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A survey of vessel dimensions in stems of tropical lianas and other growth forms

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Summary. Vessel dimensions (total diameter and length) were determined in tropical and subtropical plants of different growth forms with an emphasis upon lianas (woody vines). The paint infusion and compressed air methods were used on 38 species from 26 genera and 16 families in the most extensive survey of vessel length made to date. Within most stems there was a skewed frequency distribution of vessel lengths and diameter, with many short and narrow vessels and few long and wide ones. The longest vessel found (7.73 m) was in a stem of the liana (woody vine) *Pithecoctenium crucigerum.* Mean vessel length for 33 species of lianas was 0.38 m, average maximum length was 1.45 m. There was a statistically significant inter-species correlation between maximum vessel length and maximum vessel diameter. Among liana stems and among tree+shrub stems there were statistically significant correlations between stem xylem diameter and vessel dimensions. Lianas with different adaptations for climbing (tendril climbers, twiners, scramblers) were similar in their vessel dimensions except that scramblers tended to have shorter (but not narrower) vessels. Within one genus, *Bauhinia*, tendril climbing species had greater maximum vessel lengths and diameters than tree and shrub species. The few long and wide vessels of lianas are thought to hydraulically compensate for their narrow stem diameters. The many narrow and short vessels, which are present in the same liana stems, may provide a high resistance auxiliary transport system.

Key words: Lianas – Vessel diameter – Vessel length – Water conductivity – Wood

Vessel diameter and vessel length may be two of the most important parameters determining the efficiency of xylem conduction in plants (Zimmermann and Brown 1971; Zimmermann 1983). There is evidence that, at least in large woody plants, xylem conductivity may be an important factor constraining plant growth, development, and distribution in nature (Hellkvist et al. 1974; Schultz and Matthews 1988; Tyree 1988; Ewers 1985; Ewers et al. 1989).

Vessel dimensions, which directly affect conductivity, have been correlated to extremes in growth form. A number of surveys have found that vessels of lianas (woody vines) are wider than in closely related trees (Ayensu and Stern 1964; Carlquist 1975; Klotz 1978; Van Vliet 1981; Bamber 1984; Ter Welle 1985; Ewers 1985). Similarly, Gartner et al. (in press) reported that in Jalisco, Mexico, naturally growing lianas had greater maximum vessel diameters than trees growing in the same dry hillside forest. However, there is a paucity of information on vessel lengths in lianas. Here we are referring to the total length of a vessel, not to the length of individual component vessel members (elements) for which there is much published information. Data on vessel member lengths have, in our opinion, limited value for functional or ecological studies since the entire vessel acts as the conductive unit. If an air bubble enters a single vessel member, the entire vessel becomes embolized and hence, nonconductive (Zimmerman and Brown 1971; Zimmerman 1983). Aside from our recent papers (Ewers and Fisher 1989a, b), vessel lengths have been published for only three lianas: two species of *Vitis* (Scholander 1958; Zimmermann and Jeje 1981; Sperry et al. 1987) and one species of *Tetracera* (Scholander 1958).

In recent papers we investigated methods for measuring vessel lengths and diameters in woody plants (Ewers and Fisher 1989a) and, in six species of lianas, we examined within-stem and within-species variation in vessel dimensions (Ewers and Fisher 1989b). In the present paper we survey vessel dimensions in 31 species of tropical and subtropical lianas, and two non-woody monocotyledonous climbers, *Asparagus falcatus* and *Luzuriaga latifolia.* For convenience, these large monocots, although not truly "woody" were classified as lianas.

There is little previously published information to compare vessel dimensions in lianas with different structural adaptations for climbing, such as twiners (species

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Offprint request to: F. Ewers

Table 1. Survey of vessel dimensions. For habit, SC = scrambler, SC/TEN = scrambling habit with occasional branch tendrils, SH = shrub, TEN = tendril climber, TR = tree, TW = twiner. For method, A = air, P = paint

