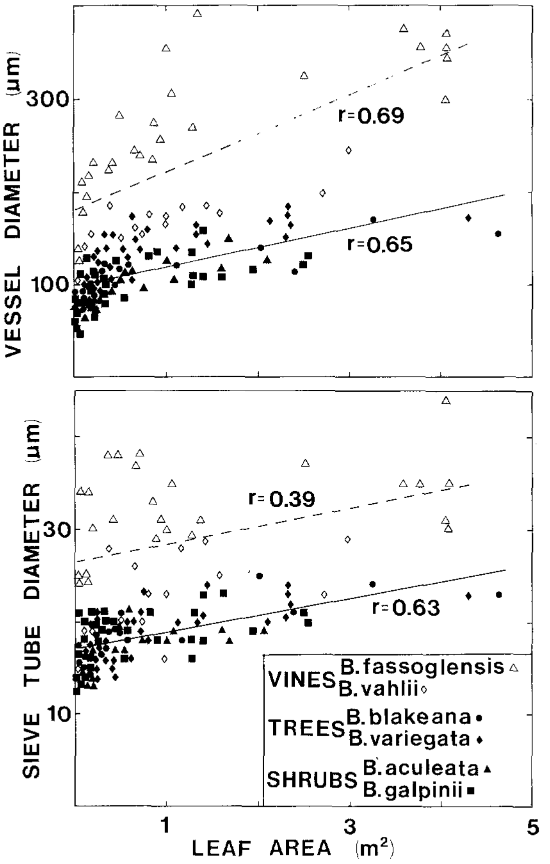

Fig. 3. Maximum diameters of vessels and sieve tubes as functions of the leaf area distal to a stem segment. Each point is from the widest vessel or sieve tube in a single transverse section of a stem segment. The dashed regression line and open symbols are for liana stems, the solid regression line and closed symbols are for tree + shrub stems

toppling the host (Putz 1984; Stevens 1987; Peñalosa 1984).

Phloem is the tissue responsible for long-distance transport of carbohydrates in the plant. The data indicate phloem sieve tubes as well as xylem vessels were wider in vines than in trees or shrubs (Fig. 3). We know of no previous reports of sieve tubes being wider in vines than in other growth forms, but there are previous reports demonstrating this trend for vessels (Ayensu and Stern 1964; Carlquist 1975; Ewers 1985; Gartner 1991; Ewers et al. 1990).

All four tree and shrub species of *Bauhinia* produced tangential rows of fibers within the phloem, whereas both vine species lacked lignified phloem fibers. Fibers are cells that are specialized for mechanical support and protection. Although the phloem is usually not considered to be of great mechanical importance to the plant, the lack of phloem fibers in the vine species is consistent with the "mechanical parasite" concept.

The wide vessels in vines are thought to compensate hydraulically for their narrow xylem area (Putz 1983; Ewers 1985; Ewers et al. 1991). This is because, by Poiseuille's law for ideal capillaries, hydraulic conductance is proportional to the vessel diameter to the fourth power (Zimmermann 1983). In *Bauhinia,* the mean maximum vessel diameter was 234 µm (SE = 12.3) for vines versus 116 µm (SE = 3.1) for the free-standing growth forms. If all else were equal, based upon Poiseuille's law, the liana vessels would be about 16 times more efficient than the tree and shrub vessels. This by itself would largely compensate for lianas having only 1/19th of the transverse xylem area.

A similar analysis could be applied to the phloem sieve tubes. The mean maximum sieve tube diameter was 29.0 µm (SE = 1.03) for vines versus 18.6 µm (SE = 0.28) for the free-standing growth forms. By Poiseuille's law, the vine sieve tubes would be 5.9 times more efficient, which would compensate for the vines having only 1/5th of the transverse phloem area. We have not yet quantified sieve plate pore size and number in the different growth forms, but in all growth forms sieve plates would tend to make conductive efficiency less than the theoretical predicted by Poiseuille's law.

