

## Interspecific variation in xylem vulnerability to cavitation among tropical tree and shrub species

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**Summary** In tropical moist forests, seasonal drought limits plant survival, productivity and diversity. Drought-tolerance mechanisms of tropical species should reflect the maximum seasonal water deficits experienced in a particular habitat. We investigated stem xylem vulnerability to cavitation in nine tropical species with different life histories and habitat associations. Stem xylem vulnerability was scored as the xylem water potential causing 50 and 75% loss of hydraulic conductivity (P50 and P75, respectively). Four shade-tolerant shrubs ranged from moderately resistant (P50 = –1.9 MPa for *Ouratea lucens* Kunth. Engl.) to highly resistant to cavitation (P50 = –4.1 MPa for *Psychotria horizontalis* Sw.), with shallow-rooted species being the most resistant. Among the tree species, those characteristic of waterlogged soils, *Carapa guianensis* Aubl., *Prioria copaifera* Griseb. and *Ficus citrifolia* Mill., were the most vulnerable to cavitation (P50 = –0.8 to –1.6 MPa). The wet-season, deciduous tree, *Cordia alliodora* (Ruiz & Pav.) Oken., had resistant xylem (P50 = –3.2 MPa), whereas the dry-season, deciduous tree, *Bursera simaruba* (L.) Sarg. was among the most vulnerable to cavitation (P50 = –0.8 MPa) of the species studied. For eight out of the nine study species, previously reported minimum seasonal leaf water potentials measured in the field during periods of drought correlated with our P50 and P75 values. Rooting depth, deciduousness, soil type and growth habit might also contribute to desiccation tolerance. Our results support the functional dependence of drought tolerance on xylem resistance to cavitation.

**Keywords:** drought tolerance, hydraulic conductivity, tropical rainforest, water potential, water stress, xylem cavitation.

### Introduction

In terrestrial plants, sustained xylem water transport is critical for physiological functioning and survival. Xylem hydraulic conductance ( $k$ ,  $\text{kg s}^{-1} \text{MPa}^{-1}$ ) is usually reduced by water stress. Strong evidence indicates that increased tension in the

water column causes cavitation of the xylem conduits through the replacement of functional conduit water with air (Sperry and Tyree 1990, Cochard et al. 1992, 1994). Tyree et al. (2003) reported that loss of xylem conductance in the range of 50 to 75% can induce severe stress and that losses in excess of 80% can cause death. Thus, the relationship between increased xylem tension and the loss of  $k$ , known as the vulnerability curve, might be useful in predicting the ecological boundaries for a particular species. For example, vulnerability curves of Sonoran desert species show that riparian species may be less capable of conducting water at low water potentials than non-riparian species (Pockman and Sperry 2000). This suggests that insight into plant distributions can be obtained from the xylem cavitation vulnerability during periods of water stress.

Great species richness and high precipitation characterize tropical rain forests, but both vary spatially. Tree and shrub distributions in the tropics are associated with environmental gradients (Gentry 1992, Levin 1992, Condit et al. 2000, Harms et al. 2001). For example, variation in total rainfall and its seasonality play a deterministic role in the composition and structure of tropical plant communities (see Gentry 1988, Condit et al. 1996, Gilbert et al. 2001). There is increasing evidence that hydraulic limitations during periods of water stress constrain physiological processes, such as gas exchange, at the leaf level (Sperry and Tyree 1988, 1990, Brodribb and Feild 2000, Brodribb et al. 2002, 2003, Santiago et al. 2004). For example, leaf-area-based photosynthetic rates ( $A_{\text{area}}$ ) were correlated to leaf specific hydraulic conductivity ( $K_L$ ) among 20 canopy tree species from central Panama (Santiago et al. 2004). Consequently, the spatiotemporal variation in soil water availability and its effect on hydraulic properties determines photosynthetic capacity (Brodribb and Field 2000), a critical factor in determining species distribution. Therefore, drought resistance, including limitations to water transport during water stress, may be a factor determining species distributions.

In this study we investigated interspecific variation in xylem hydraulic capacity in relation to water stress. We hypothesized

that the hydraulic operational limits of a species should correspond to the minimum leaf water potential experienced during periods of drought. In particular, we surveyed xylem vulnerability to cavitation and  $K_L$  in relation to the minimum seasonal leaf water potential ( $\Psi_{\text{leaf,min}}$ ) reported for nine tropical species with different life histories and habitat associations. We compared three light-demanding species with six shade-tolerant species, two tree species from waterlogged soils with six species from well-drained soils and one dry-season deciduous canopy tree with one wet-season deciduous species. We discuss whether knowledge of hydraulic limitations imposed by seasonal drought can contribute to our understanding of distribution and habitat specialization of tropical tree and shrub species.

## Materials and methods

### Study site

Measurements of xylem vulnerability were conducted on Barro Colorado Island (BCI), Smithsonian Tropical Research Institute (9°7.5' N, 79°52' W), in central Panamá and at the University of Utah, Salt Lake City (SLC), Utah, USA. Vegetation on BCI is semi-evergreen, tropical moist forest, with about 10% of the canopy trees becoming leafless during the dry season (Leigh et al. 1996). Mean annual rainfall is 260 cm with a pronounced 3–4 month dry season from mid-December to mid-April (Windsor 1990). Detailed descriptions of the BCI flora, geology and climate can be found in Croat (1978) and Leigh et al. (1996).

### Study species and plant material

Five tree and four shrub species were studied (Table 1). Among the trees, *Prioria* and *Carapa* are dominant components of seasonally inundated habitats from Nicaragua to northern South America, but can also be found in non-inundated habi-

tats (Condit et al. 1993, T.A. Kursar, personal observation). The other tree species, *Cordia*, *Ficus* and *Bursera* are conspicuous members of tropical rain forests, with broad geographical distributions, although *Bursera* appears to be better represented in tropical dry forests (Gillespie et al. 2000). *Bursera* and *Cordia* are deciduous trees, dropping all their leaves during the dry and wet seasons, respectively. The shrub species are common in the BCI understory but differ in rooting depth (Table 1). Seedlings of *Prioria* (SLC) and *Carapa* (BCI) were raised from seeds in pots. All other plant samples were collected from around the BCI laboratory clearing, or from the adjacent peninsulas of Buena Vista and Gigante. Samples from the four shrubs were collected in the understory, and from *Cordia*, *Ficus* and *Bursera* in light gaps.

