# Root pressure and specific conductivity in temperate lianas: exotic *Celastrus orbiculatus* (Celastraceae) vs. native *Vitis riparia* (Vitaceae)[1]

Tim J. Tibbetts[2] and Frank W. Ewers

Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48824 USA

The exotic temperate liana (woody vine) *Celastrus orbiculatus* has become a weed in Michigan, occurring in many of the same habitats as the native liana *Vitis riparia*. However, *C. orbiculatus* frequently develops into extensive monospecific infestations, while *V. riparia* does not. Freezing-induced embolism may be responsible for limiting liana distribution. Root pressure has been observed in numerous tropical lianas and temperate species of *Vitis* and has been implicated as vital to the recovery of xylem function in wide vessels following winter freezes. For both of these co-occurring lianas we investigated root pressure and water conductance as possible explanatory factors for their differential spread. According to our hypothesis, *C. orbiculatus* should have produced greater or more frequent root pressures than *V. riparia*. However, the reverse proved true, indicating that root pressure is not a prerequisite for weedy proliferation of *C. orbiculatus*. Additionally, the seasonal patterns of specific conductivity of stem xylem indicate that each species responds differently to environmental constraints. *Vitis riparia* establishes conductivity early in the growing season, before the leaves emerge, using root pressure to reverse embolism, but loses conductivity with the first freeze in early autumn. *Celastrus orbiculatus* is slow to establish conductivity, depending on new wood production, but leafs out sooner than *V. riparia* and maintains green leaves after the first freeze. Vulnerability curves of xylem to cavitation caused by water stress for the two species indicate that they respond similarly to dehydration. These results indicate that root pressures are not responsible for the invasive success of *C. orbiculatus* and suggest that other factors must be key to its prolific invasion.

**Key words:** Celastraceae; *Celastrus orbiculatus*; hydraulic conductivity; invasive; liana; root pressure; specific conductivity; Vitaceae; *Vitis riparia*; water transport.

Lianas (woody vines) comprise ~1% of the Michigan flora (29 species of a total of 2465 as reported by Voss, 1972, 1985, 1996). Native lianas, e.g., *Parthenocissus, Vitis,* and *Toxicodendron,* are capable of reaching the tops of tall trees and shading out their hosts. These vines rarely develop into thick monospecific stands that exclude other nontree species. However, some exotic vines have become weeds, capable of extensive infestations that may affect community structure (Penfound, 1966). *Pueraria lobata* (kudzu) is one such vine common in the southeastern United States (Wechsler, 1977), while another, *Celastrus orbiculatus* (Oriental bittersweet), appears as far north as Michigan and Connecticut (Patterson, 1974). *Celastrus orbiculatus* is native to China, Japan, and Korea (Hou, 1955). Exotic species may proliferate for various reasons such as escape from their native herbivores, pathogens, and seed predators, as well as enhanced growth in novel environments. We were interested in examining whether water transport properties could be implicated in the success of *Celastrus orbiculatus* over *Vitis riparia* in Michigan.

Lianas are much more prevalent in tropical than in temperate ecosystems, both in terms of biomass and as a percentage of species in the flora (Gentry, 1991). It has been suggested (Ewers, 1985; Sperry and Sullivan, 1992) that low temperature limits the distribution of lianas, possibly via freeze-induced air bubble formation in xylem vessels. When the water in the vessels freezes, the solubility of dissolved gases decreases and bubbles form. If thawing occurs more rapidly than the air can redissolve, the bubbles remain and may increase in size due to the tension of the transpiration stream (Zimmermann, 1983). These air bubbles (emboli) occlude the vessels and prevent further conductance of water. The likelihood of embolism occurring due to freezing increases with vessel diameter (Sperry and Sullivan, 1992; Davis, Sperry, and Hacke, 1999), and vines characteristically have wide vessels.

Embolism may also be caused by water stress. Air may enter conductive vessels through intervessel pit membranes as the xylem pressure decreases (Sperry and Tyree, 1988). This relationship can be expressed as a vulnerability curve, showing an increase in embolism as xylem pressure decreases. This vulnerability curve has been shown to be characteristic for given species and can be informative regarding likely species response to the xylem pressures typically experienced by the species under field conditions (Sperry, Tyree, and Donnelly, 1988; Davis et al., 1999).

Root pressure may be a repair mechanism of plants with wide vessels, such as lianas, that are at high risk of winter embolism. Without a mechanism to remove emboli, vessels will remain permanently dysfunctional. Root pressure is one manner by which conductance can be restored in embolized vessels. Water is taken into the roots osmotically and then forced up through the plant. Emboli may be quickly pushed out by the water, pushed through dry pit membranes, or more slowly dissolved when pit membranes are wetted (Sperry et al., 1987). Examples of positive root pressure include the exudation of water through hydathodes (guttation) and the ''bleeding'' of severed stems. These occurrences are generally limited to conditions of minimal transpiration, such as before dawn, when the stomata are closed, and during periods when relative humidity is at or near 100%, such as during rain. Positive root pressure has been observed in many plants, such as *Vitis* (Sperry et al., 1987), *Acer* (Sperry, Donnelly, and Tyree,

1988b), and many tropical species (Ewers, Cochard, and Ty-ree, 1997; Fisher et al., 1997).

