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# Xylem Conductivity and Anatomical Traits in Diverse Lianas and Small Tree Species from a Tropical Forest of Southwest Mexico

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**Abstract:** Seven lianas and four small trees collected from a tropical rainforest of Southwest Mexico were studied to relate vessel diameter and vessel frequency to the relative hydraulic conductivity (RC), vulnerability to cavitation and anatomical traits on the secondary xylem. The seven liana species and four small tree species represented ten different families. Two liana species (*Passiflora ligularis* A. Juss. and *Vitis tiliifolia* Humb. and Bonpl.) showed the highest vessel diameters, RC and vulnerability to cavitation. A small tree (*Petrea volubilis* L.) presented the lowest values for vessel diameter, RC and cavitation. Narrow vessels determined the vessel frequency per mm$^2$ (-0.58) while wider vessels showed low influence (-0.24). Wider and narrow vessels determined RC and vulnerability to cavitation ($r = 0.59$ to $0.76$). Generally, wider vessels presented solitary distribution on the secondary xylem in liana and small tree species and narrow vessels were grouped in clusters. Liana species presented parenchyma in diverse forms, while parenchyma was scanty in the small tree species. The eleven species showed a broad range in RC and vulnerability to cavitation and showed diversity in anatomical traits on secondary xylem indicating that they have different anatomical adaptations with similar growth habit.

**Key words:** Cavitation, vessel diameter, vessel frequency, relative hydraulic conductivity

## INTRODUCTION

Lianas are an abundant and diverse group of plant species that constitutes approximately 25% of woody plants (Gentry, 1991). The evolution of lianas has involved changes in vessel size to increase water conductivity in thin and large stems (Ewers *et al*., 1997). Angiosperm trees and lianas are an example of convergent evolution in relation to vessel dimension because both groups have developed wider and larger vessels (Wheeler *et al*., 2006; Ewers *et al*., 1991). Hydraulic conductivity is highly efficient in wider vessels with simple perforation plates that offer low resistance to the water movement from roots to leaves in lianas and trees (height >20 m) (Zimmermann, 2003; Carlquist, 1991; Tyree, 1997). However, wider and longer vessels in lianas are more efficient in the water conduction compared to trees or shrubs (López-Portillo *et al*., 2000). Some disadvantages of wider vessels are found because they are highly susceptible to diseases (attack of bacteria, fungi and insects), freezing by low temperatures and cavitation on the water column (Zimmermann, 2003; Tibbets and Ewers, 2000). Cavitation takes place on vessels when water is frozen, when vapor pressure is increased and when oxygen solubility decreases (Tyree, 1997). In addition, cavitation occurs in plants under natural growth conditions by seasonal or environmental changes that cause water deficit stress and water freezing on plants (Tibbetts and Ewers, 2000). Even though the disadvantages of wider vessels in lianas, Swaine and Grace (2007) established that they are highly efficient for accessing to the water in deeper soil layers increasing their distribution in tropical forests and probably lianas will be more abundant in the flora in future decades.

Hydraulic conductivity and vulnerability to cavitation depend on some anatomical traits on the secondary xylem (i.e., vessel size and parenchyma cells) (Tyree and Ewers, 1991), but narrow vessels are an alternative way for water conduction when wider vessels are cavitated (Zimmermann, 2003; Ewers *et al*., 1989).

Diverse studies have estimated the hydraulic conductivity and vulnerability to cavitation in relation to vessel size on the secondary xylem (Ewers *et al*., 1989, 1997; Carlquist, 1996; Fisher and Ewers, 1995). Vessel diameters were compared finding anatomical differences in thirteen liana species compared with one tree of the

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*Gnetum* genus (Fisher and Ewers, 1995). In the family Fabaceae, vessel diameters of tree, shrub and liana species were also compared, finding considerable differences in their xylem anatomy and life growth form (Ewers *et al*., 1989, 1997). One shrub, one subshrub and seventeen liana species of the Menispermaceae family were compared in relation to successive cambia, vessel diameter and other anatomical traits (ray width and tracheid length) (Carlquist, 1996). In the present study, the main objective was to determine vessel diameter and frequency, relative hydraulic conductivity and vulnerability to cavitation in relation to some anatomical traits on the secondary xylem in seven lianas and four small trees that represented ten different families from a tropical forest of Southwest Mexico.