Taxon	Habit	Method	Xylem diameter (mm)	Vessel diameter (µm)				Vessel length (cm)		
				min	x̄	Median	max	x̄	Median	max
Dicotyledons										
Annonaceae										
Bhandari										
Artabotrys hexapetalus (L. f.)	SC	P	10	13	34	26	90	5	3	27
Aristolochiaceae										
Aristolochia gigantea Mart. & Zucc.	TW	A	4.5	4	23	12	219			171
A. maxima Jacq.	TW	A	8.5	13	116	109	306			189
A. veraguensis Duchartre	TW	A	7	19	108	42	307			260
Bignoniaceae										
Anemopaegma puberulum (Sieb.) Miranda	TEN	P	9	10	50	29	186	26	25	115
Arrabidaea corallina (Jacq.) Sandw.										
stem 1	TEN	A	6	10	28	18	143			186
stem 2	TEN	P	11	13	36	22	214	69	60	250
A. podopogon(DC) A. Gentry										
stem 1	TEN	A	8.5	6	24	13	194	55	39	154
stem 2	TEN	A	9	8	35	18	159	67	63	167
Macfadyena (Doxantha) unguis-cati (L.) A. Gentry										
stem 1	TEN	A	1.2	5	22	13	81	19	13	94
stem 2	TEN	A	2	6	21	19	71	79	25	255
stem 3	TEN	A	2.5	4	24	13	93			133
stem 4	TEN	A	2.5							123
Mansoa allicea A. Gentry	TEN	A	9	5	22	14	126			84
M. verrucifera (Schlecht.) A. Gentry	TEN	A	18	10	58	56	134	46	38	126
Pithecoctenium crucigerum (L.) A. Gentry										
stem 1	TEN	P	2.5	9	37	13	98	32	25	150[a]
stem 2	TEN	P	2.5	6	30	18	105	42	25	170[b]
stem 3	TEN	A	5	8	44	17	217	69	25	375
stem 4	TEN	P	14	10	75	27	381	108	25	525[b]
stem 5	TEN	A	19	11	74	26	360	112	25	773
stem 6	TEN	P	25.5					141	125	625[b]
Pyrostegia venusta (Ker-Gawl.) Miers	TEN	A	9	12	39	21	233			153
Saritaea magnifica Dug.										
stem 1	TEN	P	6	6	30	23	118	5	4	21
stem 2	TEN	A	14	13	56	45	157	55	37	270
Combretaceae										
Combretum paniculatum Venten.										
stem 1	SC	A	10	13	49	26	380			199
stem 2	SC	A	12							170
Convolvulaceae										
Argyreia nervosa (Burm. f.) Bojer	TW	A	12	16	64	29	401	57	62	131
Fabaceae										
Bauhinia aculeata L.										
stem 1	SH	A	5.5	8	27	25	75	3	3	34[a]
stem 2	SH	P	6	9	31	18	92	5	3	47[a]
B. blakeana Dunn.										
stem 1	TR	A	11	13	48	38	115	10	5	83
stem 2	TR	P	11.5	9	51	47	117	30	35	85
stem 3	TR	P	11.5	9	57	60	113	29	25	75
stem 4	TR	A	16.5	13	55	44	132	15	10	100
B. corymbosa Roxb. ex DC										
stem 1	TEN	P	3	8	29	16	146	7	5	55
stem 2	TEN	P	3	6	20	12	124	13	5	55
stem 3	TEN	A	4	6	20	14	182			184
stem 4	TEN	A	4.5							157

Table 1 (continued)

Taxon	Habit	Method	Xylem diameter (mm)	Vessel diameter (μm)				Vessel length (cm)		
				min	x̄	Median	max	x̄	Median	max
B. fassoglensis Kotschy ex Schweinf.										
stem 1	TEN	A	3	10	24	18	210	27	10	65[a]
stem 2	TEN	P	3	10	37	22	215	11	5	65[a]
stem 3	TEN	P	3	6	42	29	233	9	5	45
stem 4	TEN	A	3	6	23	14	213	23	5	73
stem 5	TEN	A	3.5							270
B. galpinii N.E. Br										
stem 1	SH	A	3.5	8	39	27	99	7	5	44[a]
stem 2	SH	P	3.5	7	33	22	91	9	5	55[a]
stem 3	SH	A	20	12	49	38	134	7	5	71
B. purpurea L.										
stem 1	TR	A	7	10	30	20	88	17	10	48[a]
stem 2	TR	P	7	9	40	36	109	8	5	65[a]
stem 3	TR	P	9	13	41	39	91	9	5	55
stem 4	TR	A	13	13	42	26	103	15	5	77
B. vahlii Wight & Arn.										
stem 1	TEN	A	7	7	51	43	185	17	10	81
stem 2	TEN	A	9	6	24	17	226	37	30	110
stem 3	TEN	A	11	9	43	25	211	26	13	117
B. variegata L.	TR	A	12	10	48	38	144	11	10	101
Dalbergia brownei (Jacq.) Benth.	SC/TEN	P	12	9	48	39	133	12	5	55
Derris scandens (Roxb.) Benth.	TW	P	6	4	14	10	189	37	30	150
Hippocrateaceae										
Hippocratea volubilis L.										
stem 1	SC/TEN	P	4	10	42	27	161	30	20	100
stem 2	SC/TEN	P	6	9	66	56	193	38	20	220
Malpighiaceae										
Mascagnia psilophylla (Juss.) Griseb.										
stem 1	TW	A	6.5							122+
stem 2	TW	A	7.5	10	29	20	176			100
Peixotoa glabra Juss.										
stem 1	TW	P	4.5	10	34	19	228	23	10	130
stem 2	TW	A	7	9	21	15	181			168
Stigmaphyllon cf. *periplocifolium* Juss.	TW	A	8	8	23	16	212			151
S. ellipticum (HBK) Juss.										
stem 1	TW	A	4	8	25	15	208	43	37	160[a]
stem 2	TW	P	4	6	20	14	207	27	12	87[a]
stem 3	TW	A	7	6	33	21	222			194
Nyctaginaceae										
Bougainvillea spectabilis Willd.										
stem 1	SC	A	11.5							32
stem 2	SC	A	11.5	7	27	21	107			43
Passifloraceae										
Passiflora coccinea Aubl.										
stem 1	TEN	A	1	4	26	13	128	16	5	52[a]
stem 2	TEN	P	1	7	34	20	87	10	5	45[a]
stem 3	TEN	A	3.5	4	17	12	249			179
Polygonaceae										
Antigonon leptopus Hook. & Arn.	TW	A	7	6	27	14	233			86
Sapindaceae										
Serjania polyphylla (L.) Radlk.										
stem 1	TEN	A	3	4	13	10	156			143
stem 2	TEN	A	4.5							112
stem 3	TEN	P	6	10	37	18	257	75	60	220