### Vulnerability curves

A vulnerability curve describes the relationship between %loss of hydraulic conductivity (PLC) and xylem water potential ( $\Psi_{\text{xylem}}$ ). Vulnerability curves were measured on stem segments of all species by the air-injection method, as described by Sperry and Saliendra (1994). Xylem vulnerability curves were measured between 1992 and 1994, with the exception of *Carapa* whose curves were measured in 2000. For *Prioria* and *Carapa*, potted seedlings were brought to the laboratory and 0.2-m stem segments were cut underwater. The segments were mounted in a double-ended pressure chamber with both ends protruding. The proximal end was attached via plastic tubing to a suspended water bag and the distal end to an electronic balance in order to calculate  $k$  as the flux of water through a stem section under low pressure, about  $2 \times 10^{-3}$  MPa. Once  $k$  was measured, the segment was perfused with water at 0.1 MPa for 10 min to displace air from most embolized vessels and maximum hydraulic conductance ( $k_{\text{max}}$ ) was determined. Following this, the stem segment was pressurized with air for 20 min, the pressure was then lowered and the segment

Table 1. Species name, family, growth form, habitat, light requirement, unit sampled and root depth:plant height of studied species. Nomenclature follows Missouri Botanical Garden (2004). Abbreviations: RD/PH = root depth/plant height; US = understory shrub; ECT = evergreen canopy tree; DDCT = dry-deciduous canopy tree; WDCT = wet-deciduous canopy tree; TMF = tropical moist forest; SFF = seasonally flooded forest; TDF = tropical dry forest; B = branches from saplings in the forest; S = seedlings grown in pots; and nd = not determined.

| Species  | Family       | Growth form | Habitat | Light requirement | Unit sampled             | RD/PH (m m <sup>-1</sup> ) |
|--|--------------|-------------|---------|-------------------|--------------------------|----------------------------|
| <i>Ouratea lucens</i> Kunth. Engl.                           | Ochnaceae    | US          | TMF     | Shade             | B at 1.5 m               | 1.1/1.4 <sup>2</sup>       |
| <i>Swartzia simplex</i> (Sw.) Spreng.                        | Fabaceae     | US          | TMF     | Shade             | B at 1.5 m               | 1.4/1.3 <sup>2</sup>       |
| <i>Psychotria horizontalis</i> Sw.                           | Rubiaceae    | US          | TMF     | Shade             | B at 1.5 m               | 0.3/2.0 <sup>3</sup>       |
| <i>Hybanthus prunifolius</i> (Humb. & Bonpl.) Schultze-Menz. | Violaceae    | US          | TMF     | Shade             | B at 1.5 m               | 0.6/2.0 <sup>3</sup>       |
| <i>Prioria copaifera</i> Griseb.                             | Fabaceae     | ECT         | SFF     | Shade             | S main axis <sup>1</sup> | 0.5/0.8 <sup>4</sup>       |
| <i>Carapa guianensis</i> Aubl.                               | Meliaceae    | ECT         | SFF     | Shade             | S main axis <sup>1</sup> | 0.4/0.7 <sup>4</sup>       |
| <i>Ficus citrifolia</i> Mill.                                | Moraceae     | ECT         | TMF     | Gap               | B at 2.0 m               | nd                         |
| <i>Bursera simaruba</i> (L.) Sarg.                           | Burseraceae  | DDCT        | TDF     | Gap               | B at 2.0 m               | nd                         |
| <i>Cordia alliodora</i> (Ruiz & Pav.) Oken.                  | Boraginaceae | WDCT        | TMF     | Gap               | B at 2.0 m               | nd                         |

<sup>1</sup> Seedlings were about 6 to 12 months old.

<sup>2</sup> O.R. Lopez and T.A. Kursar, unpublished data.

<sup>3</sup> Becker and Castillo 1990.

<sup>4</sup> Determined in 6-month-old seedlings growing in 0.9-m<sup>3</sup> pots; Lopez and Kursar 2003.

allowed to equilibrate before being re-measured. This procedure was repeated at progressively increasing pressures (usually 0.25 to 1.0 MPa) until the PLC was near 100%. The PLC at each pressure ( $= \Psi_{\text{xylem}}$ ) was calculated as:

$$\text{PLC} = 100 \times (1 - (k/k_{\text{max}})) \quad (1)$$

Vulnerability curves of the remaining species were obtained from one to three branches for each applied pressure using a single-ended 1.2-m-long pressure chamber, as described by Cochard et al. (1992). After pressurization, the branch was removed and 6–10 stem segments 0.05 m long and 2.5–6.5 mm in diameter were cut underwater 0.8 m from the cut end. Stem segments were then fitted to a water-tubing system and the corresponding  $k$  measured, as described previously. Stem segments were perfused with water at 0.1 MPa and then  $k_{\text{max}}$  was measured. Filtered (0.2  $\mu\text{m}$ ), degassed water was used in all experiments.

#### *Comparisons of vulnerability curves using other methods*

Because our study of xylem vulnerability extended over 8 years, we considered it appropriate to compare the reliability of three methods (i.e., air-dehydration method versus air-injected method and air-injected method versus centrifugal-force method). For the air-dehydration method, leaf-bearing branches of *Cordia* were excised, brought to the laboratory and allowed to air dry. The leaf water potential ( $\Psi_{\text{leaf}}$ ) of the branch was measured in 2–3 leaves by the Scholander pressure chamber technique. The branch was then enclosed in a plastic bag for 1 h to allow  $\Psi$  to equilibrate throughout. After opening the bag to re-measure  $\Psi_{\text{leaf}}$ , 6–10 stem segments of 0.05 m were cut underwater 0.8 m from the cut end and fitted to a water-tubing system to measure  $k$  and  $k_{\text{max}}$ . The procedure was repeated with a series of branches that had been air-dried to a range of  $\Psi_{\text{leaf}}$  values. The PLC at a xylem pressure potential ( $\Psi_{\text{xp}}$ ) at equilibrium (i.e., after being placed in a bag) was calculated as described previously. For comparison with the centrifugal-force technique, *Carapa* stem segments were excised underwater from potted seedlings at BCI, enclosed in a plastic bag and brought to Salt Lake City, UT within 60 h. Four 0.15-m stem segments were cut underwater and  $k$  and  $k_{\text{max}}$  measured as described previously. Following this, the segments were centered on a centrifuge rotor and centrifuged along their long axis at 15 °C for 4 min. Stem segments were subjected to centrifugal forces corresponding to  $-0.5$ ,  $-0.75$ ,  $-1.0$ ,  $-1.5$  and  $-2.0$  MPa. After centrifugation, the stems were fitted into a water-tubing system and  $k$  measured for each segment. The process was repeated until PLC was nearly 100%. The PLC for each segment was calculated as previously described.