## MATERIALS AND METHODS

**Study site:** Wood samples of seven liana and four small tree species were collected during 2000 (Spring and Summer seasons) from a tropical forest called El Ocote (16°41', 17°20' N, 92°56', 94°11' W, 700-1200 m above sea level). This area is classified as a rainforest with an annual mean temperature between 18-22°C and annual precipitation between 1500-2500 mm (Breedlove, 1981).

**Plant material:** The seven liana species collected were: *Cissus biformifolia* Standl. and *Vitis tiliifolia* Humb. and Bonpl. (Fam. Vitaceae, Ishiki 3032 and 3274, respectively), *Cydista diversifolia* Miers (Fam. Bignoniaceae, Hernández 3052), *Ipomoea pauciflora* M. Martens and Galeotti (Fam. Convolvulaceae, Ishiki and Hernández 2894), *Passiflora ligularis* A. Juss. (Fam. Passifloraceae, Hernández 3078), *Pfaffia hookeriana* Greenm. (Fam. Amaranthaceae, Ishiki 3051) and *Tournefortia hirtussima* L. (Fam. Boraginaceae, Ishiki 3333). The four small tree species were: *Clusia orizabae* Hemsl. (Fam. Clusiaceae, Hernández 3108), *Heteropterys laurifolia* A. Juss. (Fam. Malpighiaceae, Ishiki 3214), *Petrea volubilis* L. (Fam. Verbenaceae, Hernández 2886) and *Russelia chiapensis* Lundell (Fam. Scrophulariaceae, Hernández and Castañeda 3099). Herbarium vouchers of each liana and tree species were deposited at Colegio de la Frontera Sur Herbarium (Chiapas, México).

Wood samples were fixed in the field in a formaldehyde-acetic acid-ethanol solution (Johansen, 1940) and stored in glycerin-ethanol-water (1:1:1). Transversal segments of wood samples from pith to bark were cut (20-30 µm thick) on a slide microtome. Sections were double stained with safranin-fast green (Johansen, 1940) and mounted with synthetic resin.

Fifty individual vessel elements per sample was considered for determining diameter in 25 fields using the image analyzer Image-pro plus version 3.1 (Cybernetics, 1997). After we measured vessel diameter in all plant species, we decided to separate two types of vessel based on their diameter values, narrow and wider vessels. Diameter values below 100 µm were considered as narrow vessels and above 100 µm were considered as wider vessels. Finally, vessel frequency was determined in 1 square mm considering both types of vessels.

**Relative hydraulic conductivity and vulnerability index:** Variation on efficiency and susceptibility to damage caused by vessel diameter was estimated indirectly through the relative hydraulic conductivity (RC) and vulnerability to cavitation according to the equations proposed by Carlquist (1988). RC and vulnerability were estimated in each plant species as:

$$RC = r^4VF$$

$$\text{Vulnerability} = VD/VF$$

where, r is vessel diameter, VF is vessel frequency in a square mm and VD is vessel diameter in a square mm.

**Statistical analysis:** Vessel diameters were transformed into logarithm values and vessel frequency were transformed into squared root values to conduct analysis of variance and Tukey's test using the SAS software (SAS, 1990). The vessel diameter and frequency vessel were transformed because they do not show a normal distribution as was previously reported (Reyes-Santamaria *et al*., 2002).

## RESULTS

**Vessel diameter and frequency:** *Passiflora ligularis* A. Juss. and *Vitis tiliifolia* Humb. and Bonpl. were liana species that showed the highest diameter values for wider and narrow vessels (Table 1, Fig. 1a, d, 2a, b). The diameter of both vessel types showed an influence on vessel frequency, which was low. *Cissus biformifolia* Standl. also showed vessels with wider diameter, but narrow vessel number caused high frequency (Fig. 2c). *Ipomoea pauciflora* M. Marteens and Galeotti, *Cydista diversifolia* Miers and *Pfaffia hookeriana* Greenm. showed lower values for wider vessels that caused low vessel frequency (Fig. 1b, c, 2d-f). *Tournefortia hirtussima* L. was the liana species with the lowest diameter values for wider vessels and vessel frequency (Fig. 2g).

