

# Hydraulic architecture, water relations and vulnerability to cavitation of *Clusia uvitana* Pittier: a C<sub>3</sub>-CAM tropical hemiepiphyte

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## SUMMARY

*Clusia uvitana* Pittier (Clusiaceae) is a tropical hemiepiphyte that has been shown to display a high plasticity in the expression of CAM in response to the environment. When water is available CO<sub>2</sub> is taken up mostly during the day. This study of the water relations and hydraulic architecture has revealed that leaf water potentials,  $\Psi$ , ranged from  $-0.7$  to  $-0.9$  MPa and changed very little with time or water availability. The absolute hydraulic conductivity of stem segments ( $K_a$ ) and the specific conductivity ( $K_s$ ) were comparable to many other temperate and tropical species, but the leaf specific conductivity ( $K_l$ ) was 1/3 to 1/30 that of many other species. So stems supported high leaf areas per unit of hydraulic conductivity. *C. uvitana* was very vulnerable to cavitation, reaching 50% loss of hydraulic conductivity at stem  $\Psi = -1.3$  MPa. The species survives in spite of low  $K_l$  and high xylem vulnerability, because the CAM physiology insures low transpiration rates and high ability to evade dehydration.

Key words: *Clusia uvitana*, water relations, hydraulic architecture, cavitation.

## INTRODUCTION

*Clusia uvitana* is a tropical hemiepiphyte that has been shown to display a high plasticity in the expression of CAM in response to the environment (Winter *et al.*, 1992; Zotz & Winter, 1993, 1994a). It can establish itself in trees up to 40 m above ground and also on rocks or fallen logs along lakes and rivers. While growing in the epiphytic stage, water is usually limiting at the same time that light intensities are high, because it often grows in trees that are deciduous for all or part of a dry season. Aerial roots

grow from the plant but may take several years to reach the forest floor. Once *Clusia* is established as a rooted hemiepiphyte, water resources become more available. Even when established in a large tree 40 m above ground, *Clusia* can grow to become a large shrub up to 6 m tall and 10 m diameter in this rooted hemiepiphytic stage. *Clusia* displays a predominately C<sub>3</sub> metabolism when water is freely available or when light intensities are low and water resources are only somewhat limited. But when water resources diminish over several days or weeks, *Clusia* gradually shifts to a CAM pattern of gas exchange (Winter *et al.*, 1992).

Very little is known about the water relations of hemiepiphytes (Putz & Holbrook, 1986) and we know of no reports of the hydraulic architecture and vulnerability to cavitation in such species. Various conflicting hypotheses are possible. For example, it might be argued that hemiepiphytes must have a xylem system with high hydraulic efficiency. This would permit hemiepiphytes to transport water from limited water sources with minimal pressure potential ( $\Psi_{xpm}$ ) gradients. Alternatively, it might be

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Abbreviations:  $A_l$  &  $A_w$ , leaf area and sapwood area, respectively (m<sup>2</sup>);  $D$ , wood diameter (mm);  $d\Psi_{xpm}/dx$ , pressure potential gradient in xylem;  $E$ , evaporative flux density;  $K_a$ , hydraulic conductivity of stem segments (kg s<sup>-1</sup> m MPa<sup>-1</sup>);  $K_l$ , leaf specific conductivity of stem segments (kg s<sup>-1</sup> m<sup>-1</sup> MPa<sup>-1</sup>);  $K_m$  &  $K_i$ , maximum and initial  $K_a$ , respectively;  $K_s$ , specific conductivity of stem segments (kg s<sup>-1</sup> m<sup>-1</sup> MPa<sup>-1</sup>); PLC, percent loss hydraulic conductivity; VC, vulnerability curve;  $\Psi$ , water potential (MPa);  $\Psi_p$ , turgor pressure potential (MPa);  $\Psi_{xpm}$ , xylem pressure potential (MPa);  $\Psi_m$ , osmotic potential (MPa).

argued that an efficient xylem is unnecessary, since many epiphytes and hemiepiphytes are CAM plants and thus transpire little water. Since CAM plants are usually less efficient than  $C_3$  plants in net carbon gain, perhaps hemiepiphytes cannot afford to invest much carbon in xylem and thus may have an inefficient xylem system.

Xylem vessels are prone to drought-induced dysfunction. When  $\Psi_{xp}$  drops too low, vessels cavitate, i.e. air bubbles are rapidly sucked into the vessel and the lumen becomes air filled. Air bubbles prevent water flow in vessels and decrease the hydraulic conductivity of stems. Then a more negative  $\Psi_{xp}$  must be generated in leaves to draw water from the rooting substrate. So it could be argued that hemiepiphytes might be very resistant to cavitation events. Alternatively, if CAM species can effectively protect roots and leaves from excessive water loss to the environment when water resources are limited (Gihson & Nobel, 1986; North & Nobel, 1991; Nobel & Cui, 1992), then it might be argued that a very negative  $\Psi_{xp}$  might never be reached; hence species might cavitate at a relatively high  $\Psi_{xp}$ .

