

## Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax septenatum*

JOSE-LUIS MACHADO<sup>1,2</sup> and MELVIN T. TYREE<sup>3,4</sup>

<sup>1</sup> Department of Botany, University of Vermont, Burlington, VT 05405, USA

<sup>2</sup> Current address: Department of Forest Resources, University of Minnesota, 115 Green Hall, 1530 North Cleveland Avenue, St. Paul, MN 55108, USA

<sup>3</sup> Northeastern Forest Experiment Station, PO Box 968, Burlington, VT 05402, USA

<sup>4</sup> Author to whom correspondence should be addressed

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### Summary

Many authors have attempted to explain the adaptive response of tropical plants to drought based on studies of water relations at the leaf level. Little attention has been given to the role of the xylem system in the control of plant water requirements. To evaluate this role, we studied the hydraulic architecture and water relations parameters of two tropical canopy trees with contrasting leaf phenologies: deciduous *Pseudobombax septenatum* (Jacq.) Dug and evergreen *Ochroma pyramidale* (Cav. ex Lamb) Urban, both in the family Bombacaceae. The hydraulic architecture parameters studied include hydraulic conductivity, specific conductivity, leaf specific conductivity, and Huber value. Water relations parameters include leaf water potential, stem and leaf water storage capacitance, transpiration, stomatal conductance, and vulnerability of stems to cavitation and loss of hydraulic conductivity by embolisms. Compared to temperate trees, both species showed a pattern of highly vulnerable stems (50% loss of conductivity due to embolism at water potentials less than 1 MPa) with high leaf specific conductivities. The vulnerability of xylem to water-stress-induced embolism was remarkably similar for the two species but the leaf specific conductivity of petioles and leaf-bearing stems of the evergreen species, *Ochroma* (e.g., 9.08 and  $11.4 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$ , respectively), were 3.4 and 2.3 times higher, respectively, than those of the deciduous species, *Pseudobombax* (e.g., 2.64 and  $5.15 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$ , respectively). A runaway embolism model was used to test the ability of *Ochroma* and *Pseudobombax* stems to maintain elevated transpiration rates during the higher evaporative demand of the dry season. The percent loss of leaf area predicted by the runaway embolism model for stems of *Pseudobombax* ranged from 5 to 30%, not enough to explain the deciduous phenology of this tree species without analysis of root resistance or leaf and petiole vulnerability to embolism.

*Keywords:* leaf phenology, Panama, vulnerability to embolism, water stress, xylem.

### Introduction

Tropical forest types have been classified according to the seasonality of the climate, i.e., in terms of the amount of rainfall and length of the dry season (Schimper and Faber 1935, Walter 1971). The phenology (leaf production and senescence) of tropical tree species has been related to seasonal changes in rainfall and soil water content, the principal determinants of tree water status (Richards 1952, Frankie et al. 1974, Alvim and Alvim 1978, Reich and Borchert 1984, Longman and Jenik 1987,

Bullock and Solis-Magallanes 1990). In contrast, the phenology of temperate forests has been attributed to changes in day length and temperature (Addicott 1982, Hicks and Chabot 1985). Other phenological events in the tropical forest, such as flowering, bud break and shoot elongation, are not directly correlated with seasonal precipitation patterns, indicating the existence of endogenous control within the plant (Wright and Comejo 1990, Borchert 1992). The only notable exception is the phenology of flowering of *Hybanthus prunifolius* (Violaceae) and some *Tabebuia* spp. (Bignoniaceae), which is cued by rainfall after a dry period (Augspurger 1982, Reich and Borchert 1982, 1984). Interaction of other abiotic factors, such as edaphic conditions, photoperiod and temperature (Medina 1984, Longman and Jenik 1987), may also be involved in determining phenological events in tropical forests.