Table 1: Vessel diameter, vessel frequency (VF), relative hydraulic conductivity (RC) and vulnerability to cavitation in seven lianas and four small trees from a tropical forest of Southwest Mexico

| | Vessel diameter (µm) | | | | | Anatomical differences | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Narrow | Wide | VF (mm$^2$) | RC | Vulnerability | Wide vessels | Parenchyma | Rays | Others |
| **Lianas** | | | | | | | | | |
| *Passiflora ligularis* A. Juss. | 93a | 340ab[†] | 5g | 27708992a | 41.5a | Solitaries | Unlignified | Wide | Centripetal cambia |
| *Vitis tiliifolia* Humb. and Bonpl. | 73ab | 359a | 22f | 11137322b | 18.4b | Solitaries | Unlignified | Narrow | Tyloses and deposits |
| *Cissus biformifolia* Standl. | 32ef | 293bc | 91b | 1234010c | 3.7efg | Solitaries | Bands | Narrow | |
| *Ipomoea pauciflora* M.M. and G. | 20g | 270cd | 30d | 1168030c | 5.4cdef | Solitaries | Vasicentric and bands | Narrow | Gelatinous fibers |
| *Cydista diversifolia* Miers | 49cd | 251ed | 42bc | 1025263cd | 3.9def | Solitaries | Scarce | Narrow | Furrowed phloem |
| *Pfaffia hookeriana* Greenm. | 39ed | 212e | 36cd | 480738d | 3.6efc | Radial rows | Bands | Narrow | |
| *Tournefortia hirtussima* L. | 64bc | 207e | 21e | 1301218c | 7.6cde | Sheathed by fibers | Bands | Narrow | |
| **Small trees** | | | | | | | | | |
| *Heteropterys laurifolia* A. Juss. | 33ef | 173f | 39e | 539791d | 5.4cde | Solitaries | Scanty | Wide | Gelatinous fibers |
| *Clusia orizabae* Hemsl. | 78ab | 167f | 34e | 970752c | 7.1cde | Solitaries | Scanty | Wide | Gelatinous fibers |
| *Petrea volubilis* L. | 29f | 149f | 106a | 43743e | 0.9g | Radial rows | Scanty | Narrow | |
| *Russelia chiapensis* Lundell | 42ed | 121g | 21f | 636218d | 9.1c | Solitaries | Confluent | Narrow | |
| Liana species | 52.8a | 276.2a | 28.1b | 6293653a | 12.1a | | | | |
| Tree species | 45.1b | 152.9b | 39.2a | 547626b | 5.6b | | | | |

