Table 1. Range in cell lumen diameters (μm) of vessels, tracheids and fibers of the twiner (*L. japonica*), scrambler (*L. sempervirens*) and shrub (*L. maackii*)

Growth forms	Vessels $n = 170$	Tracheids $n = 70$	Fibers $n = 220$
Twiner	7.6–103.0	3.8–17.6	2.5–11.3
Scrambler	10.1– 52.9	7.6–15.1	1.3–11.3
Shrub	7.6– 58.0	5.0–13.9	1.3–10.1

Table 2. Range in cell wall thickness (μm) of vessels, tracheids and fibers of the twiner (*L. japonica*), scrambler (*L. sempervirens*) and shrub (*L. maackii*)

Growth forms	Vessels $n = 170$	Tracheids $n = 70$	Fibers $n = 240$
Twiner	0.6–2.5	1.3–5.0	3.2–5.7
Scrambler	0.6–2.5	2.5–3.8	2.5–5.0
Shrub	0.6–2.5	1.9–4.4	2.5–6.3

equal sample numbers and Duncan's test for multiple comparisons (Steel and Torrie 1980; Petersen 1985).

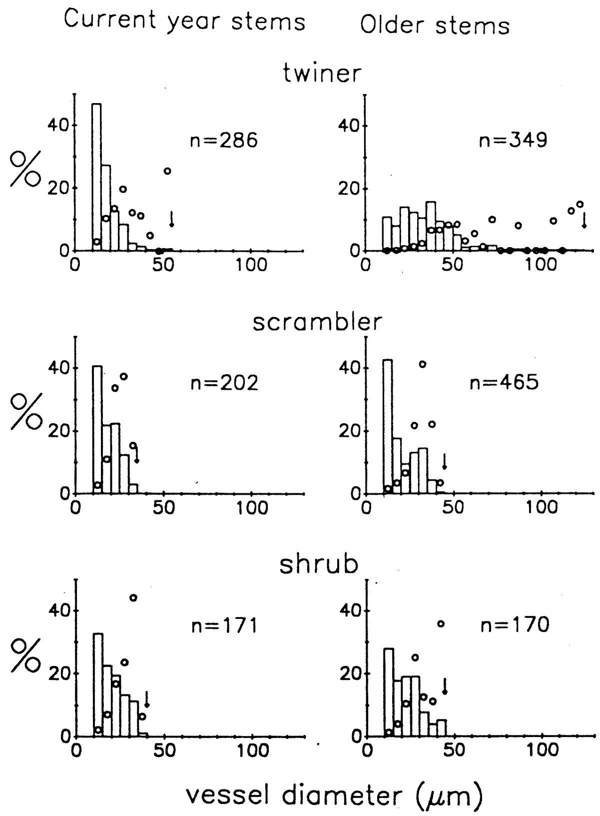

Fig. 1. Percentage of total *theoretical* K_h (*open circles*) for each class of vessel diameter and the frequency distributions of vessel diameter (histograms) in current year and 4-year-old stems of a twiner *Lonicera japonica*, a scrambler *L. sempervirens*, and a shrub *L. maackii*. Each graph is from one representative stem. *Arrows* indicate the largest vessel diameter in each sample

Results

Analysis of variance indicated that there were statistically significant differences between current year stems and older stems in most examined features for all three species. Therefore, the transectional and physiological data below are presented separately for current year and older stems.

Maceration

A comparison of cell lumen diameter (Table 1) and wall thickness (Table 2) from the macerated xylem indicated that vessels had generally wider cell lumens and thinner walls than the tracheids and fibers. However, the very narrow vessels were similar to the tracheids except for the presence of perforations. To exclude the tracheids and fibers in vessel measurements from the wood transection, below, we included only cells (vessels) that had walls thinner than 2.5 μm and lumens more than 18 μm in twiners or more than 15 μm in scramblers and shrubs.