Several authors have undertaken studies of water relations in leaves to explain the adaptive response to drought of the contrasting leaf phenologies of evergreen and deciduous tropical trees, reasoning that leaves are the main organ for energy exchange by way of photosynthesis and transpiration (Fetcher 1979, Meinzer et al. 1983, Robichaux et al. 1984, Oberbauer 1985, Sobrado 1986, Fanjul and Barradas 1987, Oberbauer et al. 1987, Rundel and Becker 1987, Becker et al. 1988, Van Rooyen 1989, Olivares and Medina 1992, Wright et al. 1992). In contrast, little attention has been given to the role of the xylem system and the hydraulic architecture of trees in the control of the water requirements for the maintenance of carbon balance by the plant. Recently, it has been suggested that trees operate near the brink of catastrophic xylem dysfunction (Tyree and Sperry 1988). This finding supports Zimmermann's segmentation hypothesis that plants are hydraulically designed to sacrifice highly vulnerable minor branches if need be, thereby improving the water balance of the remaining parts (Zimmermann 1983).

Goldstein and collaborators (1989, see also Sarmiento et al. 1985, Goldstein et al. 1987) studied the gas exchange, water relations and vascular properties of two evergreen and two deciduous trees growing in the tropical savannas of Venezuela. They found that evergreen species were more hydraulically efficient at supplying water to the leaves (their stems had higher leaf specific conductivity,  $k_L$ ) than deciduous species. Their work suggested that the more efficient transport system of the small branches of evergreen trees allowed them to maintain their leaves at a more favorable water balance (less negative water potential,  $\Psi$ ) during the high evaporative demand of the dry season than the deciduous trees, which may have to drop their leaves as a mechanism to prevent excessive embolism formation. However, their work was limited because they did not consider the hydraulic architecture and the vulnerability to embolism of the species.

The purpose of this study was to investigate the hydraulic sufficiency of stems and the vulnerability of xylem to water-stress-induced embolism of two tropical canopy trees with contrasting leaf phenologies: the evergreen tree, *Ochroma pyramidale* (Cav. ex Lam) Urban and the deciduous tree, *Pseudobombax septenatum* (Jacq.) Dug, both in the family Bombacaceae. This study addresses the following hypotheses: (1) deciduous trees are more vulnerable to embolism than evergreen trees; (2) evergreen trees have a more efficient hydraulic architecture than deciduous trees;

and (3) deciduous trees are incapable of maintaining the elevated transpiration rates that occur during the dry season without excessive cavitation.

**Materials and methods**

*Study site*

The study was conducted at Barro Colorado Island (BCI), in the Republic of Panama (9°09' N, 79°51' W). Trees were also collected nearby from Orchid and Lesseps Islands in Gatun Lake, which encompass the Barro Colorado Nature Monument (BCNM). Average annual rainfall was 2600 mm with a pronounced dry season from mid-December through April. During the dry season of 1991, the month of highest rainfall was March, with 174 mm (Figure 1). Mean maximum and minimum air temperatures recorded in the clearing in which the laboratory was located reached their lowest values in November (29.4 °C) and December (23.8 °C), respectively,