Table 1 (continued)

Taxon	Habit	Method	Xylem diameter (mm)	Vessel diameter (μm)				Vessel length (cm)		
				min	x̄	Median	max	x̄	Median	max
Thunbergiaceae										
Thunbergia grandiflora Roxb.										
stem 1	TW	A	8							170
stem 2	TW	A	10							56
stem 3	TW	A	12	10	42	26	301			157
Vitaceae										
Vitis rotundifolia Michx.										
stem 1	TEN	P	4.5	10	45	23	179	12	5	85
stem 2	TEN	P	14	12	50	27	233	33	10	310
stem 3	TEN	P	16	12	63	27	287	74	70	380
stem 4	TEN	P	24	12	79	35	337	37	10	230
Monocotyledons										
Liliaceae										
Asparagus falcatus L. branches										
stem 1	SC	A	9	9	26	20	129			172+
stem 2	SC	A	11							71
leader	SC	A	12	13	57	45	170			211
Philesiaceae										
Luzuriaga latifolia (R. Br.) Poir.										
stem 1	TW	A	4.5	10	41	31	114			101
stem 2	TW	A	5							60

[a] For these stems vessel length data was from Ewers and Fisher (1989a)

[b] Length data from Ewers and Fisher (1989b)

with twining terminal shoots), tendril climbers, and scramblers (a mixed group of species which tend to fall upon their supports and which may have thorns or spines). Root climbers were excluded from this survey. In addition to examining different types of lianas, in the present study we report on tree, shrub, and liana species of *Bauhinia* (Fabaceae). The data set includes, for seven of the 38 species and for 16 of the 86 stems, data on vessel length extracted from our previous publications (see footnotes to Table 1). The vessel diameter data are all original.

The objectives were to compare vessel dimensions among various growth forms and to determine if there are inter-species correlations between vessel length, vessel diameter, and stem xylem diameter. This study provides groundwork for various ongoing studies of xylem structure, function, and ecology in lianas vis-à-vis other growth forms.

Materials and methods

The sampled species (Table 1) were all growing outdoors at the Fairchild Tropical Garden in Miami, Florida, except for *Macfadyena unguis-cati*, which was growing outdoors at the USDA Subtropical Horticulture Experiment Station, Miami. Vessel length measurements were made in the spring and summers of 1985, 1986, and 1988.

Vessel length distributions were determined by the paint or air method, (P and A in Table 1), with mean, median, and maxi-

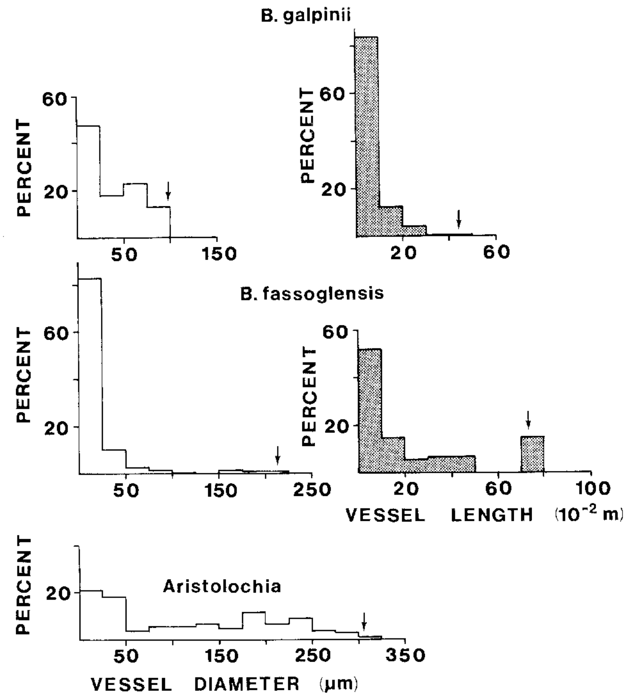

Fig. 1. Frequency distributions for vessel diameter (light bars) and vessel length (dark bars) for a stem of the shrub *Bauhinia galpinii* (stem 1 in Table 1), the liana *B. fassoglensis* (stem 4) and the liana *Aristolochia maxima*. Length distributions were not determined for *Aristolochia*. Maximum values (arrows) were greater in the liana than in the shrub. These are the best examples of stems from Table 1 with distributions that might be interpreted as bimodal

mum lengths determined for each stem. In some stems only maximum vessel lengths were measured, which is much faster than determining frequency distributions. Details of the paint and air methods, which produce similar results, are given in Ewers and Fisher (1989a).