Transections

Vessel diameter frequency distributions are shown for one representative current-year and one 4-year-old stem of the twiner, scrambler and shrub (Fig. 1). Except in the older stems of twiners, the frequency distribution of the vessel diameters tended to the Poisson distribution (Steel and Torrie 1980) with a high percentage of the narrow vessels (Fig. 1). The pattern for the older stems of twiners was a positively skewed normal distribution with many more narrow than wide vessels, and a pronounced tail to the wide vessel diameter (Fig. 1). For all the distribution patterns, a great portion of total *theoretical* K_h resulted from the wider vessels. While only 1.1% (twiners), 15.3% (scramblers), 12.2% (shrubs) of the total number of vessels in the current year stems and 0.6% (twiners), 4.7% (scramblers), 8.9% (shrubs) in the older stems were grouped in the highest 2 classes of vessel diameter in each sample, these classes contributed 30.5% (twiners), 62.7% (scramblers), 50.6% (shrubs) of the total *theoretical* K_h of current year stems and 27.7% (twiners), 25.5% (scramblers), 46.9% (shrubs) of that of older stems. Conversely, the narrow vessels were frequent but contributed little to the *theoretical* K_h (Fig. 1). When stained vessels and tracheids below the 18 μm (twiner) and 15 μm (scrambler and shrub) threshold were included, they increased *theoretical* K_h by less than 1% (data not shown).

Qualitative features of wood anatomy can be seen in Figs. 2–4. Based on the examination of vessel diameter in 56 stem segments, the twiner had the greatest maximum vessel diameter (Fig. 5) but also many small vessels (Figs. 1, 2a, b). As stems aged, the outer growth rings of xylem contained the widest vessels (Fig. 2b). The means of maximum vessel diameter for twiners, 65.8 μm in current year stems and 94.7 μm in older stems, were significantly greater than those of the other growth forms (Fig. 5).

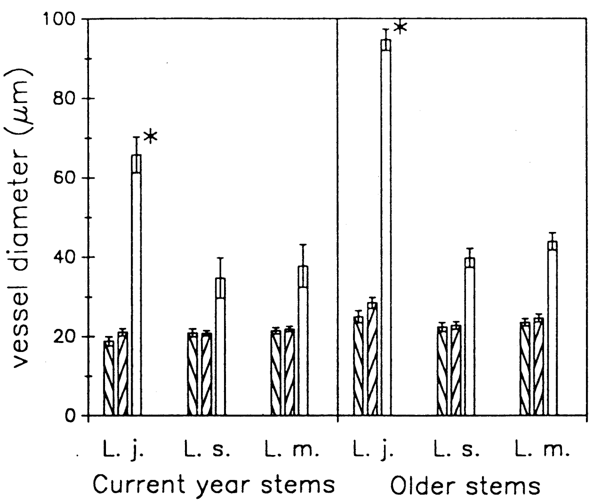

Fig. 5. Comparison of vessel diameter among different growth forms: a twiner *Lonicera japonica*, a scrambler *L. sempervirens* and a shrub *L. maackii*. *Bars* indicate ± standard error. *Asterisks* indicate the statistically significant difference between species. ▧ median; ▨ mean; ▭ maximum

Stems of the scrambler contained relatively narrow vessels (Figs. 1, 3a, b). In this species, for each growth ring the widest vessels occurred at about the 5th to 7th cell layer outside the previous year's latewood (Fig. 3b). Unlike the twiner, when the stems became older, the maximum vessel diameter did not increase by much (Figs. 1, 3b, 5). In shrubs (Fig. 4a, b), in going from earlywood to latewood, vessel diameter consistently decreased and the number of tracheids and fibers consistently increased. As with the scrambler, when the stems became older, the diameter of maximum vessels increased little in the older growth rings (Figs. 4b, 5). The anatomical characters of the scrambler were generally similar to those of the shrub. However, in the scrambler, there was a wider distribution area of moderate vessel diameters throughout the growth ring (Figs. 3, 4), a greater number of very small vessels (Fig. 1), a smaller xylem area and a higher percentage of stem conductive xylem area (Table 3). For all growth forms, the median vessel diameter was usually lower than the mean vessel diameter (Fig. 5). The difference between median and mean vessel diameter was greatest in the twiners (Fig. 5).

The shrub had greater stem xylem diameters than the twiner and the scrambler species. Likewise, the xylem diameter increment and total xylem area increment per year were greatest in shrubs (Table 3). The ratio of conductive xylem area to total xylem area (percent conductive xylem area) was lowest in the shrubs (Table 3). The greatest vessel frequency (vessels·mm^{-2}) occurred in scramblers, especially in current year stems, and the least occurred in twiners, especially in older stems (Table 3).

Wood moisture content

In the current year stems, the shrub had the highest moisture content of fresh wood and the twiner had the lowest (Table 3). However, the decline of moisture content of fresh wood from current year to older stems was greatest in the shrubs and least in the twiners (Table 3). For the older stems, there was no statistically significant difference in moisture content among the different species.