The purpose of this study was to obtain some initial information on the hydraulic architecture and the vulnerability to cavitation of *Clusia uvitana* and to relate these properties to its water relations.

## MATERIALS AND METHODS

### Field site and measurements

Investigations were conducted on Barro Colorado Island (BCI) (9° 10' N, 79° 51' W), Republic of Panama. The tropical moist forest on this 15 km<sup>2</sup> biological reserve receives about 2600 mm of annual precipitation with a pronounced dry season from late December to April. Detailed descriptions of vegetation, climate and ecology are provided by Croat (1978) and Leigh, Rand & Windsor (1982).

Measurements of water vapor flux density were performed on fully developed leaves of *Clusia uvitana* Pittier (Clusiaceae) (= *C. odorata*; Croat, 1978; Hammel, 1986). *Clusia* plants sampled or measured in the field were studied at four different sites. The individuals at all sites were fully rooted hemiepiphytes. Three individuals were located at a lake front site in the bay containing the docks on BCI; these sites will be referred to as Lakel through Lake3. The fourth site (*Ceiba*) was in the crown of a tree of *Ceiba pentandra* (L.) Gaertn, Fruct. & Sem. The plants studied were growing on *C. pentandra* branches 0.5 m diameter approximately 35 m above the forest floor. Access to the tree was via climbing ropes with the aid of a triangular climbing tower situated parallel to the trunk. The *C. pentandra* tree is leafless during the transition from rainy to dry season.

Evaporative flux density of leaves (E) was studied with a CO<sub>2</sub>/H<sub>2</sub>O-Porometer (model CQP 130, Walz,

Effeltrich, Germany). Leaves were clamped between an aluminium ring and the 16 cm<sup>2</sup> opening of a PMK10 gas exchange cuvette (Walz, Effeltrich). The hypostomatic leaf itself provided a seal for the cuvette, with the upper leaf surface exposed to ambient conditions, and the lower surface, facing the interior of the gas exchange chamber. All other instruments were kept in two aluminium boxes no more than 5 m away from the study leaves to minimize the length of the pneumatic system. The gas exchange equipment was used in a continuous open flow mode. The flow rate of air was 300 to 500 cm<sup>3</sup> min<sup>-1</sup>. External temperature was automatically tracked inside the leaf cuvette. Water vapor exchange was measured with an IRGA operating in differential mode (Binos 100, Rosemount, Hanau, Germany). Zero checks (ambient gas streaming through both the measuring and reference cells of the differential analyzer) were performed at 1 h (during daytime) and 6 h (during nighttime) intervals. A cold trap (model KF18/2, Walz, Effeltrich) was used to keep the air entering the leaf chamber below ambient to balance transpirational water loss, to keep cuvette humidity equal to ambient, and to avoid condensation inside the pneumatic system. A datalogger collected a full data-set at 5 minute intervals for calculations of gas exchange parameter.

### Laboratory measurements

**Water potential.** Measurements of leaf water potential,  $\Psi$ , and osmotic potential,  $\Psi_{\pi}$ , of the leaf sap were made psychometrically on leaf discs at 30 °C with 5 thermocouple psychrometers (model C-52) and a microvoltmeter (model HR-33T, Wescor, Logan, Utah). Following measurement of  $\Psi$ , leaf disks were frozen and thawed, which permitted determinations of  $\Psi_{\pi}$ . Leaf turgor pressure,  $\Psi_p$ , was calculated from the difference between  $\Psi$  and  $\Psi_{\pi}$ .

**Hydraulic data and native state loss of conductivity.** The hydraulic parameters that define the hydraulic architecture of *Clusia* and the native state of loss of hydraulic conductivity due to embolisms were all measured on the same branches. Eight branches were harvested (30 to 45 mm basal wood diameter and 2 to 4 m long), two were taken from each of the three lake sites and two from the *Ceiba* site (see materials section above). The branches were returned to the laboratory and recut under water. Stem segments were cut from various places in the branch and a record was kept of wood diameter,  $D$ , segment length,  $L$ , and total leaf area located to the apex of the segment,  $A_L$ , measured with a model LI-3100 leaf area meter (LiCor, Inc., Lincoln, Nebraska).

Stem segments were placed in a conductivity apparatus described elsewhere (Sperry, Donnelly & Tyree, 1987) which permitted the measurement of the rate of flow of solution ( $w$ , kg s<sup>-1</sup>) in response to

the pressure difference ( $P$ , MPa). The solution perfused through the segments was 10 mM oxalic acid in degassed solution that was filtered through a 0.1  $\mu\text{m}$  porosity filter. Initial hydraulic conductivity was measured with  $P = 40\text{--}60$  kPa and calculated from:

$$K_i = wL/P. \quad (1)$$

$K_i$  is a measure of absolute hydraulic conductivity of the segment (flow rate per unit pressure gradient) and is sometimes referred to as  $K_p$  (Tyree & Ewers, 1991). Then the segment was flushed for 10 to 15 min with solution under a pressure of 150 kPa to dissolve air bubbles in embolised vessels. After the flush  $K_n = wL/P$  was again measured. The process was repeated until a maximum conductivity,  $K_m$ , was achieved (usually after one or two flushes). Percent loss of hydraulic conductivity due to embolisms, PLC, was computed from

$$\text{PLC} = 100(K_m - K_i)/K_m. \quad (2)$$

The stem segments were perfused with 0.03% safranin and cut to determine the cross sectional area of wood  $A_w$  involved in water transport (after embolisms were dissolved). The stained area,  $A_w$ , was measured on a bit pad using SigmaScan software (Jandel Scientific, San Rafael, California).

