

WATER TRANSPORT PROPERTIES OF VINE AND TREE STEMS IN A TROPICAL DECIDUOUS FOREST¹

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ABSTRACT

Excised stem segments of vines had higher specific hydraulic conductivities (flow rate per pressure gradient per stem transverse area) than did trees during the dry season in a deciduous forest in Jalisco, México. Vine species averaged from 2.7 to $203 \times 10^{-3} \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$ and tree species from 0.8 to $5.1 \times 10^{-3} \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$. Only three of the 20 species retain their leaves during part or all of the dry season, and these included the vine and the tree with the lowest conductivities within their growth forms. An index of the mean diameter of the six widest vessels per sample was positively and significantly correlated with specific conductivity for the vines but not the trees. Stem density (g cm^{-3} , dry weight/wet volume) was not correlated with either specific conductivity or vessel diameter index for vines or trees.

RESUMEN

Segmentos cortados de tallos de bejucos presentaron conductividades específicas hidráulicas (taso de flujo por unidad de gradiente de presión y área transversal) más altas que árboles durante la época de sequía en un bosque cauducifolio de Jalisco, México. Los bejucos mostraron valores de conductividades específicas entre $2.7\text{--}203 \times 10^{-3} \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$ y los árboles entre $0.8\text{--}5.1 \times 10^{-3} \text{ m}^2 \text{ MPa}^{-1} \text{ s}^{-1}$. Solo tres de las 20 especies mantienen sus hojas durante parte o la totalidad de la época seca, y estas incluyeron el bejuco y el árbol con la conductividad más baja dentro de su respectiva forma de crecimiento. Un índice de diámetro medio de los seis vasos más grandes por muestra fue positiva y significativamente correlacionado con la conductividad hidráulica de los bejucos. Este fenómeno no fue observado en los árboles. La densidad del tallo (g cm^{-3} , peso seco/volumen fresco) no mostró correlación ni con la conductividad ni con el índice de diámetro de vasos tanto para bejucos como para árboles.

THE XYLEM presents a substantial part of the total resistance to water flow through the soil-plant-atmosphere continuum (Tyree, Caldwell, and Dainty, 1975; Gibson et al., 1985; Tyree, 1988). Quantifying the magnitude and location of this resistance to flow has helped elucidate aspects of plant architecture and water use physiology (Nobel and Jordan, 1983) such as indicating which parts of a plant are favored hydraulically during water stress and which parts are most likely to be shed (Huber, 1928; Zimmermann, 1978; Sperry, 1986). Trees produce xylem which serves the dual roles of providing mechanical support and conducting water. In vines the role of providing support is much reduced. Comparing vines and trees

will help explain the trade-offs that occur from one growth form to another in xylem function and, ultimately, may shed light on the biology of plants of different growth forms. In this study we surveyed branches of vines and trees to compare the ability of their wood to transport water by measuring their specific hydraulic conductivities; that is, we quantified the volume of water passing a given xylem transverse area per time for a known pressure gradient across excised twigs of vines and trees.

In general, climbing plants have been shown to have higher specific conductivities than self-supporting plants (Ewers, 1985; Ewers, Fisher, and Chiu, 1988; Ewers, Fisher, and Fichtner, in press) or to have anatomical characteristics that theoretically would allow higher conductivities (Haberlandt, 1909; Carlquist, 1975, 1985, in press; Zimmermann and Jeje, 1981; Bamber, 1984; ter Welle, 1985; Baas and Schweingruber, 1987). These characteristics include wide vessels, long vessels, or many vessels per stem transverse area.

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Most studies, however, are based on specimens of vines and trees that are not strictly comparable. For example, the trees and vines are taken from different topographic sites or climatic regions, have different phenologies, or were grown in botanic gardens that are unlike natural growth conditions. In this study we control for habitat by comparing ten vine and ten tree species from the same dry hillside forest to learn if as a class vines differ from trees in their specific conductivities and to learn the range of specific conductivities within a growth form.

We also wanted to determine whether several simple measurements made on the wood are good predictors of a stem's specific conductivity. Conductivity results from a complex set of wood characteristics including vessel widths, lengths, and numbers per mm², type and orientation of perforation plates between vessels (Bolton and Robson, 1988), the degree of sculpting on the inside of vessel walls, and characteristics of the pores between vessels (Schulte and Gibson, 1988). However, in the simplest cases specific conductivity should be positively correlated with vessel diameter and negatively correlated with stem density (dry weight per wet volume).