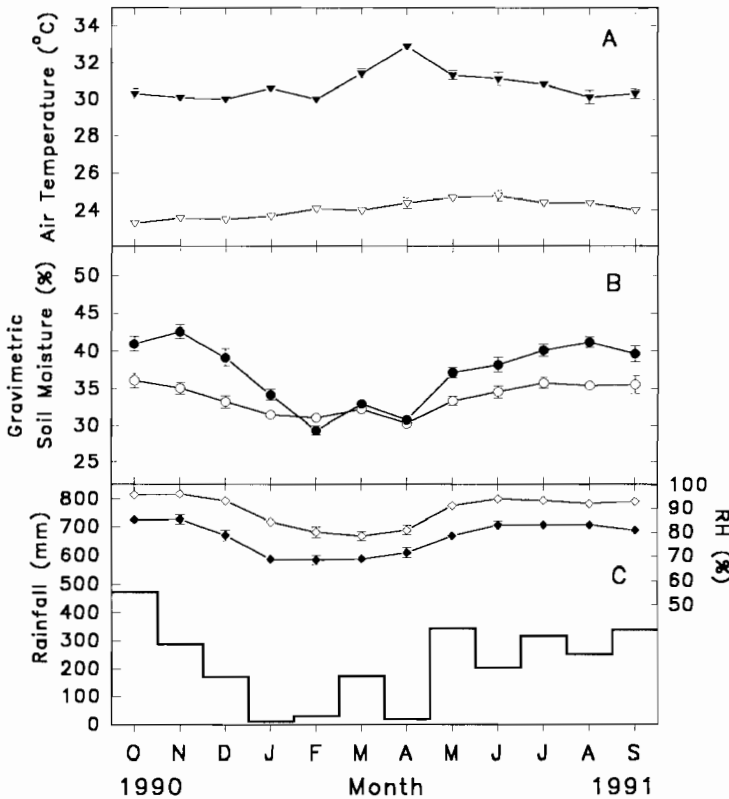


Figure 1. Main climatic features of the Barro Colorado Island (BCI) during the study period of October 1990–September 1991: A. Monthly maximum air temperatures (▼) and monthly minimum air temperatures (▽); B. Monthly gravimetric soil moisture at 10 cm depth (●) and at 40 cm depth (○); C. Monthly rainfall (open histogram) and monthly midday relative humidity in the forest understory (◇) and in the lab clearing (◆). Error bars = 1 SEM (Environmental Science Program, STRI, unpublished data).

and climbed steadily over the dry season to their highest values in April (32.9 °C) and June (24.8 °C), respectively. There was a strong seasonality in relative humidity (RH). Average monthly, midday RH during the wet season ranged from 90 to 95% in the forest understory and 80 to 85% in the laboratory clearing (Figure 1). Average monthly, midday RH during the dry season ranges from 75 to 85% in the forest understory and 60 to 75% in the laboratory clearing (Windsor 1990). During breaks in the dry season, soil water potentials at a 20-cm depth can fall to  $-2.0$  MPa (Becker et al. 1988). Gravimetric soil water at 10- and 40-cm depths was about 42 and 35%, respectively, during the wet season and about 32 and 30%, respectively, by the end of the dry season (Figure 1). The vegetation on BCI has been classified as a tropical moist forest (Holdridge and Budowski 1956) with both deciduous and evergreen trees in the canopy. Detailed descriptions of the BCI forest can be found in Croat (1978) and Leigh et al. (1982).

### Species

*Ochroma pyramidale* (Cav. ex Lam) Urban (Bombacaceae) is an evergreen, or leaf-exchanging tree, which averages 12 m in height but can reach up to 30 m in older forests. It is native to the new world and common along the lake-shore or in disturbed areas (Croat 1978). The leaves are simple with a mean leaf area of about 220 cm<sup>2</sup>. The petioles are 9 to 40 cm long and 5 to 7 mm wide. Leaves fall and are replaced throughout the year. The flowering and fruiting periods extend from August to May and February to August, respectively (Croat 1978).

*Pseudobombax septenatum* (Jacq.) Dug. (Bombacaceae) is a deciduous tree, which averages 25 m in height and is common throughout tropical moist and dry forests from Nicaragua to Brazil and Peru. The leaves are palmately compound with six to seven leaflets and a mean leaflet area of about 70 cm<sup>2</sup>. The petioles are 10 to 56 cm long and 3 to 5 mm wide. Leaves normally fall in January and grow again in May. The flowering and fruiting periods extend from January to March and February to April, respectively (Croat 1978).

### Hydraulic architecture parameters

The following parameters associated with hydraulic architecture and xylem anatomy of the whole tree were measured: (1) hydraulic conductivity ( $k_h = F/[dP/dx]$ ), where  $F$  is the water flux (kg s<sup>-1</sup>) through an excised stem segment, and  $dP/dx$  is the pressure gradient (MPa m<sup>-1</sup>) inducing the flow; (2) Huber value (HV =  $A_w/A_L$ ), where  $A_w$  is the wood cross-section area excluding the bark (m<sup>2</sup>), and  $A_L$  is the leaf area supported by the stem (m<sup>2</sup>); (3) specific conductivity ( $k_s = k_h/A_w$ ); and (4) leaf specific conductivity ( $k_L = k_h/A_L$ ).