#### *Native state xylem embolism, vessel length and other parameters*

Native state embolism refers to the PLC that occurs as a consequence of the water stress experienced by an intact plant in situ. Knowledge of vessel length is required to determine the native state xylem embolism. If the xylem conduits are under

tension, cutting a branch causes the water column to retreat into the vessel lumina until an inter-vessel membrane is encountered. Thus, PLC is highest near the excision point—because most of the vessels are air-filled—and decreases distally. For this reason, stems collected in the field or from potted seedlings were always re-cut underwater before PLC was estimated.

To determine the maximum length of xylem conduits, at least one to two leaf-bearing branches (about 1.3 m) of five species (*Cordia*, *Psychotria*, *Hybanthus*, *Ouratea* and *Swartzia*) were excised in the field in the morning (between 0700 and 0900 h), immediately enclosed in a plastic bag to prevent water loss from transpiration and taken to the laboratory. The branch was left in the bag for 15 min to allow the xylem sap to retreat from the excision point to the full length of the vessels. Then, stem segments were cut under water at progressive distances from the excision point, and  $k$  measured. Following this, stem segments were perfused with water at 0.1 MPa to remove embolism and  $k_{\text{max}}$  measured and PLC calculated. Maximum vessel length was estimated from the regression of PLC against distance from the excision point (Cochard et al. 1994). The PLC decreased linearly with distance from the excised point, and maximum vessel lengths were 0.5 m for *Cordia* and *Psychotria*, 0.6 m for *Hybanthus*, and 0.8 m for *Ouratea* and *Swartzia*.

During February and March of the 1993 dry season, native state embolism was measured for the same five species. At least two branches per species were cut in the morning and enclosed in a plastic bag and immediately brought to the lab. About ten 0.05-m segments of each branch were cut under water, beginning about 0.8 m distal from the excision point, and the native state  $k$  measured. Next, the segments were perfused to refill embolized conduits,  $k_{\text{max}}$  measured and the native state PLC calculated.

Seasonal  $\Psi_{\text{leaf,min}}$  values for eight of the nine study species were obtained from previously published studies conducted on individuals growing on sites similar to those described for our study species (see Tables 1 and 4). All of the published seasonal  $\Psi_{\text{leaf,min}}$  values had been measured with a Scholander pressure chamber (PMS Instruments, Corvallis, Oregon). Leaf specific conductivity ( $K_L$ ) was calculated by first standardizing  $k_{\text{max}}$  by stem length ( $K_h$ ) and then by the total leaf area distal to the measured stem segment. The maximum specific conductivity ( $K_S$ ) was calculated by dividing  $K_h$  by total stem cross-sectional area (i.e., including the pith). Thus, our  $K_S$  values might underestimate wood specific conductivity. Huber values represent the ratio of stem cross-sectional area to total leaf area.

#### *Statistical analysis*

To describe the relationship between PLC and  $\Psi_{\text{xylem}}$ , a Weibull function was fitted to the vulnerability curve data. The Weibull function was chosen because it provided a better fit for species with vulnerability curves that were not strongly sigmoidal (e.g., *Psychotria*). The Weibull function is given as:

Table 2. Means ( $\pm 1$  SE) of parameter estimates from fitting the Weibull function to the vulnerability curve. Parameter means followed by the same letter were not significantly different (Tukey-Kramer HDS test for all group comparisons). Abbreviations:  $b = \Psi_{\text{xylem}}$  at which 63% loss of conductivity occurred;  $c$  = slope of the vulnerability curve at its most negative inflection; P50 and P75 =  $\Psi_{\text{xylem}}$  for 50 and 75% loss of conductivity, respectively; and  $n$  = number of samples.

| Species           | Parameter estimates |              |               |               |     |
|-------------------|---------------------|--------------|---------------|---------------|-----|
|                   | $b$                 | $c$          | P50           | P75           | $n$ |
| <i>Ouratea</i>    | 2.6(0.1) c          | 1.3 (0.3) a  | -1.9 (0.1) b  | -3.3 (0.2) b  | 10  |
| <i>Swartzia</i>   | 3.5 (0.2) d         | 1.9(0.3) ab  | -2.8 (0.2) c  | -4.1 (0.2) c  | 9   |
| <i>Hybanthus</i>  | 3.7 (0.2) d         | 1.0 (0.3) a  | -2.6 (0.1) c  | -5.1 (0.2) d  | 9   |
| <i>Psychotria</i> | 4.8 (0.1) e         | 2.7 (0.3) b  | -4.1 (0.1) e  | -5.5 (0.2) d  | 10  |
| <i>Bursera</i>    | 1.0 (0.2) a         | 2.3 (0.3) ab | -0.8 (0.1) a  | -1.2 (0.2) a  | 8   |
| <i>Carapa</i>     | 1.1 (0.2) ab        | 1.0 (0.3) a  | -0.8 (0.1) a  | -1.4 (0.2) a  | 8   |
| <i>Prioria</i>    | 1.7 (0.2) abc       | 2.1 (0.4) ab | -1.4 (0.2) ab | -2.0 (0.2) a  | 4   |
| <i>Cordia</i>     | 3.5 (0.1) d         | 5.8 (0.3) d  | -3.2 (0.1) cd | -3.7 (0.2) bc | 10  |
| <i>Ficus</i>      | 1.7 (0.1) b         | 4.2 (0.3) c  | -1.6 (0.1) b  | -1.9 (0.2) a  | 10  |