Specific hydraulic conductivity,  $K_s$ , provides information about the hydraulic efficiency of xylem on a cross sectional area basis, and was calculated from:

$$K_s = K_i/A_w. \quad (3)$$

$K_s$  increases with the number of functional (non-embolised vessels) per unit wood area, with the diameter of vessels, and with vessel length.

Leaf specific hydraulic conductivity,  $K_L$ , provides information about the hydraulic efficiency of a stem segment on a leaf area basis, and was calculated from:

$$K_L = K_i/A_L. \quad (4)$$

It is a useful measure because it provides information about the pressure gradient,  $d\Psi_{xp}/dx$ , in the stem segment needed to maintain an average evaporative flux density,  $E$ , in the leaves to the apex of the segment, i.e. it can be shown that

$$d\Psi_{xp}/dx = E/K_L. \quad (5)$$

A hydraulically efficient stem has a high  $K_L$  and a low  $d\Psi_{xp}/dx$ .

*Hydraulic map.* One other branch was harvested from the Lakel site. It was 45 mm diameter at the base, 4 m long and had 17.7 m<sup>2</sup> of leaf area. A detailed map of the branching structure was made for calculation of  $\Psi_{xp}$  within the stems. The branch was cut into 453 segments. All cuts were made at branch insertion points. The following data were collected for each segment: (1) segment number

(starting with 1 at the base), (2) the segment number to which the segment was attached at its base, (3) the diameter of the wood of the segment, (4) segment length, (5) leaf area attached to the segment. For apical branch segments bearing leaves, the length taken was the distance from the base of the segment to the midpoint of the portion of the segment bearing leaves. All diameters were measured beyond the swelling of the branch insertions.

*Vulnerability curves.* A vulnerability curve (VC) is a plot of PLC versus the  $\Psi_{xp}$  that induced the PLC. Normally PLCs are measured by dehydrating excised branches in air to measured values of  $\Psi_{xp}$  and then stem segments are excised under water and mounted in a conductivity apparatus for measurement of  $K_i$  and  $K_n$ . Excised *Clusia* branches dehydrate far too slowly for this to be a practical method. From other studies (Cochard, Cruiziat & Tyree, 1992) we know that vulnerability curves measured by air dehydration are the same as those measured on branches dehydrated in a pressure chamber.

Branches 0.6 to 0.7 m long were collected from the Lakel site, the leaf blades were excised at the apex of the petioles, and the stem enclosed in a pressure chamber with the base protruding through a rubber seal into outside air. Different branches were pressurized for 12 to 16 h at different gas pressures. At the end of the pressurization period, the branch was removed from the pressure chamber, placed under water, and segments 20 to 30 mm long and 3 to 7 mm diameter were excised. Bark and pith were removed to prevent latex plugging of xylem vessels; all bark was stripped and the pith was removed for a distance of 3 mm from each end. PLC was measured as described above.