For each species the longest available unbranched stem segments were selected for study. In most but not all of these segments the leaves had abscised. In some cases, such as *Bauhinia vahlii*, which has regularly spaced short shoots along its main axis, small lateral branches could not be avoided. However, in every case we measured vessel length only along the main axis. For maximum vessel length determinations it was necessary to obtain stem segments longer than the longest vessel, but, as we determined *a posteriori*, this was rarely a problem since vessel lengths were not as great as we had anticipated.

Stem xylem diameter and vessel diameters were measured in the stem segment at one half the length of the longest vessel. This segment was fixed in FAA, transversely sectioned with a sliding microtome at 30 µm, and stained with safranin or safranin and fast green. A Nikon photostereomicroscope with transmitted light capabilities was used to prepare Kodachrome slides (diapositives) which were projected onto large sheets of white paper. Each vessel was marked on the paper as its inner diameter was measured with a ruler so that none were measured more than once. The projection resulted in spherical aberration errors of less than 1%. When a vessel was not circular in transverse view, the minimum and maximum diameters were averaged. For narrow stems, the diameter of every vessel in the stem was measured. However, wider stems often had well over a thousand vessels in cross sectional view. Rather than measure every vessel, we measured all the vessels in one or more sectors, with each sector having vascular rays for marginal boundaries and the pith and the vascular cambium as its inner and outer boundary, respectively. This avoided undue bias towards inner or outer vessels. When possible we sampled at least 100 vessels per stem. The above sampling procedure differs from that used in a previous study (1989b), where the diameters of only latex paint-filled vessels were measured.

Since normal distribution of the variables was highly questionable, correlations were determined using Spearman's nonparametric coefficient of rank (Steel and Torrie 1980).

Results

A summary of results for all the species examined is presented in Table 1. The common statistics of mean and median are given so that our results can be more easily compared to previously published surveys of xylem anatomy, although such values for non-normal distributions should be used with caution. Minimum vessel lengths could not be determined by our methods.

Most vessel length and vessel diameter distributions were positively skewed, with many short and many narrow vessels and few long and few wide ones (Fig. 1). This is reflected by the fact that mean vessel length was greater than the median length in 96% of the stems examined in Table 1, and the means were always less than 50% of the maximum. Similarly, the mean diameter was greater than the median diameter in 99% of the stems examined, and the mean was closer to the minimum than to the maximum in 100% of the cases.

For liana species the overall mean of the mean vessel lengths was 0.38 m (SE = 0.05), with an average median of 0.26 m (SE = 0.04) and an average maximum of 1.45 m (SE = 0.13). For all liana species the mean of the mean vessel diameters was 41 µm (SE = 3.9), with an average median of 26 µm (SE = 3.1) and an average maximum of 200 µm (SE = 13.2).

The mean ± SE stem xylem diameters of the sampled stems were as follows: all liana species, 8.1 ± 0.6 mm; tendril climbers, 8.2 ± 1.2 mm; twiners, 7.1 ± 0.6 mm; scramblers (including scramblers with occasional branch tendrils), 10.0 ± 1.0 mm. Within the genus *Bauhinia* the mean stem xylem diameters were: shrubs 7.4 ± 1.6 mm; trees, 11.2 ± 1.1 mm; tendril climbers, 5.2 ± 1.9 mm.

Table 2. Spearman's coefficient of rank (r_s) for various combinations of parameters. For ALL SPECIES, r_s is based upon the average value for each species in Table 1. For ALL LIANA STEMS and ALL TREE + SHRUB STEMS, each stem was individually incorporated into the calculations. The differences in *n* were due to incomplete data sets for many stems. NS = not significant at 0.05 level of probability

Parameters	r_s	*n*	Probability
All species			
mean vessel length × mean vessel diam	0.17	25	NS
median vessel length × median vessel diam	−0.06	25	NS
max vessel length × max vessel diam	0.62	38	<0.001
All liana stems			
stem xylem diam × mean vessel diam	0.57	60	<0.001
stem xylem diam × median vessel diam	0.59	60	<0.001
stem xylem diam × max vessel diam	0.42	60	<0.001
stem xylem diam × mean vessel length	0.48	40	<0.01
stem xylem diam × median vessel length	0.45	40	<0.01
stem xylem diam × max vessel length	0.31	72	<0.01
Bauhinia: all tree + shrub stems			
stem xylem diam × mean vessel diam	0.80	14	<0.001
stem xylem diam × median vessel diam	0.61	14	<0.02
stem xylem diam × max vessel diam	0.77	14	<0.01
stem xylem diam × mean vessel length	0.48	14	NS
stem xylem diam × median vessel length	0.51	14	NS
stem xylem diam × max vessel length	0.80	14	<0.001