[†]Different letters indicate significant differences at $p \leq 0.05$

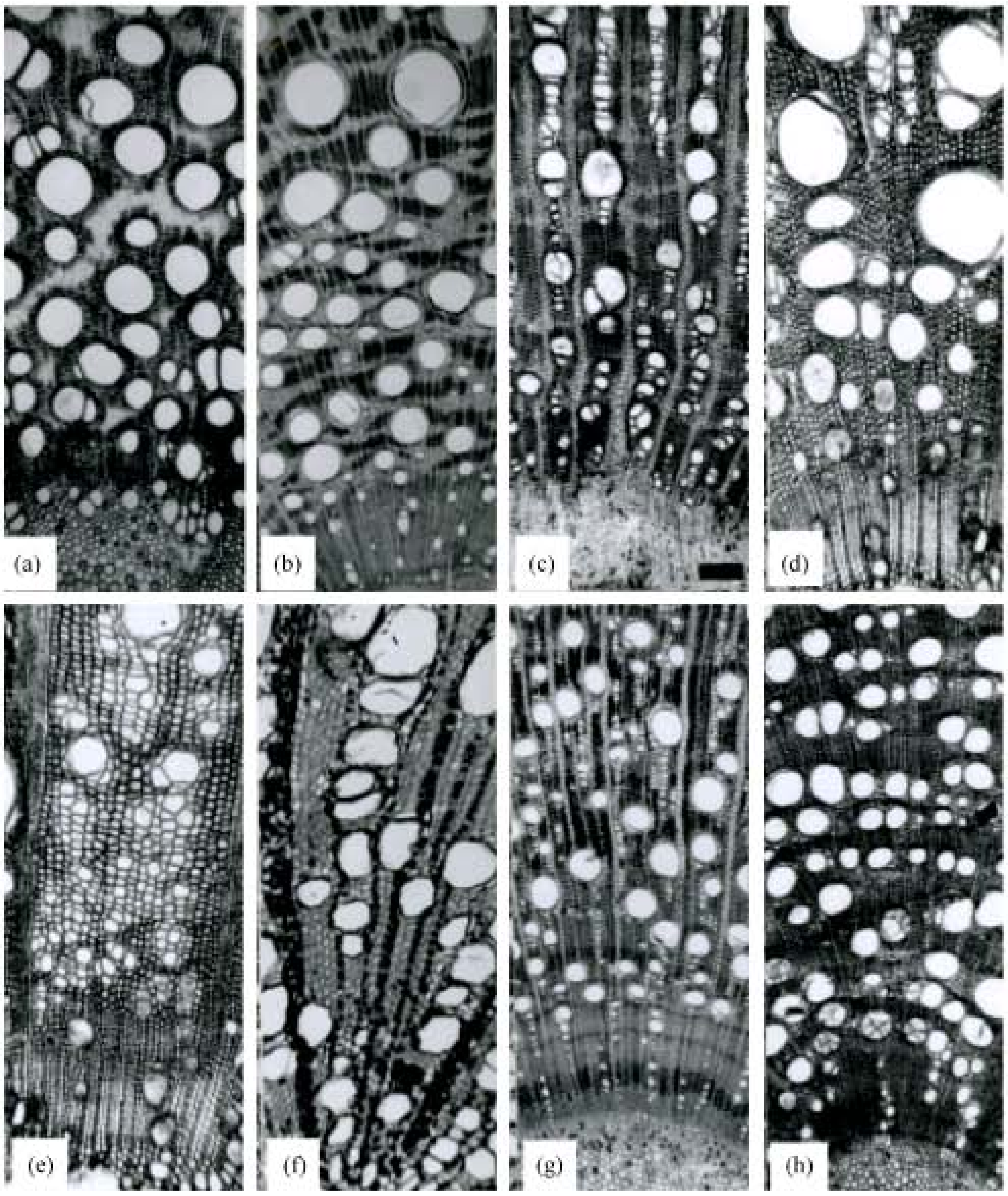

Fig. 1: Differences from pith to vascular cambium of vessels diameter of four lianas and four small tree growing in a tropical forest in Sothern Mexico, (a) *Passiflora ligularis* A. Juss, (b) *Ipomoea pauciflora* M. Martens and Galeotti, (c) *Pfaffia hookeriana* Greenm, (d) *Vitis tiliifolia* Humb. and Bonpl, (e) *Heteropterys laurifolia* A. Juss, (f) *Clusia orizabae* Hemsl, (g) *Petrea volubilis* L., (h) and *Russelia chiapensis* Lundell. Scale = 250 µm

In relation to small trees, the four species showed lower vessel diameters for narrow and wider vessels than the liana species (Table 1). Three species (*Heteropterys laurifolia* A. Juss., *Clusia orizabae* Hemsl. and *Russelia chiapensis* Lundell) showed the lowest diameter values for wider vessels of both plant groups (Fig. 1e, f, h, 3a, b, d). *Petrea volubilis* L. showed the lowest diameter values in narrow vessels that caused the highest vessel frequency (Fig. 1g, 3c).

When liana and tree species were compared as groups, lianas showed a higher diameter in wider vessels and narrow vessels than small tree species (Table 1).

**Relative hydraulic conductivity (RC) and vulnerability to cavitation:** Liana species had higher RC values than the four small tree species (Table 1). A minor vessel diameter caused high vessel frequency, low RC and low vulnerability to cavitation in both groups. *Passiflora ligularis* A. Juss. was the liana species with the biggest RC, but also with the highest vulnerability to cavitation. In contrast, *Petrea volubilis* L. (small tree species) showed the lowest RC and vulnerability to cavitation.