$$\text{PLC} = 100 - \frac{100}{\exp(-\Psi_{\text{xylem}}/b)^c} \quad (2)$$

where  $b$  and  $c$  are parameters representing the shape and slope of the curve. The parameter  $b$  indicates the  $\Psi_{\text{xylem}}$  at which 63% loss of conductivity has occurred, whereas  $c$  determines only the slope of the curve at its most negative inflection. Thus a large  $b$  means that the xylem is less vulnerable to cavitation. We also calculated the  $\Psi_{\text{xylem}}$  for 50 and 75% loss of conductivity, hereafter denoted as P50 and P75, respectively. Four to 10 vulnerability curves per species were fitted. Species differences were tested by one-way ANOVA on all parameters (i.e.,  $b$ ,  $c$ , P50 and P75). An a posteriori Tukey-Kramer HDS test for all comparisons was conducted on the parameter means and on species means of  $K_L$  and  $K_S$ . Parameter variances across species were tested for homogeneity by an O'Brien test. A Wilcoxon two-sample test was used to compare parameter means between the different techniques. Linear regression analysis was used to examine the relationship between P50 and P75 with the maximum hydraulic conductivity in relation to total leaf area and the minimum seasonal water potential and to determine the maximum xylem vessel length. In the latter case, distance from the excised point ( $d$ ) was log transformed as the natural logarithm ( $\ln$ ) of distance plus one ( $\ln(d + 1)$ ). All statistics were performed with the statistical software JMP version 3.2.1 (SAS Institute, Cary, NC).

## Results

### Vulnerability curves, parameter estimates and minimum seasonal water potentials

The study species differed with respect to all parameter estimates from fitting the Weibull function to the vulnerability data ( $b$   $F_{8,69} = 74.7$ ,  $c$   $F_{8,69} = 29.2$ , P50  $F_{8,69} = 66.2$ , P75  $F_{8,69} = 86.6$ ,  $P < 0.0001$ , ANOVA, Table 2). Vulnerability curves ranged from vulnerable, P50 = -0.8 MPa and P75 = -1.2 MPa in *Bursera* and *Carapa*, to quite resistant, P50 = -4.1 MPa and P75 = -5.5 MPa in *Psychotria* (Figure 1). The Tukey-Kramer HSD tests for all comparisons revealed species-specific differ-

ences in the mean values of the Weibull parameters (Table 2). For example, among the species, the understory shrub *Psychotria* was the least vulnerable to cavitation, requiring a mean xylem tension of -4.1 MPa to cause a 50% loss of conducti-

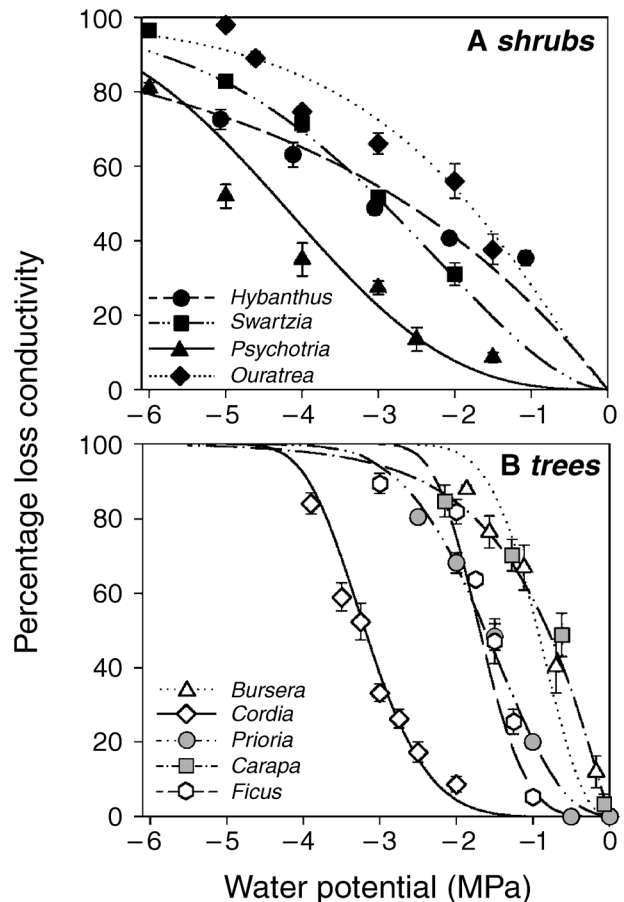


Figure 1. Vulnerability of xylem to cavitation in shrub (A) and tree (B) species, presented as the percentage loss of conductivity with decreasing xylem water potential. Gray symbols represent the two species from seasonally flooded forests. See Table 2 for comparisons of parameter estimates from the Weibull function fitting.

ity. In contrast, the seasonally flooded (swamp) forest species, *Prioria* and *Carapa*, and the dry-deciduous, tropical dry forest species *Bursera* were the most vulnerable to cavitation (Table 2). The slope of the vulnerability curve at its most negative inflection (*c* parameter) also differed significantly among species, with two of the shrubs, *Ouratea* and *Hybanthus*, and one tree, *Carapa*, having quite shallow vulnerability curves (*c* = 1.3; Table 2, Figure 1) and two trees, *Cordia* and *Ficus*, having steep vulnerability curves (*c* = 4.2; Table 2, Figure 1).

Regardless of growth form, species with similar P50 values had vulnerability curves with different slopes. For example, the shade-tolerant shrub *Ouratea* had a shallow vulnerability curve (*c* = 1.3), and its P50 was similar to that of *Ficus*, a tree with a steep vulnerability curve (*c* = 4.2; see Figure 1, Table 2). Similarly, the shade-tolerant shrub, *Swartzia*, had a shallow vulnerability curve (*c* = 1.9) and a P50 similar to that of *Cordia*, a tree with a steep vulnerability curve (*c* = 5.8; see Figure 1, Table 2). Such species-specific differences in vulnerability curve slopes (*c* parameter) might be related to the cavitation resistance of xylem elements and their distribution per cross-sectional area. A high *c* might indicate a fairly uniform distribution of xylem elements with similar vulnerabilities, whereas a low *c* could suggest the presence of xylem that, relative to P50, is highly resistant. Although, in *Cordia* the air-injection and air-dehydration techniques produced relatively similar vulnerability curves, parameters *c* and P50 were significantly different (Figure 2; Table 3). In contrast, in *Carapa* no differences were found between curves generated using the air-dehydration or the centrifugal-force technique (Figure 2; Table 3).