The risk of dysfunction may be balanced by a high hydraulic conductivity in stems with xylem dominated by wide vessels (Chiu and Ewers, 1992; Ewers, Cochard, and Tyree, 1997). Hydraulic conductivity ($k_h$) is measured as the volume of water transported through a unit length of stem per unit time divided by the pressure gradient. Specific conductivity ($k_s$) is $k_h$ per unit cross-sectional area of the xylem and reflects the efficiency of water transport (Tyree and Ewers, 1996). Liana stems provide little mechanical support, are generally narrow with respect to the leaf area they supply (Ewers, 1985; Ewers and Fisher, 1991), contain wide vessels, and are primarily committed to water transport; therefore they typically have high $k_s$ values.

The wide vessels of lianas should be prone to dysfunction when temperatures fall below 0°C, yet some lianas thrive in temperate climates and persist despite freezing. The best studied temperate lianas in this regard are *Vitis riparia* and *Vitis labrusca* L., and several authors have suggested that the success of wide-vesseled temperate lianas may depend upon root pressures (Sperry et al., 1987; Sperry, Donnelly, and Tyree, 1988b; Ewers, Cochard, and Tyree, 1997; Fisher et al., 1997). The objective of this study was to investigate whether differences in water transport characteristics were sufficient to explain the differences in growth patterns of *C. orbiculatus* vs. *V. riparia.* We hypothesized that in co-occurring species, plants of *C. orbiculatus* would have: (1) stronger or more persistent root pressures, (2) higher $k_s$ values through much of the season, and (3) would be less vulnerable to embolism caused by water stress than the co-occurring native species *V. riparia.*

## METHODS AND MATERIALS

*Site descriptions*—Field sites were chosen based on their proximity to laboratory facilities and the presence of both *V. riparia* Michaux and *C. orbiculatus* Thunb. at each site. Plant specimens were selected based on healthy appearance and stem diameters between 1 and 3 cm. Four sites were used, which were all within a 130-km radius of the Michigan State University (MSU) campus, where all laboratory measurements were made.

*Root pressure*—Root pressure was measured on individual specimens at two sites with bubble manometers (Sperry, 1983; Ewers, Cochard, and Tyree, 1997; Fisher et al., 1997). Five healthy individuals for each species were selected, with stem diameters between 1 and 3 cm. The day prior to measurement, stems were cut and manometers containing distilled water and a distal air bubble were attached. The next day, air bubble length pre- and post-attachment to the severed stems was recorded just before sunrise to avoid the effects of transpiration. Root pressure in kiloPascals was calculated using the formula (Fisher et al., 1997)

$$P_x = 100[(L_{atm}/L_{pd}) - 1]$$

where $P_x$ = xylem water pressure, $L_{atm}$ = bubble length in manometer at atmospheric pressure, and $L_{pd}$ = bubble length prior to dawn.

*Specific conductivity*—Specific conductivity of both species was measured in 1996 and 1997, on stems collected from each of the four sites on a revolving schedule. Each site was sampled at least once a month in the spring and summer, and less frequently in the winter. On each collection date, stems of five individuals for each species were severed under distilled water in the field. Measurements were made in the laboratory following the method of Sperry, Donnelly, and Tyree (1988a) and modified according to Chiu and Ewers (1992). Field condition $k_h$ was measured on 10-cm-long segments with a pressure head always less than 1.5 kPa. Stem segments were then flushed

at 172 kPa for 20 min, and final $k_h$ (=maximum) was determined when repeated flushing yielded no increase in conductivity.

Following the conductivity measurements, all stems were perfused with a 0.5% crystal violet dye solution to mark the conductive vessels. A 5-cm column of dye of the same diameter as the stem was allowed to perfuse through the flushed segments. The time required for dye to reach the distal end of the stem segments was noted. Stem segments adjacent to those used for conductivity measurements served as field condition controls for dye descents. All the field condition control stems were then perfused with the dye eight times longer to insure that even some of the smaller vessels could potentially pass the dye. After perfusion with dye, the stems were perfused with distilled water a minimum of 15 min to prevent bleeding of dye from conductive to non-conductive vessels.

After perfusion and drying, each stem segment was severed 2 cm from the proximal end (perfusion port) and shaved smooth with a razor blade. The dyed growth rings and total growth rings were counted using a dissecting microscope. A growth ring was considered conductive if it had five or more stained vessels.

Sapwood area, as demarcated by the dyes in transverse view, was measured using a caliper with a digital micrometer. Bark was removed, and the maximum and minimum xylem diameters were averaged and used to calculate the xylem cross-sectional area. The pith and heartwood area, demarcated by a lack of dye, was also measured and subtracted from the xylem area to obtain the area of conductive xylem. The field condition and maximum $k_h$ values calculated above were divided by the conductive xylem area to obtain $k_s$ values. The percentage embolism was taken as the difference between maximum $k_s$ and initial $k_s$, and standardized by dividing by the maximum $k_s$.