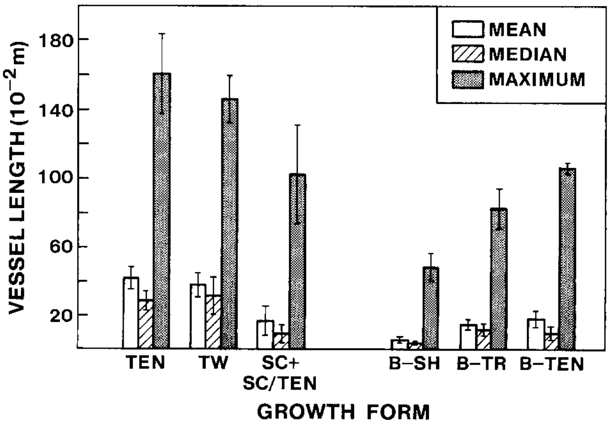

Fig. 2. The mean ± SE of the mean, median, and maximum vessel lengths in different growth forms, based upon the mean values for each species in Table 1. The number of species sampled were as follows: tendril climbers (TEN) = 15, twiners (TW) = 12, scramblers + scramblers with occasional branch tendrils (SC + SC/TEN) = 6, *Bauhinia* shrubs (B-SH) = 2, *Bauhinia* trees (B-TR) = 3, *Bauhinia* tendril climbers (B-TEN) = 3

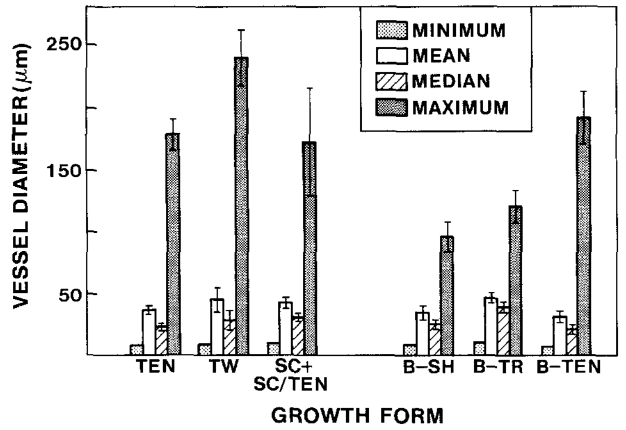

Fig. 3. The mean ± SE of the minimum, mean, median, and maximum vessel diameters in different growth forms, based upon the mean values for each species in Table 1. Sample sizes and abbreviations are as given in Fig. 2

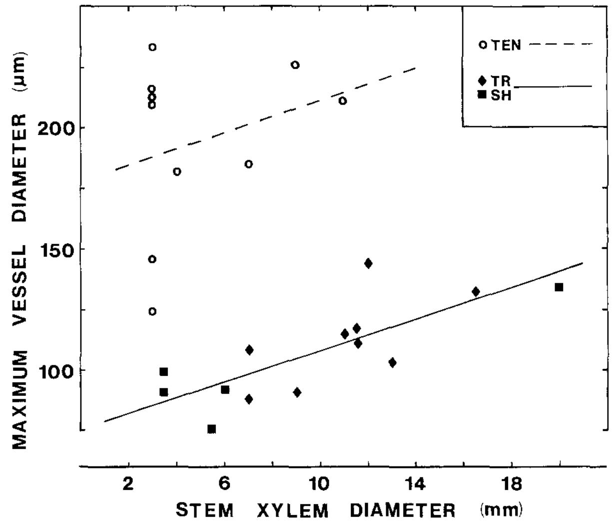

Fig. 4. Maximum vessel diameter as a function of stem xylem diameters for tendril climbers (TEN), shrubs (SH), and trees (TR) of *Bauhinia*. Each point represents a single stem segment, regression lines are shown for tendril climbers (*dashed line*) and trees + shrubs (*solid line*)

Among liana stems there were statistically significant positive correlations between stem xylem diameter and mean, median, and maximum vessel length and vessel diameter. There were similar correlations for tree + shrub stems of *Bauhina*, but the correlations were not statistically significant in all cases (Table 2).

Based upon averaged results, tendril climbers, twiners and scramblers had roughly similar, although quite variable, vessel dimensions with the following exceptions: although the scrambler stems that were sampled tended to be greater in xylem diameter than those of the twiners and tendril climbers, scramblers tended to have shorter (Fig. 2), but not narrower vessels (Fig. 3). Twiners had slightly greater maximum vessel diameters (Fig. 3) but slightly lower maximum vessel lengths (Fig. 2) than tendril climbers.