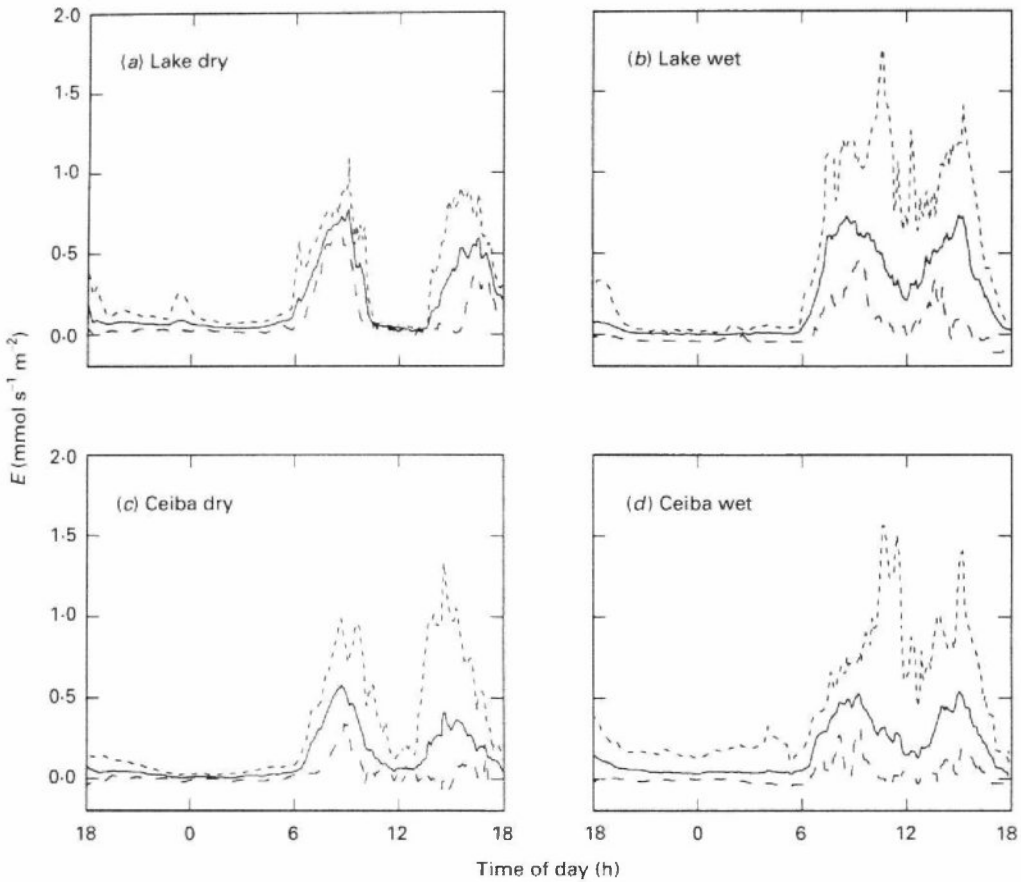
## RESULTS

### Transpiration

Evaporative flux density,  $E$ , was measured at 5 minute intervals at two sites in both the wet and dry seasons for five, seven and 10 days (Fig. 1). There were two peaks in  $E$  each day, one at about 08.00 h and the other at about 16.00 h. The mid-day reduction in  $E$  was due to a large fall in stomatal conductance (data not shown). Stomata opened at night to allow nocturnal CO<sub>2</sub> uptake, but  $E$  was low because of low leaf to air vapor pressure deficits at night.

### Water potential

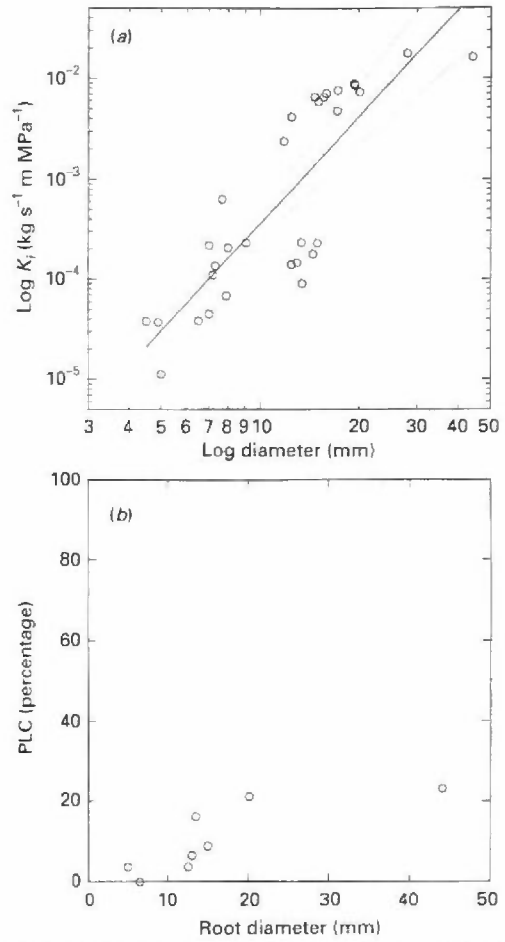
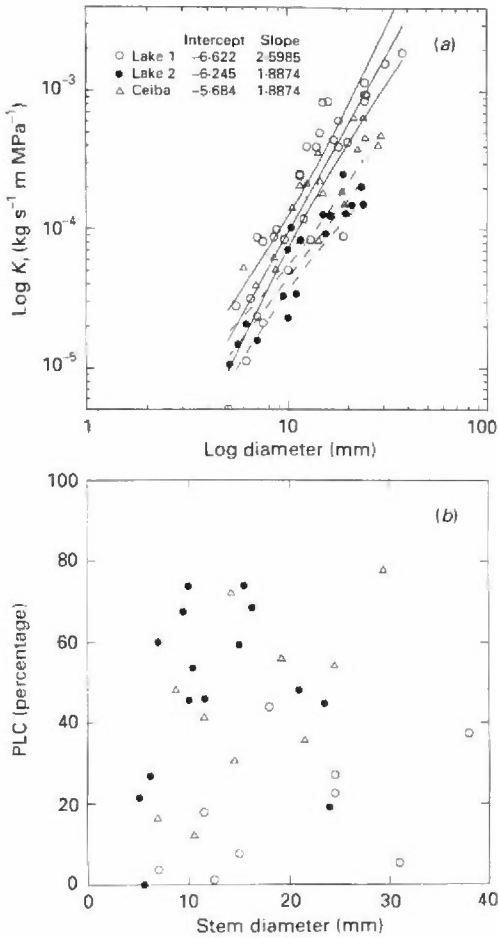
The 24 h mean  $E$  and 95% confidence intervals are shown in Table 1 together with  $\Psi$ ,  $\Psi_n$  and  $\Psi_p$  at 06.00 h and 13.00 h in each season. Most of the values in Table 1 were measured on leaves in the upper crown of *Clusia* where maximum light