The conductivity data obtained were plotted against date and phenological data collected throughout the year to determine whether the relationship varied between the two species. Phenological data were summarized for all sites and included date of bud break, leaf out (first leaf fully expanded), flowering, and first leaf drop.

*Vessel diameter measurements*—Two stems for each species were used to determine the distribution of vessel diameters. The tangential diameters of all vessels in four equivalent quadrants per stem were measured in transverse view with an optical micrometer. Quadrants were bounded by rays. Vessel diameter distributions were compared with an unpaired, two-tailed *t* test. Theoretical conductivity was calculated for each vessel diameter class using the Hagen-Poiseuille equation following Chiu and Ewers (1992).

The maximum tangential diameter in transverse view was recorded for the ten largest vessels in these distributions. Maximum vessel diameter between the two species was compared with an unpaired, two-tailed *t* test.

*Vulnerability curves*—Stems were cut in the field between July and October 1997, transported to the laboratory, and allowed to dehydrate for various lengths of time ($N = 30$ for *C. orbiculatus, N = 5$ for *V. riparia*). The stems were then bagged and allowed to equilibrate in the bags overnight following Sperry, Donnelly, and Tyree (1988a). Stem segments were cut to be longer than the maximum vessel lengths. The mean xylem pressure was determined using a pressure bomb on five shoots from each stem after equilibration. The stem segments were then severed under water into ten 10-cm lengths. Specific conductivity and percentage embolism were determined as described above.

## RESULTS

In undertaking this study we expected to find differences between the two species that would relate to the success of *C. orbiculatus* as an invasive weed. We found that only *V. riparia* frequently demonstrated measurable root pressure during both 1996 and 1997 (Fig. 1). Root pressure was greatest early in the spring, then declined into summer.

*Celastrus orbiculatus* had almost no measurable root pressures (Fig. 1). Positive, but minor root pressures were observed on a very few occasions. Large air bubbles were frequently observed in the manometers, indicating negative pres-
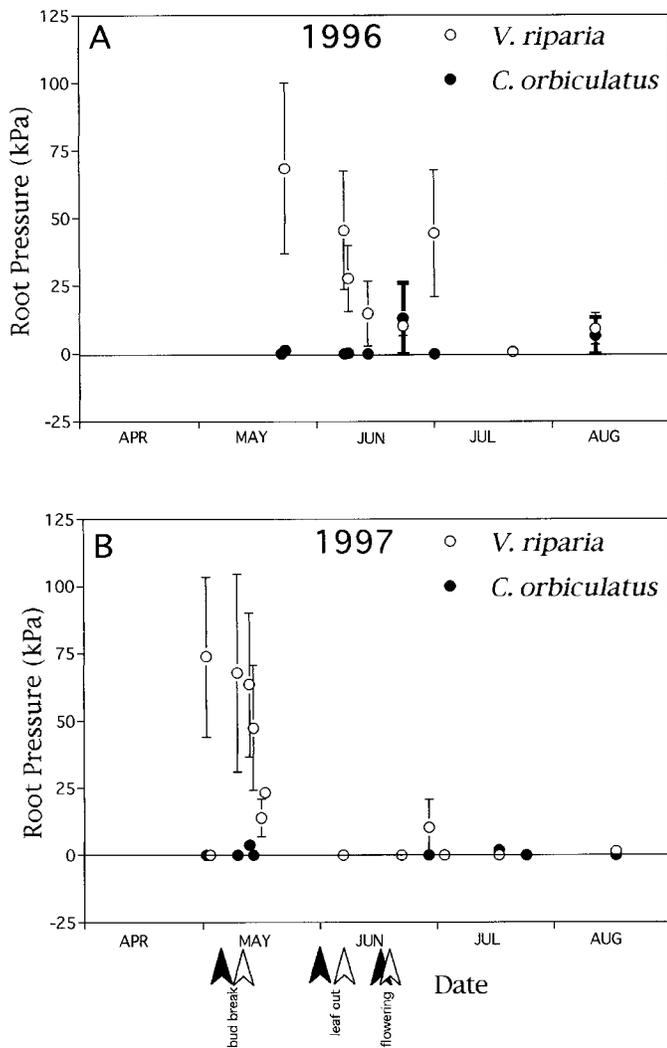
Fig. 1.  Root pressure. (A) 1996. (B) 1997. Each symbol represents the mean for five stems. The range for *V. riparia* is 0–145 kPa. Error bars represent ±1 SE. Where error bars are not visible, they are smaller than the plotted symbol. Relative phenological events are indicated by arrows (white arrows = *V. riparia,* and black arrows = *C. orbiculatus*).