Stems were collected early in the morning (usually right after dawn), recut immediately under water in Gatun Lake and brought back to the laboratory clearing. Hydraulic conductivity ( $k_h$ ) of stems less than 30 mm in diameter was measured with a conductivity apparatus described by Sperry et al. 1988a. Stem segments more than 30 mm in diameter were measured as described by Tyree et al. 1991. In brief, sections of rubber tire inner tube were fitted to the basal section of the stems. The stems were

held vertically and water flux ( $\text{kg s}^{-1}$ ) was measured gravimetrically at 60-s intervals. The pressure gradient ( $\text{MPa m}^{-1}$ ) was computed from the gravitational potential gradient. All stem segments measured were longer than most vessels. Vessel lengths were determined by the methods of Zimmermann and Jeje (1981, see also Tyree 1993). For *Ochroma*, 90% of the vessels were shorter than 300 mm, and for *Pseudobombax*, 95% of the vessels were shorter than 350 mm.

### *Hydraulic maps*

A large tree ( $\approx 13$  m tall) of each species was cut into numbered segments to create the data set for the hydraulic map as described by Tyree (1988). Data collected for each numbered segment were: (1) the number of the segment connected to its base, starting with zero; (2) the basal diameter excluding the bark; (3) the length of the segment (usually stems were cut to lengths that included the length of the junctions); and (4) the leaf area attached to the segment. Leaf areas were recorded with a model LI-3100 leaf area meter (Li-Cor, Lincoln, NE). In addition, four large branches (2 to 3 m long) were collected from different trees of each species to quantify the number, diameter, length, and leaf area of petioles attached to leaf-bearing stems.

Hydraulic maps of entire trees were used to calculate the steady-state profile of water potentials (Tyree et al. 1991) and the runaway embolism cycle (Tyree and Sperry 1988).

### *Water flux density measurements*

*Ochroma* and *Pseudobombax* canopy level branches were collected with a rope-driven saw chain (Forestry Suppliers Inc., Jackson, MS). The method (Tyree et al. 1991) required a fishing line attached to fishing weights that were shot over the branches with a slingshot. The fishing line was used to haul up the rope and saw. This method was used in combination with the expertise of a local tree climber. Branches were collected early in the morning.

Daily courses of water uptake ( $E$ ) were measured on excised branches bearing 1 to  $2.5 \text{ m}^2$  of leaves, with a computer-controlled potometer described by Tyree et al. (1991). In brief, water was delivered to the branches through a water-filled plastic pipe from a 2-liter container resting on a digital balance (range, 5 kg; readability  $\pm 1 \times 10^{-2}$  g). Simultaneously, basic climatic data were collected with a data logger (Datataker DT100; ZI-TECH Institute Corp., Mountain View, CA), e.g., net radiation with a net radiometer (Micromet Institute, Bothell, WA), and air temperature and relative humidity with a custom-made, aspirated psychrometer. Measurements were made every 20 s and recorded as means every 300 s. Midday  $\Psi_{\text{leaf}}$  of excised branches was measured with a Scholander-Hammel pressure bomb.

### *Leaf tissue characteristics and stem capacitance*

Large branches of each species were enclosed in plastic bags and the base of each branch was put in water and allowed to rehydrate overnight. Individual leaves and leaflets of *Ochroma* and *Pseudobombax*, respectively, were weighed to obtain a full turgor weight. Pressure-volume curves were generated by enclosing individual

leaves and leaflets sealed in plastic bags in a custom-made, 10-chamber apparatus fitted with a single pressure gauge. The chambers were pressurized with compressed air, and the pressure was raised in steps of 0.2 MPa. The extracted sap was collected every 30 min in small vials and weighed to the nearest 0.1 mg (Meinzer et al. 1990). Foliage samples were weighed, oven dried and then weighed again, and the data were used to calculate relative water content (RWC). Plots of inverse balance pressure versus RWC were used to determine the water relations parameters such as osmotic potential at zero ( $\Psi_{\pi}^0$ ) and at full turgor ( $\Psi_{\pi}^{100}$ ), relative water content at turgor loss point ( $RWC^{tlp}$ ), and tissue elastic modulus ( $\epsilon$ ) as described elsewhere (Tyree and Jarvis 1982, Robichaux et al. 1984). Leaf water capacitance ( $Q_{leaf}$ ) was calculated as the initial slope from plots of balance pressure versus water loss per unit leaf area (Tyree et al. 1991).