**Figure 1.** Evaporative flux density ( $E$ ) from leaves of *Clusia uvitana* measured at lake sites and Ceiba-tree site during wet and dry seasons. Solid lines are mean  $E$  for 5 days (a), 7 days (b, c), and 10 days (d). Only one leaf was monitored each day but leaves were changed daily. Dashed lines indicate minimum and maximum values recorded (modified from Zotz & Winter, 1994b).

**Table 1.** Values of leaf water potential,  $\Psi$ , leaf solute potential,  $\Psi_{\pi}$ , turgor potential,  $\Psi_p$ , and 24 h average  $E$  at different sites and season (modified from Zotz & Winter, 1994b). Errors are 95% confidence intervals on the means except for Lake site water potential values where sample size was too small so only SD is given.  $N = N1, N2$  where  $N1 =$  number of samples for  $\Psi$  terms and  $N2 =$  number of days for average  $E$ . Most values are for upper crown leaves exposed to the most sunlight. Shade leaves were lower crown and shaded most of the time ( $1 \text{ mmol s}^{-1} \text{ m}^{-2} = 1.8 \times 10^{-5} \text{ kg s}^{-1} \text{ m}^{-2}$ )

	MPa 06.00 h			MPa 13.00 h			Average $E$ ( $\text{mmol s}^{-1} \text{ m}^{-2}$ )
	$\Psi$	$\Psi_{\pi}$	$\Psi_p$	$\Psi$	$\Psi_{\pi}$	$\Psi_p$	
Ceiba wet mean	-0.78	-1.37	0.59	-0.68	-1.27	0.58	0.159
Error ( $n = 27,10$ )	0.07	0.13	0.13	0.05	0.11	0.09	0.020
Ceiba dry mean	-0.82	-1.38	0.56	-0.79	-1.21	0.42	0.127
Error ( $n = 16,7$ )	0.10	0.09	0.09	0.12	0.15	0.10	0.022
Lake wet mean	-0.76	-1.36	0.60	-0.82	-1.45	0.63	0.211
Error ( $n = 6,7$ )	0.20	0.15	0.14	0.30	0.18	0.16	0.038
Lake dry mean	-0.93	-1.39	0.46	-0.77	-1.24	0.40	0.188
Error ( $n = 4,5$ )	0.23	0.17	0.15	0.11	0.15	0.05	0.032
Shade dry	-1.0	-1.1	0.1				0.029
Error ( $n = 2,4$ )							0.008
Shade wet	-0.8	-1.0	0.2				0.028
error ( $n = 4,9$ )	0.10	0.19	0.09				0.009



**Figure 2.** (a) Initial absolute conductivity,  $K_i$ , of *Clusia* stem segments collected from different sites versus diameter of wood. Values are presented as Log-Log plots. Straight lines are linear regressions and curved lines are 95% confidence intervals on the regressions. Regression values are shown in the figure. (b) Native state percent loss conductivity, PLC, versus stem diameter measured on selected segments used in (a).

**Figure 3.** As for Figure 2 except for segments of aerial roots.  $\text{Log}(K_i) = -6.993 + 3.544 \cdot \text{Log}(D)$ .

intensities occurred. The 24 h average  $E$  in the wet season was more than the dry season value (> 95% confidence) at both the *Ceiba* and Lake sites. The 24 h average  $E$  in the Lake sites always exceeded that in the *Ceiba* (> 95% confidence) when comparing wet to wet and dry to dry season. Shade leaves (leaves in the understory of a *Clusia* crown) had a 24 h average  $E$  that was five to seven times less than more exposed leaves. None of the water potential parameters was significantly different.

*Hydraulic architecture*

Values of  $K_i$  (= initial  $K_h$  in other literature) are plotted versus wood diameter,  $D$ , in Figure 2a. Plots are  $\text{Log } D$  in mm versus  $\text{Log } K_i$  and linear regressions with 95% confidence intervals are shown. Branches from Lake1 and Lake3 were not

significantly different and were pooled. The trend for Lake2 was significantly different from Lake1 for  $D > 8$  mm. The branches from the *Ceiba* site were significantly different from Lake2 for all  $D$ s measured; they were also significantly different from Lake1 for  $D > 20$  mm. The lower values for  $K_i$  in Lake 2 and *Ceiba* sites were partly due to difference in native state PLC (Fig. 2b). Similar values for aerial roots are shown in Figures 3a and 3b. Native state PLC was low in aerial roots.