Published seasonal  $\Psi_{\text{leaf,min}}$  values for eight of the nine study species range from high to very low (Table 4). For example,

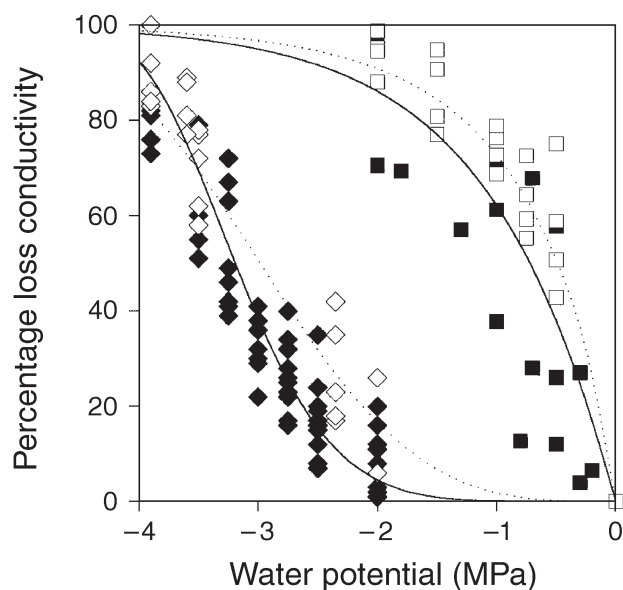


Figure 2. Comparison of vulnerability curves generated by air-injection (AI), air-dehydration (AD) and centrifugal-force (CF) techniques. Symbols: ■ = *Carapa* AI; □ = *Carapa* CF; ◆ = *Cordia* AI; and ◇ = *Cordia* AD. Refer to Table 3 for mean comparison of parameter estimates obtained by the three methods.

Table 3. Comparisons of the means ( $\pm 1$  SE) for the parameters obtained from vulnerability curves using the air-injection, air-dehydration and centrifugal-force techniques. Asterisks indicate  $P < 0.05$  between the two techniques (Wilcoxon 2-sample test). See Table 2 for abbreviations of parameter estimates.

| Technique         | Parameter estimates |            |             |            |
|-------------------|---------------------|------------|-------------|------------|
|                   | <i>b</i>            | <i>c</i>   | P50         | P75        |
| <i>Cordia</i>     |                     |            |             |            |
| Air injection     | 3.5 (0.1)           | 5.8 (0.5)* | -3.2 (0.1)* | -3.7 (0.1) |
| Air dehydration   | 3.2 (0.1)           | 4.2 (0.3)* | -2.9 (0.1)* | -3.5 (0.1) |
| <i>Carapa</i>     |                     |            |             |            |
| Air injection     | 0.7 (0.1)           | 0.8 (0.1)  | -0.4 (0.1)  | -1.0 (0.1) |
| Centrifugal force | 1.4 (0.3)           | 1.3 (0.1)  | -1.0 (0.2)  | -1.9 (0.3) |

the dry season deciduous tree *Bursera*, experiences a minimum water potential of -1.6 MPa (Brodribb et al. 2002), whereas the shallowly rooted understory shrub species *Hybanthus* and *Psychotria* sustain water potentials as low as -3.4 and -4.6 MPa, respectively (Tobin et al. 1999). The wet-soil trees and deeply rooted understory shrubs show intermediate values ranging from -1.3 to -3.3 MPa (Table 4). Interestingly, the wet-season deciduous tree *Cordia* sustains seasonal  $\Psi_{\text{leaf,min}}$  values as low as -3.7 MPa. The variation in seasonal  $\Psi_{\text{leaf,min}}$  values for eight of the nine study species was positively correlated with our estimated P50 and P75 values ( $r^2 = 0.96$ ,  $P < 0.0001$  and  $r^2 = 0.85$ ,  $P < 0.005$ , respectively; Figure 3).

*Native state embolism,  $K_L$ ,  $K_S$  and Huber values*

Native state embolism in *Cordia* and the four shrub species was moderate during the 1993 dry season, ranging from 19.3% in *Swartzia* to 35.3% in *Ouratea* (Table 3). Based on the published seasonal  $\Psi_{\text{leaf,min}}$  values for eight of the nine study species and the parameter estimates from the Weibull function, we predicted the native percentage of embolism. Previous reports have shown that pressure chamber measurements of transpiring leaves tend to overestimate stem xylem tension (cf. Bucci et al. 2004). Thus, the predicted native embolism values were

Table 4. Minimum seasonal leaf water potential ( $\Psi_{\text{leaf,min}}$ ) with its referenced sources, native state embolism ( $\pm 1$  SE) and estimated embolism. Estimated embolism was calculated based on the estimates from the Weibull function and the seasonal  $\Psi_{\text{leaf,min}}$  for each species. Letters: a = Lopez 2002; b = Brodribb et al. 2002; c = Borchert 1994; and d = Tobin et al. 1999.

| Species           | Seasonal $\Psi_{\text{leaf,min}}$ (MPa) | Native state embolism (%) | Estimated embolism (%) |
|-------------------|---|---------------------------|------------------------|
| <i>Prioria</i>    | -1.7 a                                  | nd                        | 87.8                   |
| <i>Carapa</i>     | -1.3 a                                  | nd                        | 69.3                   |
| <i>Bursera</i>    | -1.6 b                                  | nd                        | 97.5                   |
| <i>Cordia</i>     | -3.7 c                                  | 21.6 (2.1)                | 99.7                   |
| <i>Psychotria</i> | -4.6 d                                  | 21.2 (2.1)                | 92.5                   |
| <i>Hybanthus</i>  | -3.4 d                                  | 31.6 (2.5)                | 60.1                   |
| <i>Ouratea</i>    | -1.7 d                                  | 35.3 (2.1)                | 57.2                   |
| <i>Swartzia</i>   | -2.9 d                                  | 19.3 (5.2)                | 79.3                   |