We can now apply the concept of safety (many narrow sieve tubes as in the trees + shrubs) versus efficiency (few wide tubes as in the lianas) to phloem anatomy for the first time. This concept has been applied often to the xylem where increased conductive efficiency by wide vessels is well characterized (Carlquist 1975; Zimmermann 1983; Ewers 1985; Ewers et al. 1991). The possible disadvantages of wide vessels are less clear and more controversial. However, narrower vessels are generally considered to be less susceptible to dysfunction via freezing-induced embolism, and perhaps more able to recover from embolism, regardless of the cause (Zimmermann 1983; Ewers 1985). In addition, the redundancy inherent with many narrow vessels may confer greater safety than a system with few wide ones (Carlquist 1975).

Unlike xylem vessels, phloem sieve tubes are living when they are conductive. However, like vessels, sieve tubes are subject to dysfunction from a variety of causes. We would thus expect there to be tradeoffs between safety and efficiency. As with the xylem, particular phloem characteristics might be favored depending upon the growth form and the environment of a species. For instance, the vine growth habit, with reduced phloem area, would tend to select for wider sieve tubes. However, attack by aphids, insects that pierce sieve tubes with their stylets in order to obtain phloem sap, might select for a safer phloem histology, with many narrow sieve tubes.

The data in Figs. 1–4 do not necessarily reflect the total genetic or environmentally-induced variability that can occur in these species. In the species *Toxicodendron diversilobum,* which grows as both a vine and a shrub, variation in xylem anatomy was found to be controlled both by genetic and environmental factors. Artificially supported shoots exhibited more vine-like features, that is, narrow stems and wide vessels, than free-standing shoots of the same genotype or even of the same individual. In addition, different genotypes of this species differed significantly in their xylem anatomy when grown under the same environmental conditions (Gartner 1991).

In the present study, the vine *B. fassoglensis* had more pronounced vinelike features than did the vine *B. vahlii:* narrower stems with wider vessels and sieve tubes. Since both species were growing in nearly identical environ-

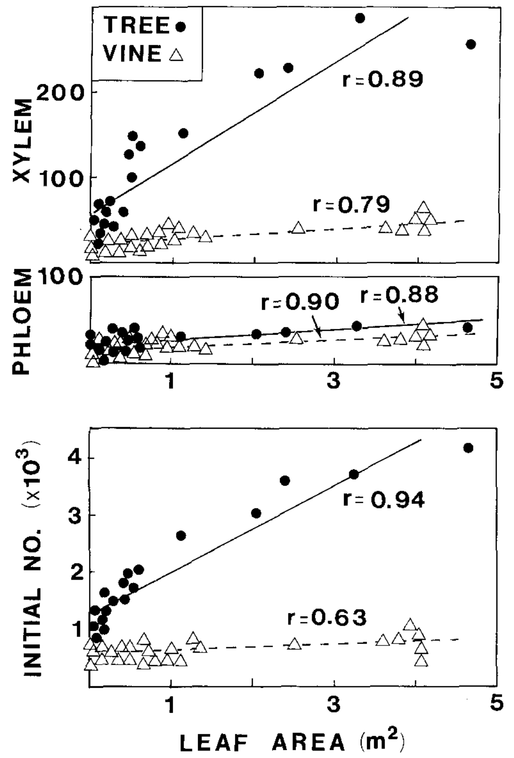

Fig. 4. Radial cell number and number of vascular cambium initials as functions of the leaf area distal to a stem segment in the tree *Bauhinia blakeana* and the vine *B. fassoglensis*. Each point represents results from a transverse section of a single stem segment

ments, the observed differences between species are assumed to be genetically controlled. The thicker stems of *B. vahlii* may be related to a searcher shoot that is more far-reaching than in *B. fassoglensis* (Ewers et al. 1991).

The evolutionary reduction in vine phloem may be caused by a developmental constaint. The vascular cambium is a cylinder which produces both secondary xylem and secondary phloem. Trees and shrubs of *Bauhinia* fit the typical pattern for secondary growth in seed plants; the vascular cambium produces several times more xylem than phloem. With less xylem production in vines, the vascular cambium does not expand in circumference nearly as much as in trees or shrubs. As a result there are many fewer cambial initials in transverse section in the vine, *B. fassoglensis,* than in the tree, *B. blakeana* (Fig. 4). Based upon radial cell counts, each initial of the vine produces a higher ratio of phloem to xylem cells (0.75) than what occurs in the tree (0.11). The number of phloem ray cells produced by an initial (i.e., radial cell number in Fig. 4) is only slightly higher in the tree than in the vine. Therefore, phloem production in vines appears to be constrained more by the reduced circumference of the vascular cambium (initial number) than by the rate of differentiation of phloem cells from the initials (radial cell number).