MATERIALS AND METHODS—*Site description*—The study area is in the Estación de Biología Chamela in the state of Jalisco, México (19°30'N, 105°03'W, 110–150 m elevation). The climate is monsoonal with 80% of the annual precipitation falling in the months of July through October (Bullock, 1986). We conducted the field work in late March 1988, or 5 months into an 8-month dry season in an average year. The woody flora is highly diverse considering the total rainfall (748 mm annually), and both floristics and structure differ strongly between moister arroyos and drier hillsides (Lott, Bullock, and Solís, 1987). Material for this study was collected from a dry hillside forest or its disturbed edge adjacent to the station.

Sampling in the field—All species sampled were dicotyledons. The vine species, all from different families (Table 1), have perennial stems and are leafless in the dry season, except *Aristolochia* which is evergreen and *Adenocalymma* which holds its leaves well into the dry season (Bullock, personal observation). Six of the species are tendril-climbers, three are twiners, and one is a scrambler (Table 1). The self-supported plants are small to large trees, all from different families (but two families are in common with the vine samples; Table 1).

All are leafless in the dry season except *Caparis* which is evergreen and shows shoot growth, leaf growth, and flowering during the dry season (Bullock and Solís, personal observation). Because most plants were leafless we could not measure leaf-specific conductivities.

Our techniques for harvesting and testing stem samples basically followed those of Farmer (1918a). All cuts were made with sharp shears. Stem segments were selected in a diameter range of about 3–20 mm and included several nodes but no branches on the longest unbranched sections we could find. In trees this length was about 0.3 m and in vines up to 2.0 m. Most of the stems were estimated (by SHB) to be at least 2 yr old. The goal of returning nonembolized samples to the lab was met in different ways for vines and trees. This first cut was on the morphological lower or proximal end. For vines this was done under water by bending the stem into a water-filled tub before cutting. Tree branches could not be bent and cut under water because of their high radius of curvature so they were cut in the air and rapidly placed in water. The proximal, submerged end was immediately trimmed by about 0.02 m and up to 0.15–0.20 m more was later removed at the laboratory (see below). The proximal end remained under water until the conclusion of conductivity measurements. The second cut was made on the distal end in the air.

Specific conductivity—At the nearby laboratory we transferred segments to a tub filled with an aqueous formaldehyde solution (0.05% formaldehyde in tap water) and then trimmed the stems to their final length of about 0.10 m. We first removed most of the excess length from the proximal end and then submerged the whole sample to trim the distal end. We used the formaldehyde solution from this point on to prevent decreases in conductivity that can occur over time when pure water is used (Sperry, Donnelly, and Tyree, 1988). In this tub, a liquid-filled connector was slipped snugly onto each newly cut end. Connectors were made of latex tubing nested around a rigid plastic rod (fitting into the siphon tube) built up to the size of the stem. We sealed the connectors to the stem with melted wax and then flushed the solution in the connectors to remove any debris.

To measure specific conductivity we attached the connector on the distal end of the stem segment to a siphon full of water (5.38-m vertical drop below the sample giving 53 kPa of vacuum; Fig. 1). We then attached the connector at the proximal end of the stem to a tube leading to a pipette or a graduated cylinder

TABLE 1. Nomenclature (following Lott, 1985) and characteristics of species used in this study in Chamela, Mexico: leaf phenology, climbing mechanism (vines), stem density (sample range and number of samples, N), vessel diameter index (sample range and N), and widest vessel. Vessel diameter index is calculated as the mean diameter of the widest six vessels per sample. Widest vessel shows the mean diameter of the widest vessel encountered