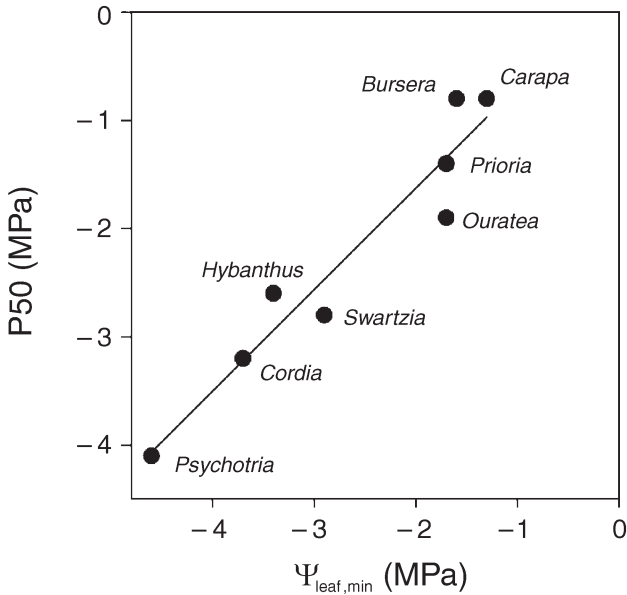


Figure 3. Correlation between P50 and published minimum seasonal leaf water potential ( $\Psi_{\text{leaf,min}}$ ) ( $r^2 = 0.96$ ,  $P < 0.0001$ ). No data on  $\Psi_{\text{leaf,min}}$  were reported for *Ficus*.

higher than those obtained in the field during the 1993 dry season and those expected from the vulnerability curves (Table 3). The degree of native state embolism in five of the study species did not agree with either the P50 or P75 or the seasonal  $\Psi_{\text{leaf,min}}$  previously reported for those species.

Leaf specific hydraulic conductivity was, on average, 5× greater for the three light-demanding trees than for the shade-tolerant species (Figure 4). The gap species *Cordia* and *Bursera* had significantly higher  $K_L$  than the wet-soil species *Prioria*, *Carapa* and *Ficus* and the shade-tolerant shrubs (all pairs comparisons Tukey-Kramer HSD,  $Q = 3.05$ ,  $\alpha = 0.05$ ; Figure 4). Similarly,  $K_S$  in the gap species was on average 2.5× higher than in the rest of the species, and among the shade-tolerant shrubs species *Psychotria* had significantly lower  $K_S$  than *Swartzia* (all pairs comparisons Tukey-Kramer HSD,  $Q = 3.04$ ,  $\alpha = 0.05$ , data not shown). Although, no relationship between  $K_L$  or  $K_S$  and P50, P75 and the seasonal  $\Psi_{\text{leaf,min}}$  was found, the leaf area to sapwood area ratio ( $A_L:A_S$ ), which could be regarded as the proportion of transpirational demand to xylem conducting capacity, was negatively related to both P50 and the seasonal  $\Psi_{\text{leaf,min}}$  reported for seven of the study species ( $r^2 = 0.68$ ,  $P < 0.04$  and  $r^2 = 0.61$ ,  $P < 0.01$ , respectively; Figure 5; no  $K_S$  was determined for *Ficus* or *Prioria*). Contrary to the patterns observed in  $K_L$  and  $K_S$ , understory species had Huber values 1.5 times greater than gap species, indicating greater allocation to xylem conductive area per unit of leaf area ( $F_{1,148} = 11.15$ ,  $P < 0.001$ , ANOVA).

**Discussion**

The ability of xylem conduits to sustain water transport during seasonal droughts is critical for plant growth and survival (Condit et al. 1996, Lopez 2002, Engelbrecht and Kursar 2003, Tyree et al. 2003, Santiago et al. 2004) Consequently,

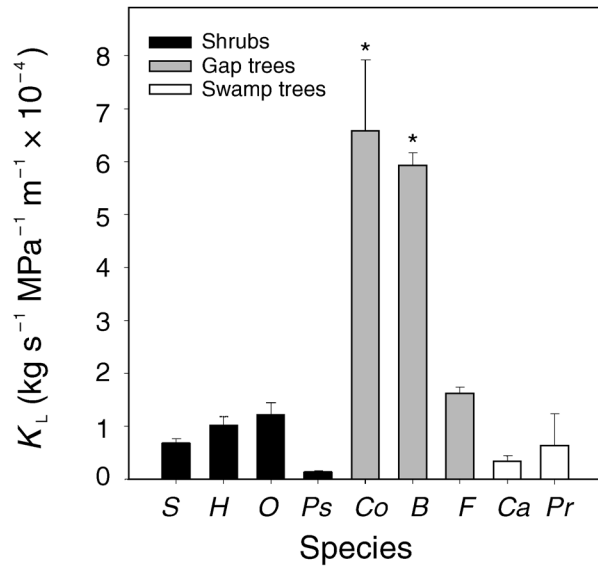


Figure 4. Leaf-area-specific conductivity ( $K_L$ ) of all species ( $\pm 1$  SE). *Cordia* and *Bursera* differed significantly from the other the species (Tukey-Kramer HSD, all means comparisons test). Shrub and tree samples were collected from plants in the understory and light gaps, respectively, except *Carapa* and *Prioria*, which were raised in the greenhouse. Species abbreviations: S = *Swartzia*; H = *Hybanthus*; O = *Ouratea*; Ps = *Psychotria*; Co = *Cordia*; B = *Bursera*; F = *Ficus*; Ca = *Carapa*; and Pr = *Prioria*.

variation in drought severity during the dry season plays a deterministic role in delimiting the ecological boundaries and distribution of tree species in tropical rain forests. Our data on tropical shrub and tree species contribute to the increasing evidence of a close relationship between the physiological limits

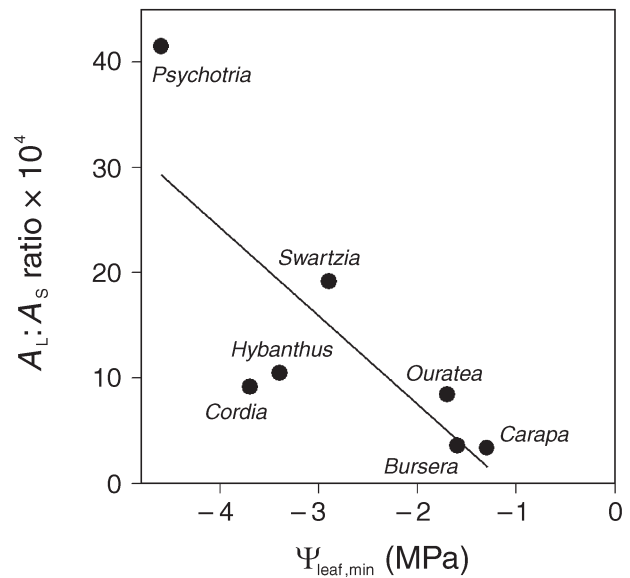


Figure 5. Correlation between leaf area:sapwood area ratios ( $A_L:A_S$ ) and published minimum seasonal leaf water potential ( $\Psi_{\text{leaf,min}}$ ) for seven of the study species ( $r^2 = 0.61$ ,  $P < 0.001$ , ANOVA). Data on seasonal  $\Psi_{\text{leaf,min}}$  and diameter specific conductivity were not determined for *Ficus* and *Prioria*, respectively.