Within the genus *Bauhinia*, as noted above, the sampled stems of the tendril climbing species tended to have smaller xylem diameters than those of the tree or shrub species. However, despite the positive correlations between stem xylem diameter and vessel dimensions (Table 2), the sampled tendril climbers tended to have greater maximum vessel lengths (Fig. 2) and greater

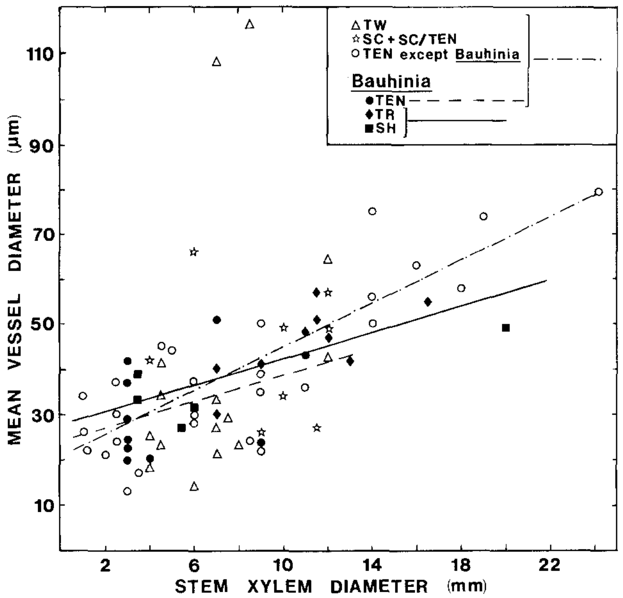

Fig. 5. Mean vessel diameter as a function of stem xylem diameter in twiners (TW), scramblers + scramblers with occasional branch tendrils (SC + SC/TEN), tendril climbers (TEN), trees (TR), and shrubs (SH). Each point represents the mean diameter of a single stem. Regression lines are shown for all lianas (*dot-dashed line*), tendril climbers of *Bauhinia* (*dashed line*), and trees + shrubs of *Bauhinia* (*solid line*). For tendril climbers of *Bauhinia*, Spearman's coefficient of rank was 0.40. See Table 2 for further statistical analysis

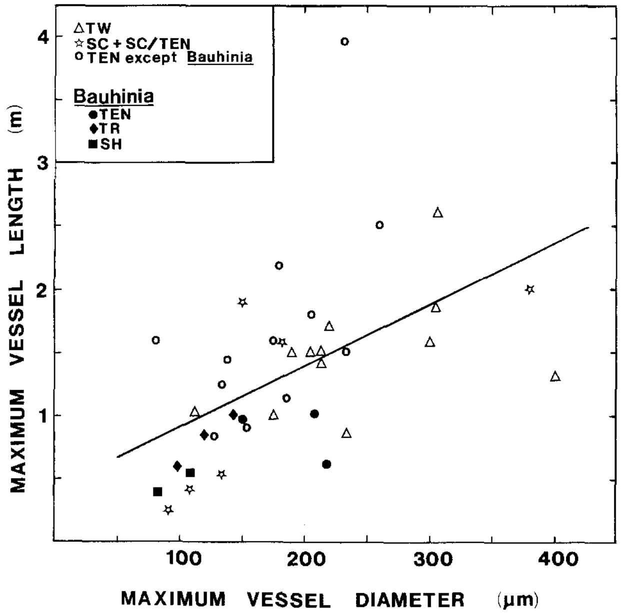

Fig. 6. Maximum vessel length as a function of maximum vessel diameter in twiners (TW), scramblers + scramblers with occasional branch tendrils (SC + SC/TEN), tendril climbers (TEN), trees (TR), and shrubs (SH). Each point represents the mean value for a single species. Based upon Spearman's coefficient of rank, the correlation for all species was significant at the 0.001 level ($r_s = 0.62$)

maximum vessel diameters than the *Bauhinia* trees or shrubs (Fig. 3). Mean and median vessel lengths were similar in trees and tendril climbers of this genus, but greater than in shrub species (Fig. 2). When compared to lianas in general, tendril climbers of *Bauhinia* were similar in vessel diameter (Fig. 3) but lower in vessel length (Fig. 2).

When expressed as a function of stem xylem diameter, maximum vessel diameters were far greater in *Bauhinia* tendril climbers than in *Bauhinia* trees + shrubs (Fig. 4). However, mean vessel diameters were nearly identical for *Bauhinia* tendril climbers, *Bauhinia* trees + shrubs, and for lianas in general (Fig. 5).

Of the three *Bauhinia* growth forms, shrubs had, on the average, the smallest maximum vessel lengths and vessel diameters. However, the shrub stems sampled were narrower, on the average, than those of the trees. When expressed as a function of stem xylem diameter, maximum vessel diameters were quite similar for trees and shrubs (Fig. 4).