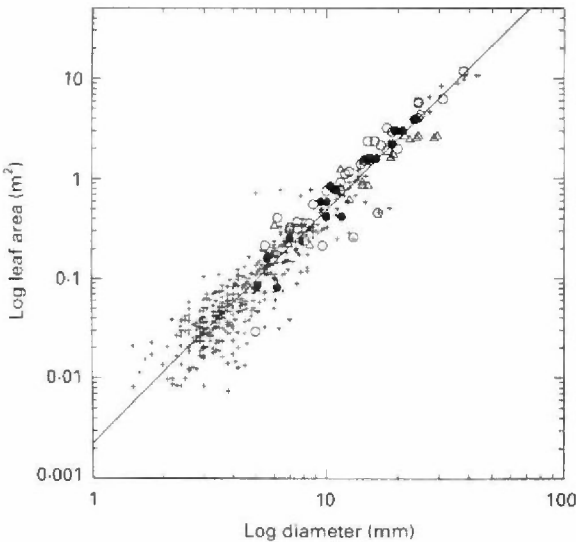
Values for specific conductivity,  $K_s$ , and leaf specific conductivity,  $K_L$ , did not show a significant dependence on  $D$  for stems so were pooled to give means and SEMs for all  $D$ s (Table 2). In roots  $K_s$  increased with  $D$ . Stem  $K_s$  was about the same as for other tropical and temperate species but  $K_L$  was much less than for most tropical species and less than for *Acer saccharum*. The lower  $K_s$  values for the Lake2 and for the *Ceiba* sites probably reflected the higher PLC at these sites.

All branches from all sites had about the same relationship between leaf area,  $A_L$ , and basal diameter of the branch bearing the leaves (Fig. 4). So

**Table 2.** Means and SEMs for  $K_s$  (specific conductivity) and  $K_l$  (leaf specific conductivity in  $kg\ s^{-1}\ m^{-1}\ MPa^{-1}$ ). For comparison purposes, values for other tropical species for stems 20 to 40 mm diameter (and for the temperate *Acer*) are given. Values for *Schefflera* and *Acer* are from (Tyree et al., 1991). Values for *Ochroma*, *Pseudobomax* are from (Machado & Tyree, 1994b) and *Ficus* are unpublished results from Barro Colorado Island, Panama (Sandra Patiño)

Species sample (site)	$K_s$ (SEM,N)	$K_l$ (SEM,N) $\times 10^4$
<i>Clusia</i>		
Roots (Lake1)	27.3 (2.2,14)*	—
Roots (Lake1)	13.4 (1.5,31)†	—
Stems (Lake1)	2.14 (0.28,12)	2.39 (0.22,19)
Stems (Lake2)	0.66 (0.05,16)	0.93 (0.14,18)
Stems ( <i>Ceiba</i> )	1.07 (0.10,20)	1.89 (0.19,20)
<i>Schefflera morototoni</i>	2.2	30
<i>Ochroma pyramidale</i>	2.1	20
<i>Pseudobombax septenatum</i>	1.6	18
<i>Ficus</i> (range for 7 spp.)	4–14	5–30
<i>Cassipourea elliptica</i>	1.3	—
<i>Rhizophora mangle</i>	1.9	—
<i>Acer saccharum</i>	2.5	5

\*  $D_{min} > 20$  mm.  
 † All roots.

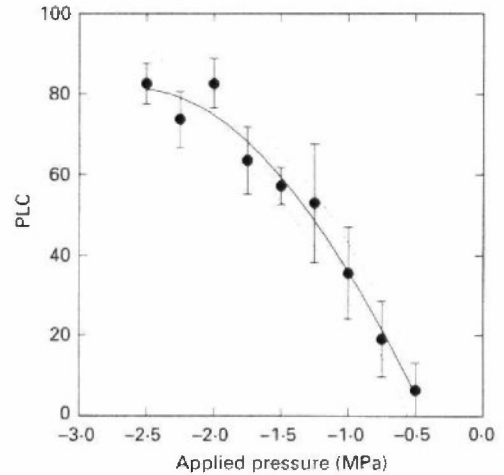


**Figure 4.** Plot of leaf area on branches versus basal wood diameter of the branch. + = values indicate area versus diameter measured on the branch cut up for the detailed hydraulic map. Other symbols indicate site from which branches were collected (O, Lake1; ●, Lake2; Δ, *Ceiba*). The regression for all data is  $\text{Log}(A_l) = -2.6489 + 2.3378 \cdot \text{Log}(D)$ ,  $R = 0.964$ .

the reduced hydraulic conductivity as expressed in  $K_r$ ,  $K_s$  and  $K_l$  observed in the Lake2 and *Ceiba* sites did not influence the amount of leaves supported by *Clusia* plants at the different sites.

*Vulnerability to cavitation*

The vulnerability curve, VC, for *Clusia* is shown in Figure 5. All measurements were done on segments



**Figure 5.** Vulnerability curve for 3–7 mm diameter stem segments of *Clusia uvitana*. Percent loss hydraulic conductivity (PLC) is plotted versus the pressure causing the observed PLC. Applied pressure on the x-axis may be interpreted as  $\Psi_{xp}$  but refers to the pressure applied in a pressure bomb to dehydrate branches before stem segments were excised under water. We assume that the extra air forced into solution in the shoots does not increase its vulnerability to cavitation. Each point is the mean of 8 to 10 stem segments, error bars give SEM. The solid line is the best-fit third-order polynomial regression with 95% confidence limits (dotted line).