Measured and theoretical K_h

The relationship between *measured* K_h and *theoretical* K_h was linear and highly correlated in all 3 species. The r values of the regression lines of *measured* K_h over *theoretical* K_h ranged from 0.72 to 0.98 (Fig. 6). The mean ratios of *measured* K_h over *theoretical* K_h were 34.2% (twiner), 45.3% (scrambler), 54.6% (shrub) in the current year stems (Fig. 6a) and 25.2%, 35.0%, 24.3% in the older stems (Fig. 6b). These percentages were not statistically different among species.

Huber value, specific conductivity, LSC

The leaf area based Huber value was greatest in the current year stems of scramblers and least in the older stems of twiners (Fig. 7). In current year stems, scramblers significantly differed from twiners and shrubs in this parameter, but twiners and shrubs were not distinguishable from each other. For older stems, twiners were distinguishable from scramblers and shrubs but scramblers and shrubs were not statistically different from each other. In addition, leaf weight based Huber value was much higher in current year

Table 3. Quantitative features (mean ± standard error) of xylem in the twiner (*L. japonica*), scrambler (*L. sempervirens*) and shrub (*L. maackii*)

Age of stems / Growth forms	Leaf weight based Huber value ($mm^2 \cdot g^{-1}$)	Moisture content of fresh wood (%)	Increment of xylem diameter ($mm \cdot year^{-1}$)	Increment of total xylem area ($mm^2 \cdot year^{-1}$)	Percent conductive xylem area	Vessel frequency (per mm^2)
Current year stems:						
Twiner	1.54±0.27	36.6±2.0	1.465±0.131	1.93±0.40	87.9±3.6	774±100
Scrambler	2.64±0.20	48.0±5.6	1.728±0.162	1.57±0.32	81.5±8.0	901± 47
Shrub	1.55±0.13	56.0±4.7	3.033±0.277	3.49±0.58	65.3±8.8	787± 96
Older stems:						
Twiner	1.75±0.34	34.2±3.4	0.905±0.095	3.22±0.44	65.4±5.7	561±69
Scrambler	1.77±0.16	38.3±4.0	1.090±0.091	2.16±0.40	82.2±3.8	830±62
Shrub	1.51±0.16	33.4±1.4	2.410±0.250	13.08±2.22	59.0±5.1	738±59

the scrambler and the twiner, there was a trend of decrease in leaf area based Huber value from current year stems to older stems. It could be expected, especially in the scrambler, that older stems would have greater external support and less influence of inflorescences or fruits than the current year stems, allowing for lower Huber values in older stems.

One advantage of narrow stems in vines is that they are less likely to result in mechanical failure by the host plant (Peñalosa 1984). The wood densities were not significantly different in the three growth forms of *Lonicera* (unpublished data). The "light stem" approach, implied by low Huber values or "less wood per leaf", seems to apply to the twiner *L. japonica* but not the scrambler *L. sempervirens*. Narrow stems of *L. japonica* may allow this species to be a successful canopy weed.

The terms "ring-porous" and "diffuse-porous", as they are normally defined (Panshin and de Zeeuw 1980) do not apply well to *Lonicera* wood. Carlquist (1988) proposed at least 13 types of ring to semi-ring porous woods, based on the origin and function of growth rings (Carlquist 1988). *L. japonica* and *L. sempervirens* have "type 10" growth rings in which maximum vessel diameter is deferred until after the beginning of the growth ring. *L. japonica* has rings of markedly wide vessels but *L. sempervirens* does not. The occurrence of maximum vessel diameter not at the beginning of the earlywood also implies that growth commences during cool winter months when soil moisture is available but peak transpiration does not occur until some weeks after initation of the growth ring (Carlquist 1988). *L. maackii* has "type 7" growth rings in which vessels are wider in earlywood than in latewood. It thus had markedly enhanced earlywood conductive capacity (Carlquist 1988).

The maximum vessel diameters of the twiner *L. japonica* and the scrambler *L. sempervirens* are close to the lower end of the range for vines in general (Ewers et al. 1990). Narrow vessels are held to increase safety against freezing-induced xylem embolism (Carlquist 1985; Ewers 1985). Temperate lianas such as *L. japonica* and *L. sempervirens* might have evolved or retained relatively narrow vessels and low maximum vessel diameter due to exposure to annual periods of freezing weather. *L. japonica* is evergreen except when cultivated as far north as Michigan, where its leaves start to turn brown before April. Narrow vessels, which are more resistant to freezlng induced embolism, are compatible with the evergreen strategy which allows for a longer growing season. Temperate liana species of *Vitis* have extremely wide vessels, but in these species the wide embolized vessels are refilled by the high root pressures in the spring (Sperry et al. 1987).