Species	Family	Leaf phenology	Climbing mechanism	Stem density (g cm ⁻³)	N	Vessel diameter index (µm)	N	Widest vessel (µm)
Vines								
<i>Adenocalymma inundatum</i> Mart.	Bignoniaceae	Tardily decid.	Tendrils	0.51-0.63	3	69-81	2	98
<i>Aristolochia taliscana</i> Hook. & Arn.	Aristolochiaceae	Evergreen	Twiner	0.13-0.33	3	141-200	2	230
<i>Combretum fruticosum</i> (Loefl.) Stuntz	Combretaceae	Deciduous	Scrambler	0.59-0.68	2	93	2	121
<i>Dieterlea fusiformis</i> Lott	Cucurbitaceae	Deciduous	Tendrils	0.27	1	217	1	227
<i>Entadopsis polystachya</i> (L.) Britt.	Leguminosae	Deciduous	Tendrils	0.38-0.46	3	289-330	2	372
<i>Gaudichaudia mcvaughii</i> Anderson	Malphiaceae	Deciduous	Twiner	0.62-0.64	2	109-120	2	132
<i>Gouania rosei</i> Wiggins	Rhamnaceae	Deciduous	Tendrils	0.51-0.66	4	179-203	2	209
<i>Ipomoea bracteata</i> Cav.	Convolvulaceae	Deciduous	Twiner	0.28-0.40	3	85-246	3	266
<i>Passiflora juliana</i> MacDougal	Passifloraceae	Deciduous	Tendrils	0.44	2	108-113	2	121
<i>Serjania brachycarpa</i> Rose	Sapindaceae	Deciduous	Tendrils	0.64-0.68	2	107-108	2	124
Mean of vine means (±S.E.)				0.48 ± 0.05		155 ± 22		190 ± 27
Trees								
<i>Caesalpinia eriostachys</i> Benth.	Leguminosae	Deciduous		0.65-0.75	3	61-68	2	77
<i>Capparis indica</i> (L.) Fawc. & Rendle	Capparidaceae	Evergreen		0.55-0.57	2	59-69	2	75
<i>Cnidioscolus spinosus</i> Lundell	Euphorbiaceae	Deciduous		0.24-0.38	3	106-121	2	137
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Boraginaceae	Deciduous		0.53-0.65	2	78-59	2	88
<i>Guapira</i> sp.	Nyctaginaceae	Deciduous		0.43-0.52	3	44-50	2	54
<i>Heliocarpus pallidus</i> Rose	Tiliaceae	Deciduous		0.46-0.48	2	70-89	2	96
<i>Ipomoea wolcottiana</i> Rose	Convolvulaceae	Deciduous		0.44-0.77	2	116-193	2	201
<i>Psidium sartorianum</i> (Berg) Ndzu.	Myrtaceae	Deciduous		0.67-0.78	2	33-39	2	39
<i>Ruprechtia fusca</i> Fern.	Polyaceae	Deciduous		0.61-0.64	2	57-65	2	67
<i>Spondias purpurea</i> L.	Anacardiaceae	Deciduous		0.38-0.40	2	93-117	2	129
Mean of tree means (±S.E.)				0.55 ± 0.04		81 ± 16		96 ± 15

filled with 0.05% formaldehyde. We opened the valve leading to the siphon and measured the volume of liquid pulled through the stem in a timed interval, usually about 10 sec. All measurements were made at ambient temperature, around 20 C. For each species we repeated measurements several times and determined conductivities for two to three samples, each sample from a different plant. We next measured the segment length and xylem and pith diameters for the distal and proximal ends. We calculated transverse area by subtracting pith area from xylem area, then averaged both ends for one value per segment. We preserved a sample of each segment in a mixture of formalin, acetic acid, and alcohol (FAA) for descriptions of anatomy and stem density.

We use the term specific conductivity, L_p , ($m^2 s^{-1} MPa^{-1}$) for the water volume that passes a transverse area per unit time ($m^3 s^{-1} m^{-2}$) divided by the pressure gradient ($MPa m^{-1}$) across the segment:

$$L_p = (\Delta V / \Delta t)(A)^{-1}(\Delta P / \Delta l)^{-1}$$

where ΔV is water volume that passes the xylem transverse area, A , in the time interval Δt , and ΔP is the pressure difference across the stem segment of length Δl .

The water velocity through the siphon, different for each sample, determined the loss of pressure due to friction in the siphon. We used the Darcy-Weisbach equation (Linsley and Franzini, 1964) to calculate this loss to determine the true pressure drop across the sample (ΔP), which we used in the above equation. For the sample with the highest flow rate the pressure loss due to friction was 6% of the total pressure drop across the apparatus, but for most samples the loss was negligible.

Different workers have used different terminology to report the same hydraulic quantities, so it is important to note the units. Specific conductivity is a material property because it is normalized by transverse area and segment length. It differs from the often reported values of hydraulic conductance (volume per time divided by pressure, $m^3 s^{-1} MPa^{-1}$) and hydraulic conductance per unit length (volume per time divided by pressure gradient, $m^4 s^{-1} MPa^{-1}$, sometimes called hydraulic conductivity) which do not account for the cross-sectional area of the stem and so are structural, not material properties. For the purposes of this study specific conductivity is more relevant than hydraulic conductance because we want to compare the ability of a unit of wood material to transport water.