There was a negative significant correlation between diameter of narrow vessels and vessel frequency (Table 2). Narrow vessels had a great influence

Table 2: Correlation Coefficients between vessel diameter and vessel frequency (VF), relative hydraulic conductivity (RC) and vulnerability to cavitation in lianas and small trees

| | Lianas and small trees | | |
|---|---|---|---|
| Vessel | VF | RC | Vulnerability |
| Wide | -0.24 | 0.67* | 0.59* |
| Narrow | -0.58* | 0.71** | 0.76** |

*Correlation coefficient significant at the 0.05 level of probability. **Significance level 0.01

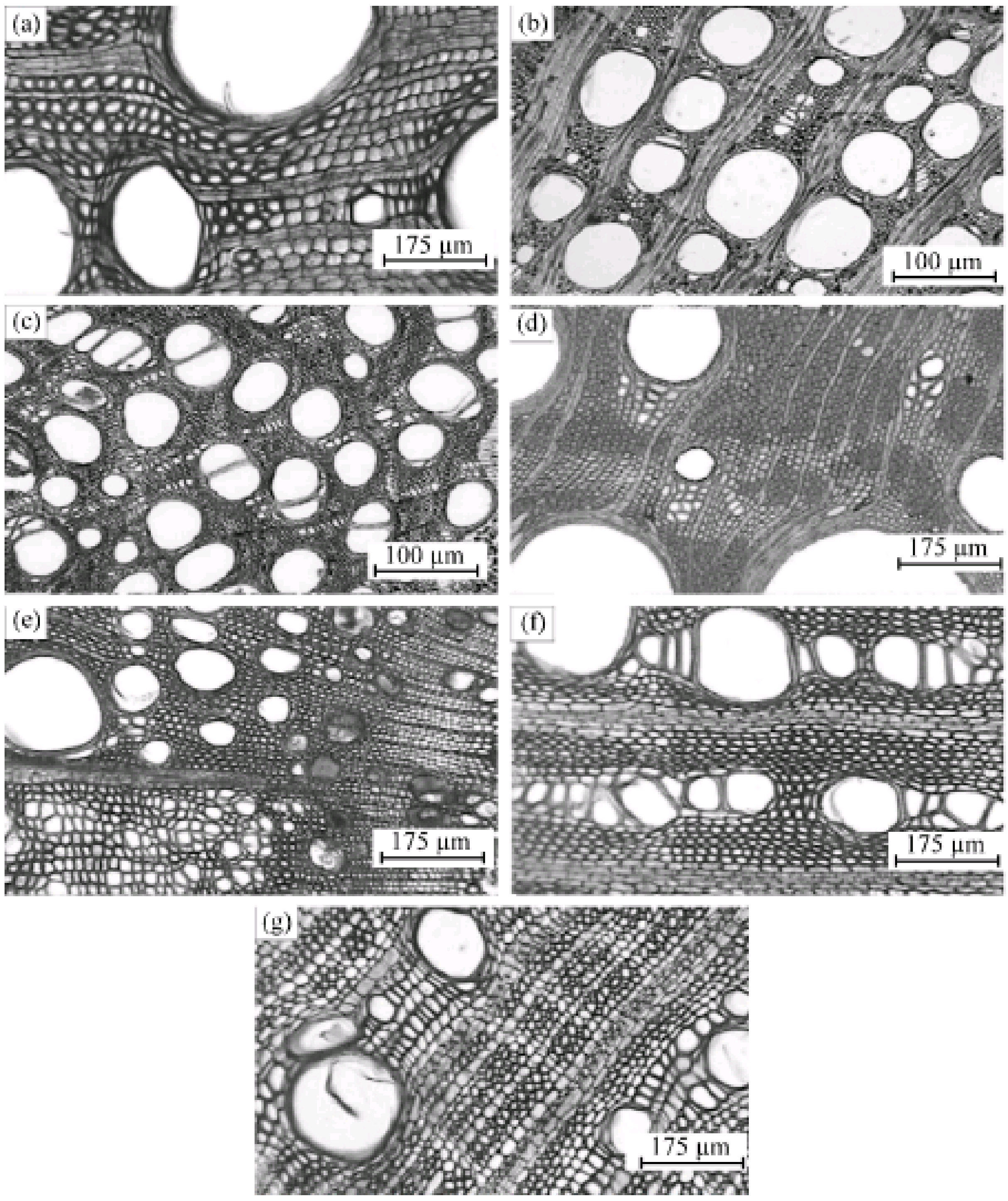

Fig. 2: Patterns of secondary xylem of lianas growing in a tropical forest in southwest Mexico. (a) *Passiflora ligularis* A. Juss., wide and narrow solitary vessels, (b) *Vitis tiliifolia* Humb. and Bonpl., clusters of narrow vessels and wide solitary, (c) *Cissus biformifolia* Standl., narrow vessels in radial rows, (d) *Ipomoea pauciflora* M. Martens and Galeotti, confluent and banded parenchyma, (e) *Cydista diversifolia* Miers, phloem wedge, (f) *Pfaffia hookeriana* Greenm., vessels in radial rows and (g) *Tournefortia hirtussima* L., narrow banded parenchyma