Fig. 2.  Percentage embolism. (A) 1996. (B) 1997. Each symbol represents the mean for five stems. Error bars represent ±1 SE. Where error bars are not visible, they are smaller than the plotted symbol. Relative phenological events are indicated by arrows (white arrows = *V. riparia,* and black arrows = *C. orbiculatus*). Some relevant minimum daily temperatures are indicated along the top.

sure. However, the bubble manometer method is not reliable for negative pressures, so these values were considered no different from zero (Ewers, Cochard, and Tyree, 1997).

Despite differences in site characteristics, the trends in conductivity were relatively uniform across sites for both species. In 1996, *V. riparia* reached its minimum percentage embolism sooner than *C. orbiculatus* (Fig. 2A). The minimum percentage embolism in *V. riparia* (37%) was reached by the beginning of June, whereas in *C. orbiculatus* the minimum (50%) occurred at the end of August. The reduction in embolism began prior to leaf out in *V. riparia,* but it did not occur until after leaf out and after maturation of new vessels in *C. orbiculatus.*

Both species produced flowers and fruit at roughly the same time. Leaf fall in *V. riparia* roughly coincided with increased embolism and the first daily minimum temperatures below 0°C. The leaves of *C. orbiculatus* remained green at some sites for over a month beyond the first frost. During the winter of 1996–1997, embolism reached 100% in both species.
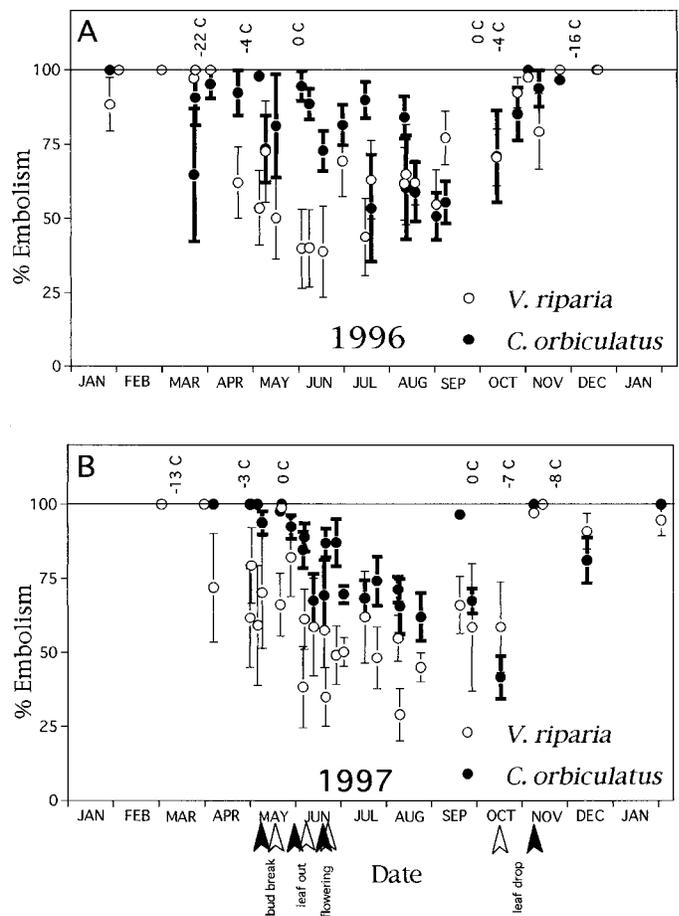
The same general patterns were observed in 1997. *Vitis riparia* reached its minimum percentage embolism sooner than *C. orbiculatus* (Fig. 2B), however, for both species the period of reduced embolism began ~1 mo earlier than in 1996, and therefore the total period of reduced embolism lasted longer than in 1996. In both species minimum embolism was slightly lower in 1997 than in 1996 and did not occur until 1 mo later. The minimum percentage embolism reached during 1997 for *V. riparia* was 29% during August, while for *C. orbiculatus* it was 42% during October. Unlike the winter of 1996–1997, embolism failed to reach 100% during the winter of 1997–1998 and, therefore, reduced embolism persisted for a longer time.