There was a statistically significant inter-species correlation between maximum vessel length and maximum vessel diameter (Fig. 6). There was not a statistically significant correlation between mean vessel length and mean vessel diameter, nor between median vessel length and median vessel diameter (Table 2).

Discussion

There are theoretical reasons to expect the vessels of lianas to be longer and wider than those of trees. Liana stems are quite narrow in relation to the amount of foliage they supply with water and minerals (Schenck 1893; Putz 1983; Ter Welle 1985; Ewers 1985). Lianas do not require wide stems for mechanical support since they are, by definition, supported by other plants. It may be that the relatively wide and long vessels of lianas, due to their great conductive efficiency, compensate for narrow stem diameters (Putz 1983; Ewers 1985; Ewers et al. 1989, in press). This relationship would appear to hold true for tropical (Putz 1983; Ewers 1985; Ewers et al. in press) as well as temperate lianas/trees/shrubs (Chiu and Ewers 1990; Gartner unpublished).

Within *Bauhinia* the liana species had greater maximum vessel lengths and diameters than did trees or shrubs, but this was not true for mean or median values. However, the wider vessels, although few in number, are the ones that are functionally the most important for determining conductive efficiency (Ewers and Fisher 1989a). This is because, by Poiseuille's law for ideal capillaries, conductivity is proportional to the summation of the vessel diameters each raised to the fourth power (Zimmermann and Brown 1971).

We know of no theoretical reason to expect lianas with different structural adaptations for climbing to have different vessel dimensions, except that scramblers may, initially at least, provide more of their own mechanical support that do twiners or tendril climbers. Gartner (unpublished) has found that unsupported stems of the liana *Toxicodendron diversilobum* tend to have greater transverse areas but narrower vessels than supported stems. In our study different types of lianas were similar in vessel dimensions, except that scramblers appeared to have shorter (but not narrower) vessels. We made no evaluation of the extent to which particular stems were self supporting.

In plants in general, narrow vessels tend to occur in plants from colder and more arid environments (Carlquist 1975, 1988). We know of no published accounts of correlations of the mode of climbing with the environment in which the lianas are found, but the shorter vessels of scramblers would, presumably, be more adapted to colder and more arid environments, where embolism may be a more severe limitation to survival.

The advantage of wide and long vessels, to increase conductive efficiency, is well known. The disadvantages are more complex, but long and wide vessels are generally considered to be "less safe" than small vessels. Embolism of a single large vessel will have much greater negative impact on conductivity than embolism of a small one. A plant with many short and narrow vessels has greater redundancy (Zimmerman 1983; Carlquist 1988). There also is evidence that larger volume conduits are more susceptible to freezing-induced embolism. Air is insoluble in ice, and larger conduits contain larger, more difficult to dissolve bubbles following a freeze-thaw cycle than do smaller conduits (Ewers 1985). However, based upon inter-specific comparisons, conduit size is *not* correlated with water stress-induced embolism (Tyree and Dixon 1986; Sperry et al. 1988; Tyree and Sperry 1989). The induction of water stress-induced embolism may be controlled by the size of pores in the pit membranes (Zimmermann 1983; Crombie et al. 1985; Sperry and Tyree 1988). Regardless of the cause of embolism, once it has occurred, larger conduits are probably more difficult to re-fill than smaller ones (Ewers 1985; Ewers and Cruiziat in press).

Earlier we reported positive *intra*-species and *intra*-stem correlations between vessel length and vessel diameter in tropical lianas (Ewers and Fisher 1989b). Now we can report a similar positive *inter*-species correlation between maximum vessel length and maximum vessel diameter (Fig. 3). This is consistent with results by Handley (1936) and Zimmermann and Jeje (1981) for temperate tree species.

These correlations might be explained as follows. If both vessel length and vessel diameter limit conductivity, evolutionary increases in vessel length might have little impact on conductivity without simultaneous increases in vessel diameter (Ewers and Fisher 1989b). Another possibility is that selective pressure to minimize embolism danger could simultaneously reduce both vessel length and vessel diameter.

The lack of a correlation with mean and median vessel lengths versus mean and median diameters (Table 3) may be a methological artifact. Given a skewed distribution pattern, errors in means and medians are easily magnified. In species where the narrow vessels are extremely short (less than 1 mm), the paint and air methods could have omitted some of the narrow vessels from the vessel length counts, since the stem surface must be trimmed to get a count of the paint-filled vessels at the infusion port (Ewers and Fisher 1989a). The mean and median vessel length values would then be erroneously elevated, with the extent of the error varying with the species. The vessel diameters were measured independently but on the same stems. This source of error would not affect the maximum vessel lengths.