3 to 7 mm diameter just below the leaf bearing portion of the branch. They began losing hydraulic conductivity at  $\Psi_{xp} = -0.5$  MPa, had 50 PLC at  $-1.3$  MPa and 80 PLC by  $-2.3$  MPa.

The data set for the branch map consists of a table of values that provide stem dimensions, locations, hydraulic conductances, and leaf areas and is too

**Table 3.** Comparison of vulnerability to cavitation of several tropical species having different growth forms.  $\Psi_{x_{p50}}$  = xylem pressure potential for 50% loss of hydraulic conductivity. (Reference No.): 0, unpublished measurements made by H. Cochard & Pilar Angulo on BCI; 1, Sperry, Tyree & Donnelly, 1988; 2, Tyree et al., 1991; 3, Machado & Tyree, 1994; 4, Cochard, Ewers & Tyree, 1994

Species (family)	$\Psi_{x_{p50}}$ MPa (Ref. No.)	Growth form
<i>Pseudobombax septenatum</i> (Jacq.) Dug. (Bombacaceae)	-1.0 (3)	Tree, drought deciduous
<i>Ochroma pyramidale</i> (Cav. ex Lam) Urban (Bombacaceae)	-1.0 (3)	Tree, gap specialist Deep rooted
<i>Schefflera morototoni</i> (Araliaceae)	-1.4 (2)	Tree, gap specialist Deep rooted
<i>Ficus citrifolia</i> P. Mill. (Moraceae)	-1.7 (0)	Tree
<i>Ouratea lucens</i> (H. B. K.) Engler (Marcgraviaceae)	-1.8 (0)	Small understory shrub (deep rooted)
<i>Cordia alliodora</i> (R. & P.) Cham (Boraginaceae)	-3.2 (0)	Tree
<i>Rhipidocladum racemiflorum</i> (Steud.) McClure (Gramineae)	-4.2 (4)	Vine-like bamboo (shallow rooted)
<i>Cassipourea elliptica</i> (Sw.) Poir. (Rhizophoraceae)	-4.8 (1)	Small tree
<i>Rhizophora mangle</i> (L.) (Rhizophoraceae)	-6.2 (1)	Small tree, mangrove
<i>Psychotria horizontalis</i> Sw. (Rubiaceae)	< -5* (0)	Small understory shrub (shallow rooted)

\* Entire VC not known but it reached 30 PLC at -5 MPa.

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#### DISCUSSION

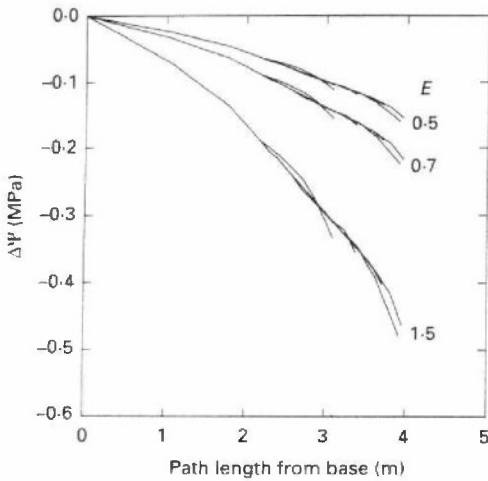
*Clusia* reaches 50 PLC at -1.3 MPa. This should be compared with the vulnerability to cavitation of several other tropical species. In Table 3, 10 species are ranked according to the  $\Psi_{x_p}$  at which 50 PLC is reached. We can now tentatively begin to identify a pattern. We can classify tropical species into two categories, drought-evaders and drought-tolerators. The drought-evaders escape drought (low  $\Psi_{x_p}$  and high PLC) by having deep roots and a highly conductive hydraulic system (Table 2); taxa that fall into this category are *Ochroma*, *Schefflera*, and perhaps *Ficus* and *Ouratea*. Alternatively they evade drought by being deciduous (*Pseudobombax*). The other species frequently reach very negative  $\Psi$ s for part or all of the year and are shallow rooted (where soils get dry) or grow in saline environments; taxa in this category are *Rhipidocladum*, *Rhizophora* and *Psychotria*. Taxa that are of doubtful classification are *Cordia* and *Ficus* because we know nothing about rooting depths or typical dry season values of  $\Psi$ . *Cassipourea* is uncertain for the same reasons, and is also unusual in beginning to cavitate at -0.5 MPa and not reaching 50 PLC until -4.8 MPa whereas most other species reach 50 PLC within 0.5 or 1.0 MPa of the start of cavitations. *Clusia* is clearly a drought-evader as would be expected for a CAM

plant; it evades low  $\Psi$  by preventing loss of water from leaves and roots during dry periods.