*Vitis riparia* achieved rates of initial (= native) specific conductivity about two to four times higher than *C. orbiculatus* (Fig. 3). The peak values (±1 SE) for *V. riparia* in 1996 were 49.4 ± 10.3, and for 1997 64.8 ± 20.1 kg • s$^{-1}$ • MPa$^{-1}$ • mm$^{-2}$. For *C. orbiculatus,* the values were 17.9 ± 5.7 in 1996, and for 1997 21.0 ± 3.5 kg • s$^{-1}$ • MPa$^{-1}$ • mm$^{-2}$. Similarly, the final $k_s$, measured after flushing the stems, was consistently higher in *V. riparia* than in *C. orbiculatus* (Fig. 4). These values did not show a clear seasonal trend in 1996, although in 1997 the values peaked in July for *C. orbiculatus.*
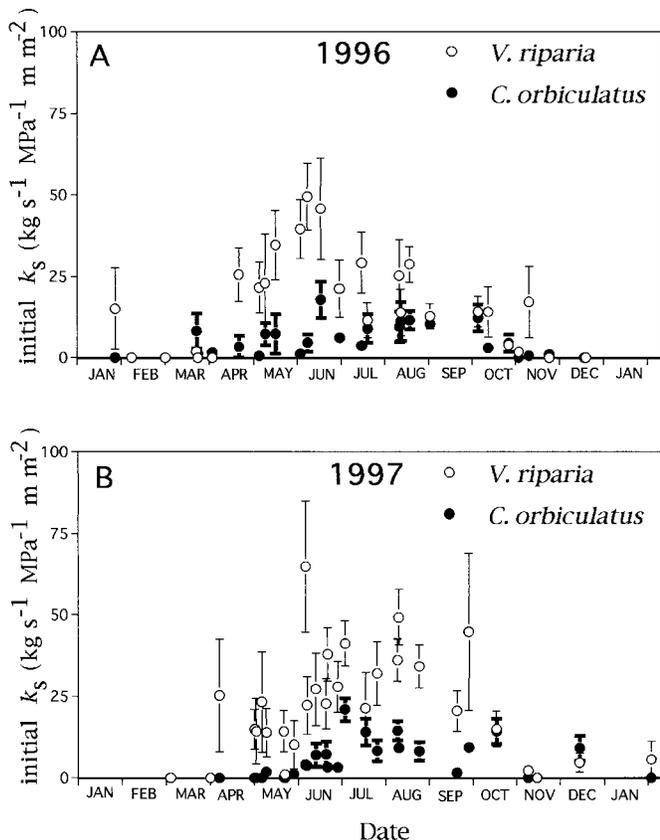
Fig. 3. Initial (native) specific conductivity ($k_s$). (A) 1996. (B) 1997. Each symbol represents the mean for five stems. Error bars represent ±1 SE. Where error bars are not visible, they are smaller than the plotted symbol.



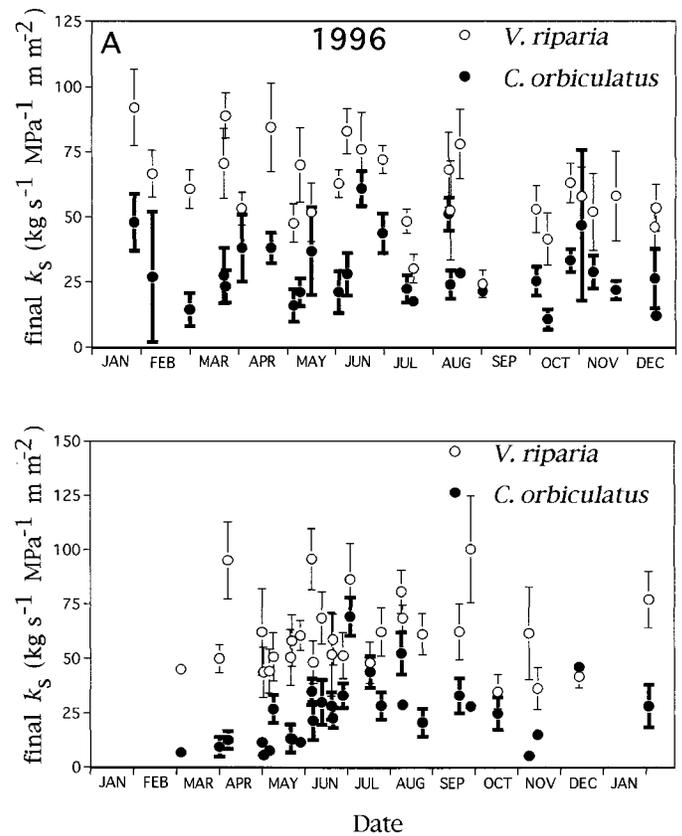Fig. 4. Final (maximum) specific conductivity ($k_s$). (A) 1996. (B) 1997. Each symbol represents the mean for five stems. Error bars represent ±1 SE. Where error bars are not visible, they are smaller than the plotted symbol.

Stems sampled for conductivity measurements ranged between 5 and 12 mm in diameter. During 1997, the mean stem diameter (±1 SE) for *V. riparia* was 7.5 ± 0.1 mm ($N = 145$) and for *C. orbiculatus* 8.1 ± 0.1 mm ($N = 145$). The difference in stem diameter was significant (two-tailed $t$ test, $P = 0.0002$). However, the mean stem age (±1 SE) for *V. riparia* was 4.2 ± 0.2 yr ($N = 140$) and for *C. orbiculatus* 3.7 ± 0.1 yr ($N = 140$). The difference in stem age was significant (two-tailed $t$ test, $P = 0.03$).

The number of active growth rings differed between the two species (Fig. 5). Stems of *V. riparia* routinely showed that in their native state (without removal of emboli), several growth rings contributed to the stem conductivity (Figs. 7 and 11), with about two to four conductive growth rings by the end of April (Fig. 7). However, for *C. orbiculatus* rarely more than one growth ring was capable of conductance (Figs. 6 and 10). High-pressure flushing to remove emboli induced conductance in additional growth rings in *C. orbiculatus* (Figs. 8 and 12), but not in *V. riparia* (Figs. 9 and 13).