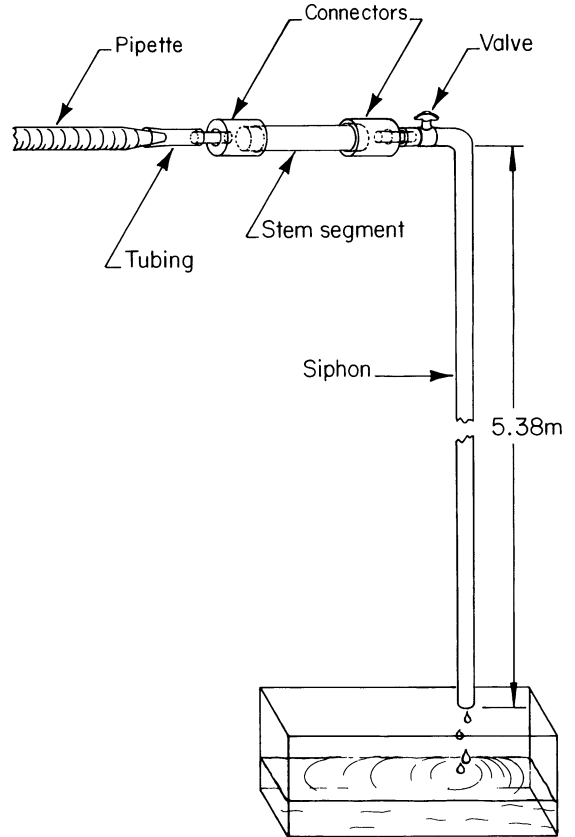


Fig. 1. Apparatus used to measure stem-specific conductivity. The pipette and tubings are filled with 0.05% formaldehyde in tap water. After opening the valve one measures the loss of water volume in the pipette over a set time interval.

Stem density—Stem samples that had been stored in FAA for 7 months were used for determination of stem density, dry weight per wet volume. We prepared samples by removing everything external to the cortex and removing pith > 2 mm in diameter. Wet volume was determined from displacement of water in a graduated cylinder. Our values for stem density may be slightly lower than for fresh samples because of possible weight loss during storage in FAA.

Vessel diameters—We determined the widest vessels per individual rather than complete vessel size distributions. Because flow rate is proportional to radius to the fourth power the majority of flow will occur through the widest vessels. Moreover, wide vessels could be identified unambiguously in all species on hand-made transverse sections. Two perpendicular vessel diameters were recorded and averaged

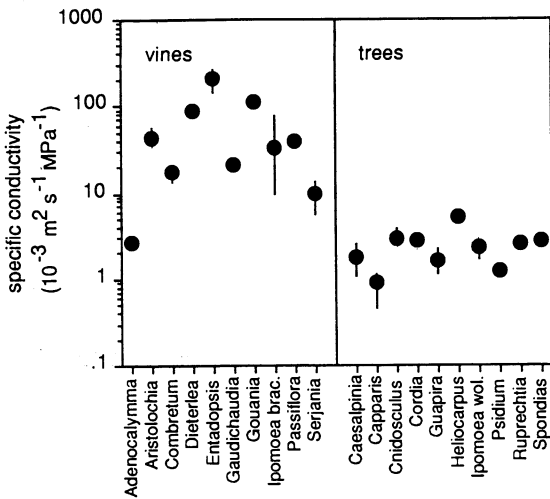


Fig. 2. Specific conductivity of stems of vines and trees with bars denoting range ($N =$ two stems except in *Aristolochia*, *Entadopsis*, *Ipomoea bracteata*, *Caesalpinia*, and *Cnidocolus* where $N =$ three). Note that conductivity is shown on a logarithmic scale.

for the widest 24 vessels encountered per slide for several samples (each a different individual) of each of the 20 species. We then averaged the highest six values of each plant for the vessel diameter index.

RESULTS—Vines averaged much higher conductivity than did trees (57 ± 19 vs. $2.4 \pm 0.4 \times 10^{-3} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$, mean \pm standard error, one-tailed t -test significant at $P < 0.05$). Nine of the ten vine species had higher specific conductivities than the tree species (Fig. 2). The trend toward higher conductivity in vines than trees is shown within the genus *Ipomoea* (*I. bracteata* vs. *I. wolcottiana*) and within the family Leguminosae (*Entadopsis* vs. *Caesalpinia*). The vine *Entadopsis* had stem-specific conductivity two orders of magnitude higher than the trees. Conductivity did not differ between twiners and tendril climbers.