over vessel frequency in lianas and tree species, while large vessel diameters had a lower influence. Both types of vessels had stronger influence over RC and vulnerability to cavitation.

**Anatomical traits of secondary xylem:** Four liana with the larger vessel diameters and four small tree species were compared in Fig. 1 where anatomical differences of both groups were clearly distinctive. Liana species showed mostly solitary vessels with wider diameter on the secondary xylem (Fig. 1-2), except for *Pfaffia hookeriana* Greenm. where vessels were distributed in radial rows (Fig. 1c, 2f). The same solitary distribution of vessels occurred in small tree species, but *Petrea volubilis* also showed wider vessels grouped in radial rows (Fig. 1g, 3c). Narrow vessels were commonly distributed in clusters in the diverse liana species (Fig. 2b-d). Species showed narrower vessels near the pith, increasing vessel diameter abruptly in most species except for *Heteropterys laurifolia* A. Juss. and *Clusia orizabae* Hemsl. (Fig. 1e, f).

Parenchyma is highly diverse in liana species (Table 1, Fig. 1-2). For example, *Ipomoea pauciflora* M. Martens and Galeotti showed vasicentric to confluent parenchyma in irregular bands with crystals surrounded by gelatinous fibers while *Vitis tilifolia* Humb. and Bonpl. presented unlignified parenchyma (Fig. 1b, d, 2b, d). *Cissus biformifolia* presented solitary wider vessels and some of them were included in thin parenchyma bands (Fig. 2c). In *Tournefortia hirtussima* L., solitary wider vessels were sheathed by fibers and distinctive 1-2 cells-wide parenchyma bands occurred (Fig. 2g). *Passiflora ligularis* A. Juss. shows centripetal successive cambia with patches of unlignified parenchyma (Fig. 1a, 2a). *Cydista diversifolia* Miers. had furrowed phloem with lignified or unlignified fibers (Fig. 2e). Rays were narrow in all liana species, except for *Passiflora ligularis* A. Juss. that presented wide rays.

Small tree species also showed solitary distribution of wider vessels while narrow vessels were commonly distributed in clusters (Fig. 3). Some xylem areas of narrow vessels were surrounded by abundant gelatinous fibers and the distinctive phloem wedges in *Heteropterys laurifolia* A. Juss. (Fig. 1e, 3a). *Clusia orizabae* Hemsl. presented solitary wider vessels with angular walls some occluded by tyloses and surrounded by gelatinous fibers (Fig. 1f, 3b). *Petrea volubilis* L. shows a stem flattered with a wider accumulation of xylem in two poles with abundant contents in the vessels lumina (Fig. 3c). Tree species showed few parenchyma cells, except for *Russelia chiapensis* Lundell that presented paratracheal confluent parenchyma (Fig. 3d).