The distributions of vessel diameters of the two species are remarkably similar ($P > 0.9$, Fig. 14). Both species have a large number of narrow diameter vessels that contribute little to the theoretical conductivity. However, the largest four vessel diameter categories (<160 μm) are responsible for ~63% of the theoretical conductivity, though numerically they only represent 8% of the total vessels in the stems of each species. The average maximum vessel tangential diameter (±1 SE) for *C. orbiculatus* was 203 ± 6 μm and for *V. riparia* was 191

± 3 μm. This difference was not statistically significant ($P = 0.08$), despite the wood of *C. orbiculatus* being ring-porous and that of *V. riparia* being diffuse-porous.

Vulnerability curves were similar for *C. orbiculatus* and *V. riparia* (Fig. 15). From the amount of scatter in the data and the high amount of native embolism, it is difficult to tell if there is any difference between the two species. If there was a difference, *C. orbiculatus* was more vulnerable to water-stress-induced embolism than *V. riparia*.
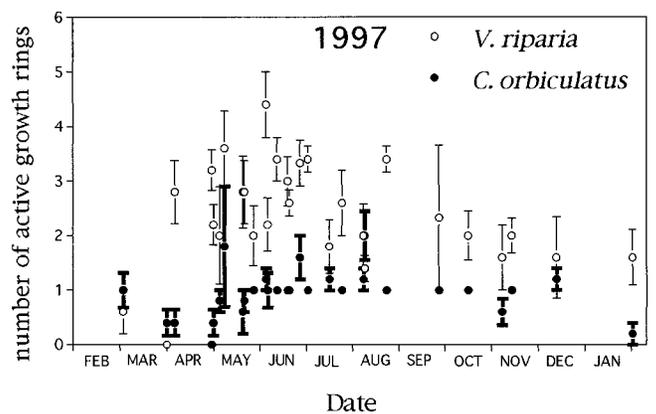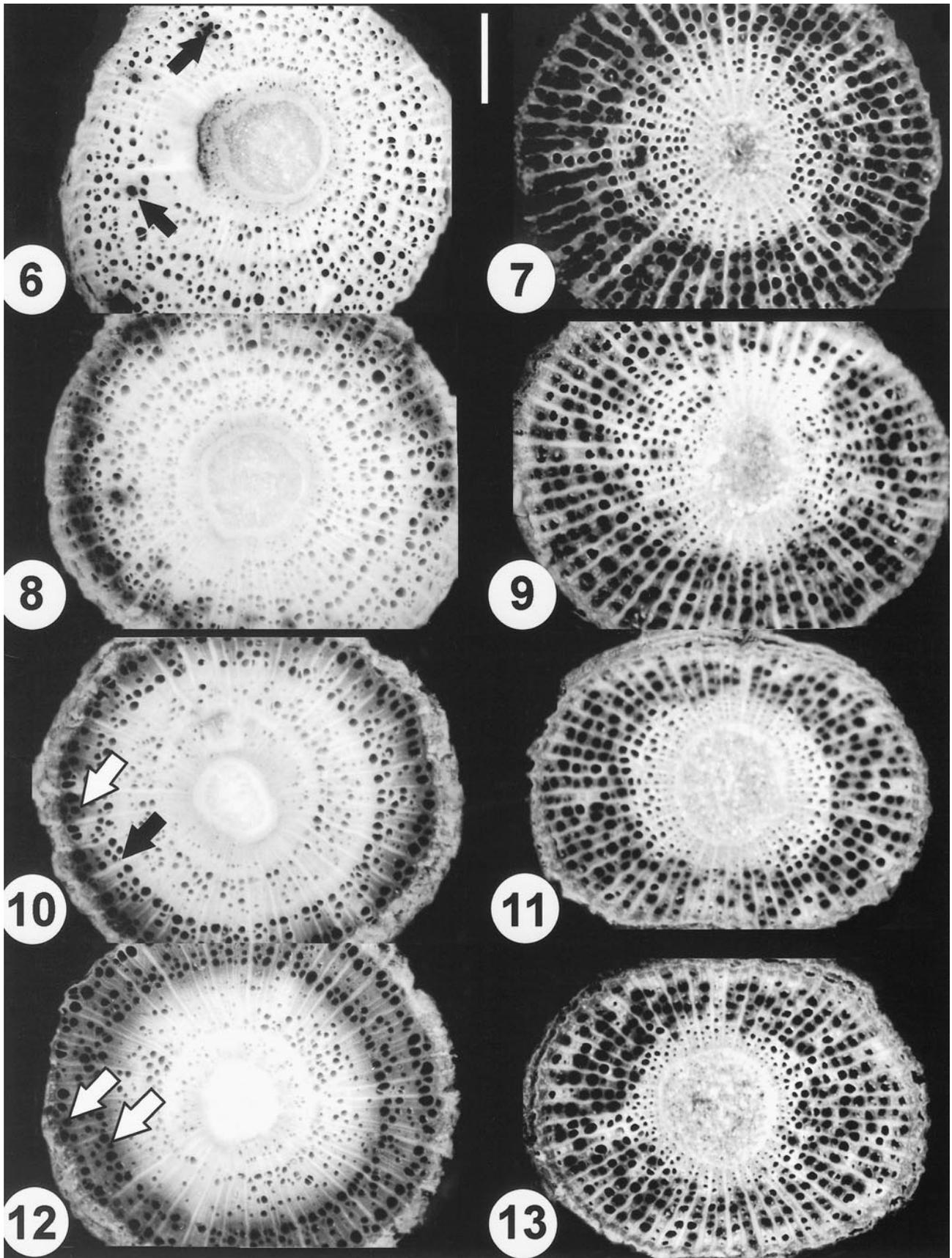