There appears to be tremendous variation in vessel length in plants. At one extreme, Fisher (1970) indirectly found, based upon maceration data for stems of the herbaceous monocotyledon *Cyperus alternifolium*, mean vessel lengths of 0.0017 m for early metaxylem vessels and 0.012 m for late metaxylem vessels. In the viny monocotyledons *Luzuriaga latifolia* and *Asparagus falcatus*, we found maximum vessel lengths of up to 1.01 and 2.11 m, well within the range of results for dicotyledonous lianas (Table 1).

Results for the subtropical species *Vitis rotundifolia* (Table 1) were similar to those reported for temperate species of this genus. Scholander (1958) reported "average vessel length" to be about 0.6 m in the temperate liana *Vitis labrusca.* Using the air method, Zimmermann and Jeje (1981) reported a maximum vessel length of 7.5 m in a stem of *V. labrusca*, with 69% of the vessels longer than 1 m. Using similar methods, Sperry et al. (1987) found that in stems of *V. riparia* the maximum vessel length was about 1.5 m, with many more short than long vessels. However, Sperry et al. (1987) used 5 mm diameter stems, which were narrower than the stem used by Zimmermann and Jeje (1981).

The liana vessel lengths were much greater than reported by Zimmermann and Jeje (1981) for temperate diffuse-porous trees and shrubs, but shorter than the maximum values reported for large temperate ring-porous trees. Zimmermann and Jeje (1981) reported maximum vessel lengths of 10 m or more in the ring-porous trees *Fraxinus americana* and *Quercus rubra*, and Greenidge (1952) found maximum vessel lengths of over 15 m in *Q. borealis* and over 18 m in *F. americana* . The greatest maximum vessel length we found was 7.73 m in the liana *Pithecoctenium crucigerum.* The common perception in the literature that lianas have extremely long vessels (Kramer and Kozlowski 1979; Zimmermann 1983) may be somewhat exaggerated. However, it should be cautioned that our measurements were from relatively small, cultivated specimens. The correlations between stem diameter and vessel dimension suggest that as stems enlarge they produce longer as well as wider vessels (Table 3; Fig. 2, 4; see also in Table 1 *P. crucigerum, Saritea magnifica, Bauhinia blakeana, B. galpinii*, and *Vitis rotundifolia* and results in Ewers and Fisher 1989b). The huge liana stems naturally growing in the tropics may have even longer and wider vessels than those reported in the present study.

Most importantly, even in those liana stems with some very long and wide vessels, most of the vessels were rather short and narrow. Similarly, Skene and Balodis (1968) and Zimmermann and Jeje (1981) reported a skewed vessel length distribution for various species of woody plants. In many studies of vessel diameter the narrowest vessels have probably been overlooked or ignored. Since the vessel length and vessel diameter distributions tend to be highly skewed, and since theoretical conductance is proportional to the vessel diameter to the fourth power, the mean vessel lengths and diameters are not the most functionally significant parameters for comparing taxa. Complete vessel length distribution and vessel diameter distribution patterns are more informative (e.g., Fig. 1).

Carlquist (1985, 1988) suggested, based upon his qualitative observations, that probably many lianas have a bimodal distribution of vessel diameters. Similarly, Baas and Schweingruber (1987) used qualitative criteria to determine that many European lianas have two or three more-or-less distinct vessel diameter classes. Observation of wood in transverse view often gives, especially in lianas, the impression of wide vessels surrounded by many small vessels. In our survey this vessel arrangement was usually found to have a positively skewed distribution pattern in which the curve extended far to the right, with more intermediate vessel diameters than one may have supposed. In Fig. 1 we show some of those distribution patterns from our survey that could most easily be interpreted as bimodal. Other examples of vessel diameter and length distributions are presented in Ewers and Fisher (1989a, b). In our opinion "positively skewed" is a better description than "bimodal" for almost all the stems we examined.

To conclude, based upon the data in the present report, and upon what literature data are available, it does appear that lianas have great maximum vessel lengths and widths, but the values for mean and median vessel dimensions are not necessarily greater than in closely related trees or shrubs. These conclusions appear to be valid for monocotyledonous as well as dicotyledonous lianas, for temperate as well as tropical lianas, and for lianas with different types of climbing adaptations. Although the maximum vessel dimensions in lianas are much greater than in temperate diffuse-porous trees, they do not appear to be greater than those reported for temperate ring-porous trees.

One implication of long and wide vessels in liana stems is that the xylem may be particularly vulnerable to dysfunction by embolism. In temperate ring-porous trees the long and wide vessels become and remain embolized after one growing season (Ellmore and Ewers 1986). In contrast, in the temperate liana *Vitis*, embolized vessels become refilled due to root pressures on a seasonal (Scholander et al. 1955; Sperry et al. 1987) and perhaps even on a diurnal basis (Schultz and Matthews 1988). As suggested by Carlquist (1985, 1988), the many narrow vessels in liana stems may represent a crucial auxiliary transport system for when the wide vessels become temporarily, or permanently, non-conductive.

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