of xylem water transport and the minimum water potential that species experience in their habitat. Among the most vulnerable species were the dry-deciduous forest species *Bursera* and the swamp tree *Carapa*, both with P50 values of  $-0.8$  MPa. At the other extreme, the shrub species *Psychotria* had a P50 value of  $-4.1$  MPa, similar to the value of  $-3.9$  MPa reported for *Artemisia tridentata* ssp. *tridentata*, the dominant shrub in the Great Basin Desert in Utah (Kolb and Sperry 1999). Thus, some rainforest plants have highly resistant xylem. Such a broad range of vulnerabilities is consistent with observations of xylem vulnerability among species of tropical dry forests and savanna in Venezuela and 28 tree species from two aseasonal (wet) lowland tropical forests in Borneo and 12 tree species from BCI and (Sobrado 1997, Tyree et al. 1998). Nevertheless, tree species from the two aseasonal Bornean forests were, on average, substantially more vulnerable to cavitation (mean P50 =  $-0.85$  MPa; Tyree et al. 1998) than the species in our study (average P50 =  $-2.1$  MPa), with those from dry forests being the most resistant (mean P50 =  $-2.5$  MPa; Brodribb et al. 2003). Together, these results illustrate the adaptive significance of xylem resistance to cavitation in relation to the severity of the dry season (cf. Maherali et al. 2004). Within a community type (e.g., wet and dry forest), however, other factors such as root depth and deciduous habit, may also be critical in determining drought tolerance.

For eight of the nine study species, variation in resistance to xylem cavitation was consistent with their seasonal  $\Psi_{\text{leaf,min}}$ . During a severe dry season on BCI, Tobin et al. (1999) reported midday  $\Psi_{\text{leaf}}$  of  $-3.4$  and  $-4.6$  MPa for established individuals (1–2 m tall) of the shallowly rooted shrubs *Hybanthus* and *Psychotria*, respectively. Such negative  $\Psi_{\text{leaf}}$  values corroborate our findings of P75 =  $-5.1$  and  $-5.5$  MPa *Hybanthus* and *Psychotria*, respectively. Similarly, the relatively high midday  $\Psi_{\text{leaf}}$  values of  $-2.9$  and  $-1.7$  MPa reported for the deeply rooted understory shrubs *Swartzia* and *Ouratea*, respectively, during the same dry season, are congruent with the relatively high vulnerability to cavitation that we found for these species; P75 =  $-4.1$  and  $-3.3$  MPa for *Swartzia* and *Ouratea*, respectively. These observations for species from four distantly related families, with similar stature and light requirements (shade tolerant), suggest that xylem vulnerability, observed  $\Psi_{\text{leaf,min}}$ , and rooting depth are correlated. Similarly, Hacke et al. (2000) studied six shrub species of the Great Basin Desert in Utah and found that the drought-deciduous, shallow-rooted species sustained the lowest water potentials and had the most resistant xylem, whereas the deeply rooted, phreatophytic shrub *Chrysothamnus nauseosus* (Pall.) Britt. (Asteraceae) was capable of maintaining high water potentials and had the most susceptible xylem. These physiological correlations indicate that, even though these are understory species and the dry season at BCI is not as severe as in tropical dry forest, drought stress is an important selective factor. In addition to xylem cavitation resistance and rooting depth, characteristics such as stem capacitance, deciduousness and stomatal closure are important components of drought resistance (Robichaux et al. 1984, Landsberg 1986, Becker and Castillo 1990, Borchert 1994).

Xylem vulnerability curves have become a standard tool for

defining relationships between xylem tension and degree of embolism (Cruziat et al. 2002). We found big discrepancies between the native state of embolism in the field and that predicted from the Weibull function and the reported seasonal  $\Psi_{\text{leaf,min}}$ . Several studies on tropical woody species have shown that pressure chamber measurements of  $\Psi_{\text{leaf}}$  on transpiring leaves can result in an overestimation of xylem tension. In the Brazilian savanna (Cerrado), Bucci et al. (2004) found that measurements on transpiring leaves of *Ouratea*, and two other genera, can result in overestimates of  $\Psi_{\text{xylem}}$  by 0.8 to 1.0 MPa when compared with measurements made on leaves that were covered and equilibrated. Similarly, in central Panama, Meinzer et al. (2003) measured  $\Psi_{\text{leaf}}$  values of  $-1.7$  MPa in covered leaves of *Cordia alliodora*, a value well above the P50 of  $-3.0$  MPa that they reported for uncovered leaves. With the exception of *Bursera*, data on seasonal  $\Psi_{\text{leaf,min}}$  was collected during an extreme El Niño Southern Oscillation (ENSO) related drought, a time when overestimation is more likely (Borchert 1994, Tobin et al. 1999, Lopez 2002). Thus, use of these seasonal  $\Psi_{\text{leaf,min}}$  values will lead to overestimates of native state embolism. Also, native state embolism was measured during the dry season of 1993, after the rainy season, a period when conditions for vessel refilling (e.g., root pressure) may have occurred (Cochard et al. 1994, T.A. Kursar, unpublished data). Although the significance of seasonal reductions in hydraulic conductivity in understory, shade-tolerant species remains to be investigated, it is known that reductions in soil water availability during the dry season are coupled with an increase in light availability, and thus, potential carbon gain.