Fig. 5. Number of active (conductive) growth rings. Error bars represent ±1 SE. Where error bars are not visible, they are smaller than the plotted symbol.

## DISCUSSION

In Michigan, *C. orbiculatus* is considered an escaped weed (Voss, 1985). Its extensive and prolific growth suggests that it possesses characteristics that set it apart from native lianas. Apparently the sampled stems of *C. orbiculatus* had significantly greater rates of secondary growth than *V. riparia* since the stems of *C. orbiculatus* were, on average, a half-year younger (3.7 vs. 4.2 yr) but 8% wider than for *V. riparia.*

Root pressure has been observed in many species (Sperry et al., 1987; Ewers, Cochard, and Tyree, 1997; Fisher et al., 1997) and may enhance conductivity by removing emboli. Root pressure may also negate liana distribution limits imposed by freezing-induced embolism. However, root pressure is frequently too small to account for the elimination of emboli in tall plants (Ewers, Cochard, and Tyree, 1997). According to our results, positive root pressures were mostly lacking in stem xylem of *C. orbiculatus* but present in *V. riparia*; thus they would not explain the weedy nature of *C. orbiculatus.*

The maximum individual root pressure measurement of 145 kPa for *V. riparia* found in this study would be sufficient, in theory, to push water 14.5 m above the ground surface. Other studies have reported root pressures for *Vitis* between 10 and 100 kPa (Sperry et al., 1987). Scholander, Love, and Kanwisher (1955) reported sap pressures of 300–500 kPa in *Vitis labrusca.* These measurements suggest that root pressure is an important mechanism for maintaining the conductivity of xylem vessels in this genus. The vessels remained conductive for up to 4 yr in the present study and up to 7 yr according to Smart and Coombe (1983). In *V. riparia,* increased embolism coincides with the onset of freezing conditions. Apparently, freeze-induced embolism reduces transport capability, which, in conjunction with defoliation induced by long nights, brings about winter dormancy. Since the probability of freeze-induced embolism increases with vessel diameter (Davis et al., 1999), 100% embolism may not be achieved because the narrower vessels in a stem may not become air-filled. Greater than 50% of the vessels in each species were narrower than 40 μm.

The wood of *C. orbiculatus* is ring-porous, as compared to the diffuse-porous wood of *V. riparia,* though the vessel diameter distributions are similar and both are dependent on wide vessels for most of their conductivity. *Celastrus orbiculatus* appears to rely on the production of new wood to reestablish conductivity instead of positive root pressure. In 1997, percentage embolism in *C. orbiculatus* decreased around the end of May, corresponding to the onset of conductivity by new sapwood. This dependency of *C. orbiculatus* on new wood production is similar to that reported for temperate ring-porous trees (Wang, Ives, and Lechowicz, 1992; Sperry et al., 1994).

For both species the values of winter embolism were essentially 100% for 1996, but often <100% for 1997. This may be unexpected due to the different xylem anatomies of the two species, but parallels the findings of Tognetti, Longobucco, and Raschi (1998) who found the same trend looking at two
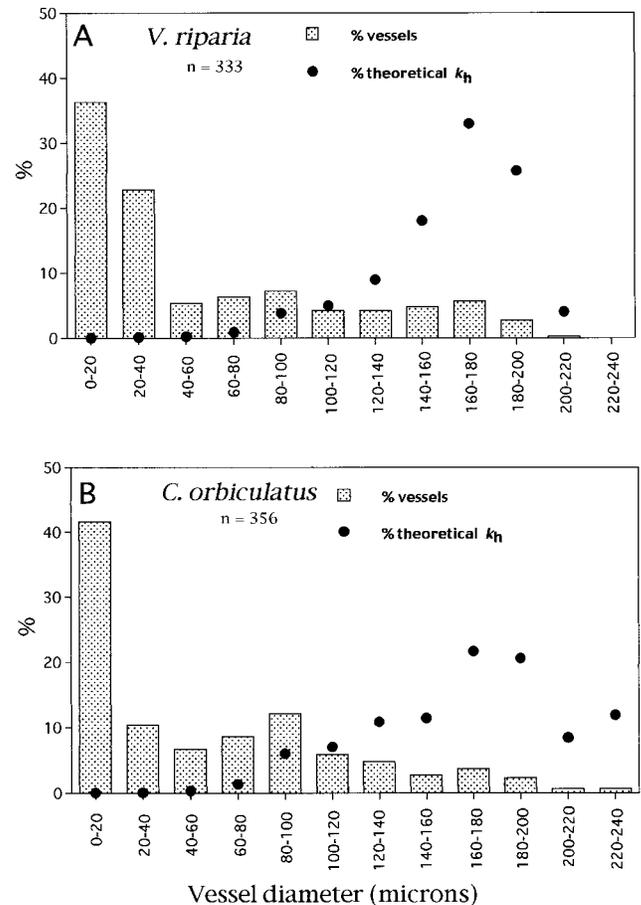