Adenocalymma, the vine with a low conductivity similar to trees, is notable in that it holds its leaves long into the dry season. The plant with the lowest conductivity was the evergreen tree *Capparis*. However, the evergreen vine *Aristolochia* had intermediate conductivity for its growth form.

We also studied three vine individuals that were growing in more mesic habitats than the others in this study. An arroyo *Entadopsis* and a *Serjania* growing near the station leachfield had more than twice the conductivities of the same species growing on the dry hillside ($417 \times 10^{-3} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$ and $30 \times 10^{-3} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$, respectively). A third species, an un-

named Vitaceae from the arroyo, had very wide vessels (widest vessel $382 \mu\text{m}$ in diameter, vessel diameter index of $327 \mu\text{m}$) and low stem density (0.22 g cm^{-3}) suggesting it had the potential for very high specific conductivity.

Vines and trees had the same ranges of stem densities for the species examined (Table 1), 0.26 – 0.65 g cm^{-3} for vines and 0.32 – 0.72 g cm^{-3} for trees (species means), and the means did not differ significantly (one-tailed t test, $P > 0.05$). Vine values are higher than those reported for the same site and species by Castellanos et al. (1989), who sampled internodal regions only, during the growing rather than dormant season, and who included bark in the samples. Three tree species had similar densities to those reported for the same site by Barajas-Morales (1985). On average the widest vessels in vines were wider than in trees, shown both by the vessel diameter index (mean of the six widest vessels) and the single widest vessel per species (Table 1). In spite of much overlap between vines and trees, the vessel diameter index was significantly higher for vines than trees (one-tailed t -test, $P < 0.01$).

Stem density was not correlated significantly with vessel diameter index or specific conductivity for either vines or trees (Table 2). The lack of correlation indicates that stem density is determined by a variety of factors and cannot be used as a simple gauge of diameter of largest vessels or of specific conductivity.

Specific conductivity was strongly and positively correlated with vessel diameter index and diameter of the widest vessel for the ten vine species but not for the ten tree species (Table 2). However, in the absence of data on vessel density (number per transverse area) and complete vessel diameter distributions, we cannot state whether vessel diameter or vessel density is more important to conductivity in the different growth forms.

DISCUSSION—The mean specific conductivity was higher for vines than trees: vine species averaged 2.7 – $203 \times 10^{-3} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$ and tree species averaged 0.8 – $5.1 \times 10^{-3} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$. These values are on the low end of the ranges summarized by Ewers (1985) for maximum conductivity of lianas (woody vines, 12 – $1,375 \times 10^{-3} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$) and dicot trees (3.6 – $366 \times 10^{-3} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}$) from around the world. Vessels tend to be wider in a plant's main axis than in its lateral branches (e.g., Zimmermann, 1978) and so one would predict greater conductivities for the main axis than the laterals. In order to compare stem segments of the same size we probably biased vine samples toward main axes and tree samples toward

TABLE 2. Correlation coefficients and their significance between wood properties for vine species ($N = 10$) or tree species ($N = 10$). Correlations were conducted on species means

Dependent variable	Independent variable	Vines r^a	Trees r
Stem density	Vessel diameter index	0.52	0.40
Stem density	Specific conductivity	0.30	0.45
Specific conductivity	Vessel diameter index	0.94**	0.27
Specific conductivity	Diameter of widest vessel	0.84**	0.30

^a No symbol = not significant at $P = 0.05$; ** = significant at $P < 0.01$.

lateral shoots. These results, then, are really saying that for stems of a given size vines had higher conductivities than trees.

Some of the difference between conductivities of vines and trees could have resulted from the different sampling methods we used, but we think this was minor. Because trees were harvested in air rather than under water, some of the vessels in tree samples may have become air-filled. We subsequently trimmed 0.15 m or more stem away from the proximal end, which probably removed most or all of the potentially air-filled vessels. We base this premise on the very high skew of vessel length distributions (e.g., Ewers and Fisher, 1989, in which 50–80% of the vessels were less than 20% the length of the longest vessel) and our crude field determination of maximum vessel lengths. Concomitant with the stem harvest for conductivity measurements, we harvested a total of nine other segments from five tree species (not more because of the difficulty of finding long unbranched stems), submerged one end in water, blew on the other end, and shortened the stem until air bubbled through the water. The longest vessels for each of the five species (nine samples total) were 0.71 m (*Spondias*), 0.39 m, 0.30 m, 0.28 m, and 0.22 m. In a comparison of greenhouse-grown *Entadopsis* and *Serjania* vines sampled with both methods, there was no evidence that conductivity was lower in segments sampled using the tree method (unpublished data).