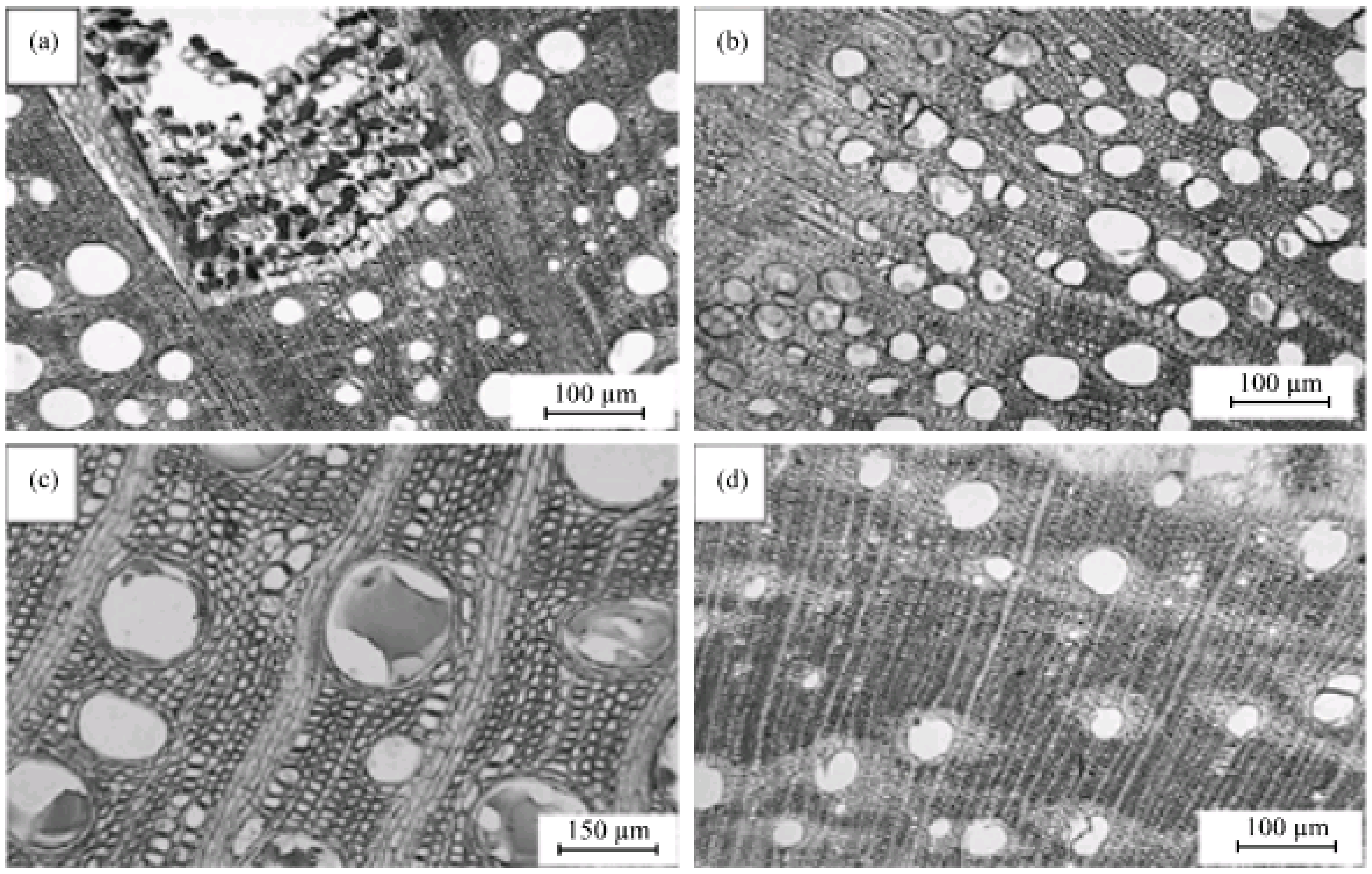

Fig. 3: Patterns of secondary xylem of small tree growing in a tropical forest in southwest Mexico. (a) *Heteropterys laurifolia* A. Juss., phloem wedge, (b) *Clusia orizabae* Hemsl., abundant tyloses, (c) *Petrea volubilis* L., dark-staining deposits occluding vessels lumina and (d) *Russelia chiapensis* Lundell, abundant aliform and confluent parenchyma

## DISCUSSION

The liana and tree species described in the present study that were collected from a tropical forest in Southwest Mexico, showed high heterogeneity in vessel diameter, vessel distribution and anatomical differences on secondary xylem characters (Table 1). Lianas and tree species showed genetic differences in their growth pattern on the secondary xylem that can be related with vessel diameter, vessel frequency, RC and vulnerability to caviation.

Narrow and wider vessels were highly correlated with vessel frequency in both plant groups (i.e., *Cissus biformifolia* Standl and *Petrea volubilis* L.) (Table 1). Both vessel types determined RC, but their diameter dimension was the determinant factor to define a low or high RC in both groups (Table 2).