Fig. 14.  Frequency distributions of vessel diameters (histograms) and percentage of total theoretical $k_h$ (filled circles). Based upon vessels from stems shown in Figs. 6, 7, 10, and 11. (A) *V. riparia.* (B) *C. orbiculatus.*

species of *Quercus* that differed in anatomy. The present study may reflect the El Niño weather patterns and the lack of severe freezing during the winter of 1997–1998.

*Vitis riparia* had higher specific conductivity, both initial and final, than *C. orbiculatus.* This is probably explained by the fact that several growth rings were capable of contributing to conductivity in the case of *V. riparia,* but not for *C. orbiculatus.* However, using perfusion at high pressure to remove emboli, additional growth rings may become conductive in some cases. This may result in higher embolism measurements by overestimating the maximum conductivity possible. Thus the high native embolism reported here may be due to refilling of permanently nonfunctional vessels, especially for *C. orbiculatus.* Whether such embolism reversal can ever occur in intact plants of *C. orbiculatus* is unclear.

Finally, the vulnerability to desiccation curves indicate that both species are similar in their sensitivity to drought-induced

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Figs. 6–13.  Transverse view of stems. Scale bar = 200 μm and applies to all figures. Perfusion of stems with crystal-violet-marked conductive vessels. Stems were collected from the same site on two different dates. Figs. 6–9. Stems collected on 30 April 1997. **6.** *Celastrus orbiculatus,* native state. The arrows indicate conductive vessels. **7.** *Vitis riparia,* native state. **8.** *C. orbiculatus,* after being flushed to remove embolism. **9.** *V. riparia,* flushed. Figs. 10–13. Stems collected on 18 June 1997. **10.** *C. orbiculatus,* native state. The white arrow indicates a conductive growth ring; the black arrow indicates a nonconductive growth ring. **11.** *V. riparia,* native state. **12.** *C. orbiculatus,* flushed. The white arrows indicate conductive growth rings. **13.** *V. riparia,* flushed.
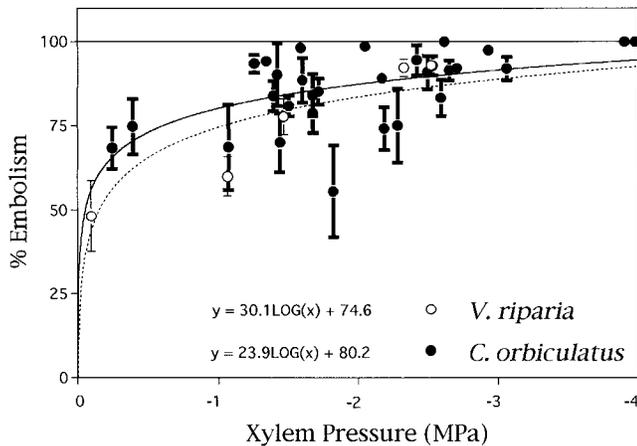
Fig. 15. Vulnerability curves. Each symbol represents the mean for five segments from one stem. Error bars represent ±1 SE. Where error bars are not visible, they are smaller than the plotted symbol.

embolism. Pawmmenter and Vander Willigen (1998) point out that there are numerous models for analyzing vulnerability curves. There is little agreement in the literature as to statistical tests for vulnerability curves. Our curve-fit approach represents the best fit available; however, it does not reflect coefficients of biological significance and should not be used to infer the native state of embolism for these species. Importantly, it is not possible to attribute the success of *C. orbiculatus* to greater resistance to drought-induced embolism.

Clearly, the *Vitis* root pressure paradigm (Putz, 1983; Sperry et al., 1987) does not apply to all successful wide-vesseled temperate vines. *Celastrus orbiculatus* has little or no root pressure and is dependent on newly produced xylem each year, similar to temperate ring-porous trees. The weedy nature of *C. orbiculatus* cannot be explained by root pressure nor exceptional conductivity. The results of this study indicate that *V. riparia* has the advantage in the hydraulic parameters measured, although it is possible that leaf or root hydraulics, not measured in the present study, may favor *C. orbiculatus.* However, there are many alternative hypotheses not related to water relations that could explain the reality of the *C. orbiculatus* spread. Among those deserving attention are: the lack of pests and diseases afflicting the exotic species, more prolific seed production and dispersal, vegetative propagation from root sprouts, and faster growth rates.

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