Because the vine growth form is freed from the constraint of providing its own structural support, over evolutionary time its wood appears to have become optimized for rapid transport of water. Within the vine growth form, twiners and tendrils did not differ in their specific conductivities. Because $\Delta V/\Delta t A^{-1}$ is equivalent to the average velocity of flow through the stem, v , ($m^3 s^{-1} m^{-2}$ equals $m s^{-1}$), the water potential gradient along a stem equals the average velocity of flow through the stem divided by specific conductivity:

$$\Delta P/\Delta l = v/L_p.$$

With the same average flow velocity through

their main stems the large measured difference in mean specific conductivity of vines vs. trees will lead to only modest differences in water potentials. For the sap flow velocity of $3.6 \times 10^{-5} m s^{-1}$ the difference between water potentials at the top of a 5-m-long vine and tree stem will be 0.07 MPa. However, the differences in specific conductivity appear more important when stems are viewed in terms of the leaf area stems can support hydraulically. If there is no water storage in the system, water flow rate across the stem of area A_s is equivalent to transpiration, E (water volume transpired per time per leaf area), times the ratio of stem area, A_s , to the leaf area supplied by that stem, A_1 :

$$(\Delta V/\Delta t)A^{-1} = E(A_1/A_s),$$

so

$$L_p = E(A_1/A_s)(\Delta P/\Delta l)^{-1}.$$

For the same transpiration rate, stem area, and pressure gradient in the stem, vines would have 24 times the leaf area of trees and 24 times the velocity of water flow through the stem.

Much of the variability in conductivity within a growth form appeared related to the evergreen vs. deciduous habit. The exception was the evergreen vine *Aristolochia*. *Adenocalymma*, which holds its leaves well into the dry season, had the narrowest vessels of the vines tested. The other eight vines were deciduous. Two of the vines growing in more mesic sites had twice the conductivities of the same species on the xeric hillside. The arroyo Vitaceae had the widest vessels of all species we measured. The only evergreen tree, *Capparis*, had the lowest conductivity of all species tested. These results are consistent with regional surveys showing that plants of xeric habitats or those active in the dry season tend to have smaller-diameter vessels and tracheids than those from more mesic sites and those active in wetter seasons (Carlquist and Hoekman, 1985). Farmer's direct measurements of specific conductivities (1918a, b) showed consistently lower conductivity in evergreen than in deciduous plants. In his comparison of conductivities of

29 types of deciduous plants (934 samples) and 27 evergreen ones (376 samples), deciduous plants averaged 3.5 times the specific conductivity of evergreen ones.

From an ecological viewpoint it is unclear why species characteristic of wet sites or wet seasons should have higher conductivities and wider conduits than those of drier sites or seasons. *Within* a species conduit diameter may be correlated with availability of water at the time of conduit development because cell turgor (a function of water availability and other factors) is a major determinant of how large the cells become. *Between* species the developmental argument is not applicable (Tyree and Sperry, 1989). The argument that wide conduits are more likely to become embolized than narrow ones may hold within an individual (Ellmore and Ewers, 1985; Salleo and LoGullo, 1986; Lewis, 1987) but is not supported by interspecific comparisons of vulnerability to cavitation (Tyree and Dixon, 1986; Sperry, Tyree, and Donnelly, 1988). The tension at which cavitation occurs is determined by the diameter of intervessel pores, which are not correlated with vessel diameters between species (Sperry, Tyree, and Donnelly, 1988).

In conclusion, vines had higher specific conductivities than did trees for stems of about the same size, but there was a wide range of conductivities within each growth form. Plants of dry seasons or dry sites tended to have lower conductivities than did plants of the same growth form living in wetter seasons or wetter sites. Further research emphasizing the whole plant profile of hydraulic properties in vines and trees is needed to examine the physiological, mechanical, and ecological tradeoffs of production of wood that optimize water transport vs. wood that also functions in mechanical support.

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