Different species of lianas may compensate for the limited phloem production imposed by the reduced vascular cambium circumference in a number of ways including: (A) Increasing the ratio of phloem to xylem produced by an initial. (B) Producing more sieve tubes and fewer fibers within the phloem. (C) Producing wider sieve tubes and/or wider pores in the sieve plate, both of which would increase transport efficiency. (D) Maintaining their sieve tubes in a conductive state for a longer time period. Lastly, (E) Evolving variant (= anomalous) growth patterns to increase phloem transverse area in narrow stems. In many lianas of the Bignoniaceae portions of the vascular cambium produce mainly secondary phloem and almost no secondary xylem, resulting in four (or later 8 or more) wedges of phloem, the "cross vine" histology. Other vine taxa produce internal phloem and/or intraxylary phloem (e.g., the Cucurbitaceae). Still others produce additional vascular cambia external to the original vascular cambium, each of which produce phloem as well as xylem. In some lianas there are multiple steles, and in others the original vascular cylinder becomes highly fragmented in older stems with vascular cambia formed within various sectors of the stem (Dobbins and Fisher 1986; Carlquist 1988; Fisher and Ewers 1989).

Variant secondary growth is relatively uncommon in trees and shrubs but quite common in dicotyledonous vines where it has previously been considered to be related to increased stem flexibility, improved grasping ability of the stem, phloem protection, increased vascular supply in stem tissue, increased storage tissue, or enhanced regeneration of vascular tissue following injury (Carlquist 1975; Dobbins and Fisher 1986; Fisher and Ewers 1989). Carlquist (1988) felt that varient types of secondary growth are likely derived and polyphyletic features representing "alternative solutions to production of secondary tissues". Most variant patterns of secondary growth have in common the potential for enhanced phloem production.

The reduction in transverse cortical/periderm area in vines may be developmentally linked, as for the phloem, to the reduction in xylem area. Cortex is composed of parenchyma cells and is involved with food and water storage. Periderm with its cork protects the stem from desiccation and pathogen invasion. In trees and shrubs, cortical area increases by the production of expansion and proliferation tissue, and thus keeps pace with the expanding vascular cylinder (Fahn 1982). Similarly, anticlinal divisions of the phellogen (cork cambium) allow the periderm to remain intact as the vascular cylinder expands. When xylem expansion is reduced, growth accommodations by the cortex and periderm are less pronounced.

Many vines have succulent stems, with a higher percentage of unlignified parenchyma cells in the xylem, than do typical trees and shrubs. Wide rays and several other forms of variant growth produce additional parenchyma cells (Dobbins and Fisher 1986; Carlquist 1988; Fisher and Ewers 1989) which might help compensate for the reduction in cortical tissue in the liana growth form.

Reduced resource allocation to stem tissue might seem advantageous for vines in any environment. Anomalous secondary growth may be particularly adaptive for vines that are regularly subjected to frequent twisting or bending injuries (Dobbins and Fisher 1986; Fisher and Ewers 1989; Fisher and Ewers 1991). However, other concomitant features of vine stems (e.g., long and wide vessels) may help limit the distribution of vine species in nature. Vines are more common in tropical than temperate ecosystems, and are rare in desert environments (Rundel and Franklin 1991; Teramura et al. 1991). Long and wide vessels may be less able to recover from drought or freezing-induced embolism than short or narrow vessels (Ewers 1985). Vines that occur in cold or arid environments may be dependent upon particularly effective root systems that can create strong root pressures to refill embolized vessels (Sperry et al. 1987; Ewers et al. 1991).

To conclude, we view the benefits derived from reduction in xylem area as the evolutionary driving force behind reductions in total stem transverse area in vines. Except for the elimination of mechanically redundant phloem fibers, we know of no advantage to the reduced phloem or cortical tissue areas in vines. The phloem and cortical reductions are less pronounced than in the xylem and may be an indirect consequence of the developmental and geometric constraints imposed by reduction in mechanical tissue. Variant secondary growth may serve to increase the relative amounts of phloem and/or storage parenchyma. Long and wide vessels of vines, which may be necessary to compensate for reduced xylem areas, might help limit the distribution of vine species in nature.