RC indicates the efficiency of vessels for conducting water and the vulnerability indicates their susceptibility to cavitation in the water column (Carlquist, 1988). Although, wider vessels conduct water more efficiently than narrow vessels, they are highly susceptible to cavitation. In our study, it is evident that lianas species with wider vessel diameters (high RC) are susceptible to cavitation (Table 1), especially if they are growing in natural conditions with variations of environmental elements (i.e., temperature and rainfall). There are several reports suggesting that cavitation occurs on the xylem during the day influenced by variations of stomatal conductance, photosynthesis and water potential (Ewers *et al*., 1991; Salleo *et al*., 1996; Hubbard *et al*., 2001). In consequence, vessels with smaller diameters are an alternative manner for conducting water. If wider vessels are cavitated, narrow vessels are an alternative way for conducting water from roots to leaves by storing and moving water in a radial and tangential direction (Ewers *et al*., 1991; Zimmermann, 2003). Gallenmüller *et al.* (2001) compared two growth form of the liana *Croton pullei* (Euphorbiaceae) in early development stages (free-standing stems)and in well-established plants (flexible-support stems) and plants with flexible stems presented a dense wood type with a major vessel number with wider diameters compared to the free-standing stems for transporting higher water amounts from roots to leaves. A large diameter vessel is essential in longer and taller stems in lianas because water needs to be transported by several meters (>20 m). Zhu and Cao (2009) described and compared three liana species and three tree species in relation to the sapwood density and hydraulic conductivity and as in our study, lianas presented larger vessel diameter and higher hydraulic conductivity than tree species. Even though lianas grow in lower light levels, they have higher growth rates compared to tree species (lianas, 86.4% and trees, 61.5%) (Chen *et al*., 2008). The liana species responded more efficiently to low radiation levels derived of a higher pigment content and they were less photo-inhibited during midday compared to tree species. Andrade *et al*. (2005) compared eight liana and tree species with similar stem diameters of a seasonally dry tropical forest and found that the daily sap flow rate was similar in both groups. In our study, we found clear differences in RC between the lianas and tree species, probably the stem length between lianas and tree was a determinant factor.

Water flow depends on traits such as vessel size and its distribution, but the presence of parenchyma cells is also critical to inverse cavitation, especially for wider and larger vessels (Tyree and Ewers, 1991; Roderick and Berry, 2001). Parenchyma cells are important to refill cavitated vessels when plant is not under adverse growth conditions (Carlquist, 1988). Parenchyma cells also give high flexibility to the stem reducing damage to the vessel elements and sieve cells (Carlquist, 1988). In the current study, the majorities of liana species showed solitary wider vessels, but in several species vessels were sheathed by fibers or parenchyma cells (Table 1). *Ipomoea pauciflora* M. Martens and Galeotti had a vasicentric and banded parenchyma (Fig. 2d). *Passiflora ligularis* A. Juss. with high RC and vulnerability to cavitation presented unlignified parenchyma cells and *Pfaffia hookeriana* Greenm. with low vulnerability shows bands of parenchyma (Fig. 2a, f).

Tree species did not show the same occurrence of parenchyma cells as occurred in lianas (Table 1, Fig. 1, 3). Metcalfe and Chalk (1989) described that abundance of parenchyma do not occur in tree species. In our study, we found that pattern, except for *Russelia chiapensis* Lundell that presented more abundant paratracheal parenchyma cells (Fig. 3c). Apparently, the occurrence of cavitation in narrow vessels in the tree species is lower compared to the liana species with vessels with wider diameters. This makes less susceptible to cavitation to the tree species described in the present study.

Liana and small tree species described in the present study with similar growth habits in the tropical forest located in Southwest Mexico showed different anatomical traits on the secondary xylem and diversity in their vessel diameters, RC and vulnerability to cavitation.

## CONCLUSION

The seven liana species and the four small tree species showed a wider range of vessel diameter and frequency, RC and vulnerability to cavitation. Lianas species showed greater RC and vulnerability to cavitation than the small tree species. Liana species which were more susceptible to cavitation by wider vessels, presented parenchyma cells in diverse forms and distributions. Parenchyma cells were scanty in the small tree species with lower vessel diameters (low susceptibility to cavitation). Both groups of plant species showed anatomical differences in vessel diameter causing variation in their RC and vulnerability to cavitation. Plant species are adapted in diverse forms to maintain high RC by presenting wider vessels (low frequency) and high number of narrow vessels (high frequency) and possibly refilling vessels with parenchyma cells.

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