Xylem vulnerability to drought-induced cavitation may also be a determinant of species distributions in waterlogged soils. The exceptionally vulnerable xylem of *Ficus*, *Carapa* and *Prioria* (P50 =  $-1.6$  MPa) may explain the association of these species with wet habitats. *Carapa* and *Prioria* are the most dominant trees in seasonally inundated (swamp) forests of Central America and northern Colombia (Lamb 1953, Linares and Martínez 1991, Grauel and Kursar 1999), whereas *Ficus* appears to be strongly associated with the shoreline of Gatun Lake in central Panama (Croat 1978, Patiño et al. 1995). Thus, species associated with wet habitats might be more vulnerable to xylem cavitation, because overall soil water availability is less likely to be a limiting factor in such environments. However, considerable water stress can develop in these habitats during unusual dry periods, with severe consequences for seedling establishment of these wet soil habitat specialists. In a seasonally flooded forest in Darién, Panamá during the dry season, first-year seedlings of *Carapa* and *Prioria* experienced mean midday  $\Psi_{\text{leaf}}$  as negative as  $-1.3$  and  $-1.7$  MPa and mortality of 97% and 50%, respectively (Lopez 2002), suggesting that drought, rather than flooding, is the major factor determining mortality in these flooded habitats. The seasonal  $\Psi_{\text{leaf,min}}$  and high mortality experienced by seedlings of *Carapa* and *Prioria* during the dry season might be the result of their high xylem vulnerability to cavitation. In addition, because P75 =  $-1.4$  and  $-2.0$  MPa in *Carapa* and *Prioria*, respectively, the lower mortality of *Prioria* seedlings may reflect its somewhat more resistant xylem. These findings led us to two conclusions. First, a close relationship between vulnerability

to drought-induced cavitation,  $\Psi_{\text{leaf,min}}$  and mortality might exist. Second, small interspecific differences in xylem vulnerability and water stress, probably linked to rooting depth, can result in substantial differences in seedling survival. Similarly, survival of shallowly rooted species during drought may be enhanced by the presence of highly resistant xylem (a low P50 value as well as a shallow slope at water potentials below the P50 value; e.g., *Hybanthus* in Figure 1A).

Somewhat unexpected was the high vulnerability of the dry-season deciduous *Bursera* (P50 =  $-0.8$  MPa), a dry forest species. The dry-season deciduous *Pseudobombax septenatum* (Jacq.) Dugand (Bombacaceae), a tree from moist and dry forests, also has highly vulnerable xylem (P50 =  $-0.8$  MPa, Machado and Tyree 1994). *Cordia*, a tree from dry, moist and wet forest and one of the few species that is deciduous during the rainy season, has resistant xylem (P50 =  $-3.2$  MPa). From these observations we infer that the dry-season deciduous habit, rather than deciduousness itself, is more likely to be associated with xylem vulnerability (but see Hacke et al. 2000). However, a high degree of variability in xylem resistance to cavitation exists among dry-deciduous species because leaf shedding is not always coupled with reduced conductivity in order to prevent xylem cavitation. Brodribb et al. (2002, 2003) found that *Calycophyllum candidissimum*, Vahl DC (Rubiaceae) experienced seasonal  $\Psi_{\text{leaf,min}}$  values beyond its P50 values, indicating that the relationship between xylem resistance to cavitation and seasonal  $\Psi_{\text{leaf,min}}$  provides no clear differentiation between deciduous and evergreen species (Sobrado 1997).

A reduction in xylem hydraulic conductance limits gas exchange (Brodribb and Feild 2000, Brodribb et al. 2002, 2003). Therefore, the physical limitations of the vascular system under tension should dictate the constraints on its supportive foliage in relation to carbon assimilation during periods of high evaporative demand (Cochard et al. 1997, Maherali et al. 1997). On average, the three gap species had  $K_L$  values 5 times greater than the shade-tolerant species. This might be explained, in part, by the microclimate (e.g., high irradiance and high vapor pressure deficits (VPD)), in which gap species grow. Because of the negative effect of increased VPD on carbon assimilation, plants growing in open microsites are expected to have higher  $K_L$  to sustain higher rates of gas exchange (Brodribb et al. 2003). In a study of 20 canopy tree species from central Panama, Santiago et al. (2004) found that  $A_{\text{area}}$  and stomatal conductance were tightly coupled with  $K_L$ , indicating that carbon assimilation is ultimately linked to hydraulic function (see also Brodribb et al. 2002). The negative relationship between seasonal  $\Psi_{\text{leaf,min}}$  and the ratio of leaf to sapwood area ( $A_L:A_S$ , Figure 5), suggests that, as transpirational demands in relation to xylem conductive capacity increase, seasonal  $\Psi_{\text{leaf,min}}$  becomes more negative. Therefore, we predicted that species with greater transpirational demands in relation to hydraulic capacity (e.g., *Psychotria*) not only experienced the greatest xylem tension, but also exhibit the most resistant xylem.

Fast-growing species adapted to high irradiances may have lower wood density (Givnish 1995, Enquist et al. 1999) as well

as greater susceptibility to xylem cavitation (Hacke et al. 2001) than slow-growing, shade-tolerant species. Results from a long-term study on BCI suggest that fast-growing, high-light-adapted species that colonize open areas have higher mortality rates than non-colonizer species during periods of severe drought (Condit et al. 1995). The available data suggest that many of these species have vulnerable xylem, with P50 values of  $-0.7$  to  $-1.2$  MPa (*Bursera* and *Ficus* in this study and three other species reported in Machado and Tyree 1994 and Tyree et al. 1991). Our results on xylem vulnerability curves offer a general perspective on the operational limits of the conductive tissue. However, as shown for temperate species, cavitation resistance, wood density, growth strategy and species distribution also appear to be interrelated in tropical species. For example, wood density is negatively correlated with photosynthesis and hence,  $K_L$  among 20 species from lowland forests in Panama (Santiago et al. 2004). Therefore, hydraulic efficiency and its limitations during periods of water stress appear to reflect physiological trade-offs imposed by life-history strategies, with light-demanding, fast-growing species having higher  $K_L$  and  $K_S$  than shade-tolerant, slow-growing species.

We have found relationships between xylem vulnerability to cavitation and seasonal  $\Psi_{\text{leaf,min}}$  for four understory shrubs, two light-demanding trees and seedlings of two swamp species. In a previous study, vulnerability to cavitation was related to mortality for two wet-soil species (Lopez 2002). Taken together, these relationships are consistent with the idea that xylem resistance to cavitation is related to the lowest  $\Psi_{\text{leaf,min}}$  observed in the field (Pockman and Sperry 2000) and to drought-caused mortality (Davis et al. 2002). In addition, Tyree et al. (2003) report that the loss of 50–75% of xylem conductivity can induce severe stress and losses in excess of 80% can cause death. Furthermore, the severity of the dry season and its effect on xylem vulnerability may play a key role in determining desiccation tolerance and the distribution of plant species.

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