Acknowledgements. We thank F.E. Putz for valuable discussions on vine biology, S.-T. Chiu, M. Kowalska, and L. Stultz for technical assistance, and J.H. Beaman, R. Hammerschmidt and M.A. Murry for critical review of the manuscript. The work was supported by the National Science Foundation (Grant BSR-8506370) and by an MSU All-University grant. We thank Mrs. E.C. Sweeney and the Kampong Fund for providing housing for FWE in Miami.

References

Ayensu ES, Stern WL (1964) Systematic anatomy and ontogeny of the stem in Passifloraceae. Contr US Nat Herb 34:45–71

Carlquist S (1975) Ecological strategies of xylem evolution. Univ Calif Press, Berkeley

Carlquist S (1988) Comparative wood anatomy. Springer, Berlin

Dobbins DR, Fisher JB (1986) Wound responses in girdled stems of lianas. Bot Gaz 147:278–289

Ewers FW (1985) Xylem structure and water transport in conifer trees, dicot trees, and lianas. Int Assoc Wood Anat Bull 6:309–317

Ewers FW, Cruiziat P (1990) Measuring water transport and storage. In: Lassoie JP, Hinckley TM (eds) Techniques and Approaches in Forest Tree Ecophysiology. CRC Press, Boca Raton 91–116

Ewers FW, Fisher JB, Chiu S-T (1990) A survey of vessel dimensions in stems of tropical lianas and other growth forms. Oecologia 84:544–552

Ewers FW, Fisher JB, Fichtner K (1991) Water flux and xylem structure in vines. In: Putz F, Bullock S, Mooney HA (eds) The Biology of Vines. Cambridge University Press, New York 119–152

Fahn A (1982) Plant Anatomy, 3rd ed. Pergamon Press, Oxford

Fisher JB, Ewers FW (1989) Wound healing in stems of lianas after twisting and girdling injuries. Bot Gaz 150:251–265

Fisher JB, Ewers FW (1991) Structural responses to stem injury in vines. In: Putz F, Bullock S, Mooney HA (eds) The Biology of Vines. Cambridge University Press, New York 119–152

Gartner BL (1991) Stem hydraulic properties of vines vs. shrubs of western poison oak, *Toxicodendron diversilobum*. Oecologia 87:180–189

Gartner BL, Bullock SH, Mooney HA, Brown VB, Whitbeck JL (1990) Water transport properties of vine and tree stems in a tropical deciduous forest. Am J Bot 77:742–749

Gentry A (1991) The distribution and evolution of climbing plants. In: Putz F, Bullock S, Mooney HA (eds) The Biology of Vines. Cambridge University Press, New York

Huber B (1928) Weitere quantitative Untersuchungen über das Wasserleitungssystem der Pflanzen. Jahrb Wiss Bot 67:877–959

Peñalosa J (1984) Basal branching and vegetative spread in two tropical rainforest lianas. Biotropica 16:1–9

Putz FE (1983) Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro Basin, Venezuela. Biotropica 15:185–189

Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713–1724

Rundel PW, Franklin T (1991) Vines in arid and semi-arid ecosystems. In: Putz F, Bullock S, Mooney HA (eds) The Biology of Vines. Cambridge University Press, New York

Schenck H (1893) Beitrage zur Biologie und Anatomie der Lianen. II. Beitrage zur Anatomie der Lianen. Bot Mitt Trop 4:1–248

Sperry JS, Holbrook NM, Zimmermann MH, Tyree MT (1987) Spring filling of xylem vessels in wild grapevine. Plant Physiol 83:414–417

Stevens GC (1987) Lianas as structural parasites: the *Bursera simaruba* example. Ecology 68:77–81

Teramura AH, Forseth IN, Gold WG (1991) Physiological ecology of mesic, temperate vines. In: Putz F, Bullock S, Mooney HA (eds) The Biology of Vines. Cambridge University Press, New York

Welle BJH TER (1985) Differences in wood anatomy of lianas and trees. Int Assoc Wood Anat Bull 6:70

Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer, Berlin