The minimum vessel diameters in *Lonicera*, of 7.6 μm, are not surprising, given that vessels as narrow as 4 μm were reported for the lianas *Macfadyena unguis-cati* (L.) A. Gentry, *Derris scandens* (Roxb.) Benth., and *Serjania polyphylla* (L.) Radlk. (Ewers et al. 1990). In tropical lianas, the narrower vessels in stems, although quite numerous, contribute an insignificant amount to the *theoretical* K_h (Ewers and Fisher 1989). Likewise, the exclusion of the narrowest vessels in our sampling of *Lonicera* dropped the *theoretical* K_h by less than 1%. However, ignored narrow vessels would affect measurements of the vessel frequency, mean and median vessel diameters, and physiological functions such as water storage and lateral transport.

The mean vessel frequency of the three *Lonicera* species ranged from 561 to 901 vessels mm^{-2}. Despite the fact that we excluded the narrowest vessels, this is much higher than reported for 35 species of Caprifoliaceae of Japan. For instance, the vessel frequency for *L. maackii* was reported as only 230 $\cdot$ mm^{-2} (Ogata 1988). One possibility is that Ogata ignored the narrower vessels, which we found to resemble tracheids in transverse view. The highest vessel frequency previously recorded within the Caprifoliaceae was 737–741 in *Zabelia mosanensis* (Ogata 1991). Carlquist (1988) claimed that vessel frequency above 500 $\cdot$ mm^{-2} was unusual for plants in general, but these high frequencies had been found in plants of notably cold or dry habitats (Miller 1975; Michener 1981, 1983; Carlquist and Hoekman 1985). Those reported above 1000 in shrubs are 1350 in *Romneya racemosa* Harv. of the Papaveraceae (Carlquist and Hoekman 1985) and 2673 in a species of *Cassiope* of the Ericaceae (Wallace 1986). In vines, 901 vessels $\cdot$ mm^{-2} in current year stems of *L. sempervirens* may be the highest vessel frequency thus far recorded, compared to 8–90 in 25 vine species of the Bignoniaceae (Gasson and Dobbins 1991), 24.1 in *Vitis girdiana* Munson of the Vitaceae, and 425 in *Clematis lasiantha* Nutt. of the Ranunculaceae (Carlquist and Hoekman 1985).

In our studies, the *measured* K_h was approximately 24 to 55% of the *theoretical* K_h, with values not significantly different in the different growth forms. This is similar to what most researchers have found in plants in general. However, Berger (1931) reported a value of 100% for three species of vines. Zimmermann (1983) suggested this high ratio might be due to long vessels that behaved more like ideal capillaries than did short vessels.

Why is the *measured* K_h not equal to 100% of *theoretical* K_h? The Hagen-Poiseuille equation, which is based on an ideal capillary, is not adjusted for changing vessel diameter along the vessel length, and does not consider resistance of the vessel ends, the pits and the perforation plates along the pathway of conduction. Furthermore, it assumes non-turbulent flow. From the present report, and the study on the liana *Bauhinia fassoglensis* (Ewers et al. 1989), it does not appear that liana vessels behave differently than in other growth forms.

With LSC and maximum transpiration rates (E), one can predict the maximum pressure gradient ($dP/dx = E/LSC$) that should occur in stems (Zimmermann 1978; Ewers and Cruiziat 1991; Tyree and Ewers 1991; Ewers et al. 1991). The LSC of the twiner, *L. japonica*, is much lower than in other vines (Ewers et al. 1991; Gartner 1991b; North 1992), and E is near the upper end of the range (Ewers 1985; Bell et al. 1988; Ewers et al. 1991; Gartner 1991b; North 1992). The mean LSC for *L. japonica* was also lower than that for dicotyledonous trees and most conifers (Ewers 1985) except *Thuja occidentalis* (Tyree et al. 1991). We found a maximum E value for *L. japonica* of $1.5 \cdot 10^{-7}$ $m^3 \cdot m^{-1} \cdot s^{-1}$ (unpublished data), which is in the range reported by Bell et al. (1988). This is higher than reported in most other vines (Gartner 1991b; North 1992). The predicted pressure-potential gradient

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