In terms of hydraulic architecture, the  $K_x$  values of *Clusia* were comparable with those of other tropical species (Table 2). This means that the xylem of *Clusia* was about as efficient on a wood area basis as other species. But  $K_x$  of *Clusia* was 1/5 to 1/30 that of other species, so stems were less efficient on a per unit leaf area basis. From this we can conclude that *Clusia* branches supported a large leaf area per unit stem area, i.e. it invested relatively little carbon in stems. *Clusia* can afford to invest less carbon in stems because of its very low  $E$  values and because it needs less biomechanical support as a hemiepiphyte. The average maximum  $E$  at 08.00 h or 16.00 h are about  $0.7 \text{ mmol s}^{-1} \text{ m}^{-2} = 1.2 \times 10^{-5} \text{ kg s}^{-1} \text{ m}^{-2}$ . This value should be compared to  $E$  values for tropical trees that range from 5 to  $8 \times 10^{-5} \text{ kg s}^{-1} \text{ m}^{-2}$  from 10.00 h to 15.00 h (Tyree et al., 1991 and Machado & Tyree, 1994).

Using the tree map we can calculate steady-state profiles of  $\Psi_{x_p}$  in *Clusia* branches as explained in several other studies (e.g. Tyree, 1988; Tyree et al., 1991). The results of this calculation are shown in Figure 6. *Clusias* are frequently shrublike in appearance, having many branches up to 6 m long emerging from the base. Figure 6 shows that during steady state transpiration  $\Psi_{x_p}$  would decline about 0.15 or 0.2 MPa from the base of the shoots to a leaf near the top of the shrub. *Clusia* leaves were thick (1 mm) and fleshy and presumably had a large water storage capacity. So it was unlikely that *Clusia*





**Figure 6.** Computed pressure potential profiles for steady-state flow of water through a *Clusia vitata* branch calculated from the hydraulic map. The y-axis gives the change in water potential ( $\Delta\Psi$ ) from the base of the branch to any given point along the branch. The x-axis is the distance along the branch in m. Six pathways from the base of the branch to 6 different apices were selected at random and plotted. The numbers to the right of each plot is the average evaporative flux density from leaves,  $E$  ( $\text{mmol s}^{-1} \text{m}^{-2}$ ), used for each calculation. Since *C. vitata* leaves have high water storage capacity, it is unlikely that steady-state is ever reached so gradients are likely to be less than shown here.

branches would have reached steady state flow at peak transpiration. The 24-h average values of  $E$  were about 1/3 to 1/5 of the peak values (Table 1). So the 24-h average gradients in  $E$  would be about 1/3 to 1/5 that in Figure 6. The longest hydraulic path in the *Clusia* at the *Ceiba* site was in the aerial roots. The aerial roots were about 35 m long. The root diameters ranged from 20 to 100 mm and tended to be thicker near the top of the aerial roots. The combined cross section of the roots was  $430 \text{ cm}^2$  averaged over the entire length of the root system. From stem diameters in the crown and the relation between stem diameter and leaf area (Fig. 4) we estimated the total leaf area of this individual to be  $900 \text{ m}^2$ . Using this value of leaf area, and combined cross section of aerial roots and the  $K_s$  of aerial roots in Table 1 it is possible to estimate the gradient of  $\Psi_{xp}$  in aerial roots from:

$$d\Psi_{xp}/dx = -0.01 - E_a A_L / (A_r K_s), \quad (6)$$

where  $-0.01$  is the gradient needed to overcome gravity. We estimated  $E_a = 0.1 \text{ mmol s}^{-1} \text{m}^{-2} = 1.8 \times 10^{-6} \text{ kg s}^{-1} \text{m}^{-2}$  averaged over 24 h and averaged over sun and shade leaves. Setting  $A_L$  to  $900 \text{ m}^2$ ,  $A_r$  (the aerial root wood area) to  $0.043 \text{ m}^2$  and  $K_s$  (the specific conductivity of aerial roots) to  $27 \text{ kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$ , the calculated value of gradient was  $0.0114 \text{ MPa m}^{-1}$  or a total drop of  $0.4 \text{ MPa}$  over 35 m. Most of this drop in water potential was due to gravity. Adding on the decline in the shoots we have

a total computed change in  $\Psi_{xp}$  in the vascular system of *Clusia* to be  $0.45 \text{ MPa}$  on a 24-h basis. This compares favourably with the leaf  $\psi_s$  of  $-0.7$  to  $-0.9 \text{ MPa}$  (Table 1). This leaves a driving force of  $0.25$  to  $0.45 \text{ MPa}$  to extract water from dry soils and for the  $\Psi$  decline for radial flow across roots.

There is a strong possibility that flow of water through aerial roots versus  $E$  from leaves are strongly decoupled in time. The driving forces for water flow through roots may be relatively uniform over a 24 h period because of the large water storage capacity in leaves compared to the low transpiration rate and because of the nature of CAM. At times of peak  $E$  which should lower leaf turgor and thus lower leaf  $\Psi$ , there may also be a rise in solute potential due to metabolism of acids during photosynthesis. These two affects might cancel out causing little change in leaf  $\Psi$ .

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