The diurnal course of  $\Psi_{leaf}$  was determined during a clear and sunny day at the end of the dry season on April 4, 1991. Leaves were shot down with a shotgun and  $\Psi_{leaf}$  determinations were made with a portable pressure chamber (PMS Instruments, Model 1000, Corvallis, OR), at four 3-h intervals beginning before sunrise (pre-dawn).

Stem water capacitance ( $Q_{stem}$ ) was measured as described by Tyree and Yang (1990), and Tyree et al. (1991). Two sets of stems ( $n = 3$  for each species) were used. One set was allowed to rehydrate for two days to evaluate the maximum storage capacitance, and the other set was allowed to rehydrate for no longer than 3 h to return the stems to a xylem pressure potential ( $\Psi_{xp}$ ) of 0 MPa. Stems were then allowed to dehydrate in air under laboratory conditions. Stem water potentials were measured by a temperature-corrected stem hygrometer (Dixon and Tyree 1984), and cavitations were monitored with an ultrasonic acoustic emission (AE) counter (Model 4615 Drought Stress Monitor; Physical Acoustic Corp., Princeton, NJ) for a period of 5 to 7 days while water loss was recorded gravimetrically.

The stem and leaf water capacitance data allowed us to evaluate the likely contribution of water-storage to the daily evaporative demands during the dry and wet seasons.

#### *Leaf stomatal conductance versus leaf-to-air vapor pressure difference*

Leaf stomatal conductance at light saturation was measured with a steady-state porometer (LI 1600M, Li-Cor Inc., Lincoln, NE). Measurements were made on the abaxial surface of all the leaves and leaflets on small excised branches of *Ochroma* and *Pseudobombax*, respectively. The branches were fed with tap water during the experiment. Different air vapor pressure deficits (VPD) were obtained by adjusting the relative humidity inside the porometer chamber from 90 to 60% at 30-min intervals. The xylem of small branches (e.g., less than 10 mm in diameter) slowly became plugged as a result of the exudation of mucilage from the cut surface of the stem, allowing us to measure stomatal conductance at different values of  $\Psi_{leaf}$ .

#### *Vulnerability to embolism*

Branches (1.5 to 2 m long) of each species were used to develop vulnerability curves,

the relationship between  $\Psi$  and the reduction of  $k_h$  due to the development of embolisms (Sperry et al. 1988b, Cochard et al. 1992). Entire stems (8 to 30 mm in diameter) were dehydrated to a desired  $\Psi$  and then cut underwater to prevent air from entering the severed vessels. An initial hydraulic conductivity ( $k_h = k_i$ ) was measured by the method described by Sperry et al. (1988a). Stems subsequently were flushed with a  $10 \text{ mol m}^{-3}$  oxalic acid solution at 140 kPa for 10-min to remove existing embolisms and  $k_h$  was recorded. Flushes were repeated until  $k_h$  reached a maximum ( $k_{\max}$ ). The percent loss of conductivity (PLC) was calculated from  $\text{PLC} = 100(k_{\max} - k_i)/k_{\max}$ . The  $k_{\max}$  for *Ochroma* stem segments was difficult to obtain because of plugging of the xylem conduits. Exudation of mucilage from the pith of the wood probably caused the plugging. The  $k_{\max}$  for *Ochroma* stem segments was obtained from a linear regression of stem diameter versus  $k_h$  (initial conductivity), where  $k_{\max}$  was taken as  $k_h$  measured on non-dehydrated stems with  $\Psi_{\text{xp}} \approx 0 \text{ MPa}$ .

## Results

### Hydraulic architecture

Stem hydraulic conductivities ( $k_h$ ) in the native state versus stem diameters (excluding bark) for *Ochroma* and *Pseudobombax* are shown in Figure 2. The linear regression models of  $\log k_h$  ( $Y$ ) versus  $\log$  stem diameter ( $X$ ) yielded  $Y = 2.44X - 6.19$

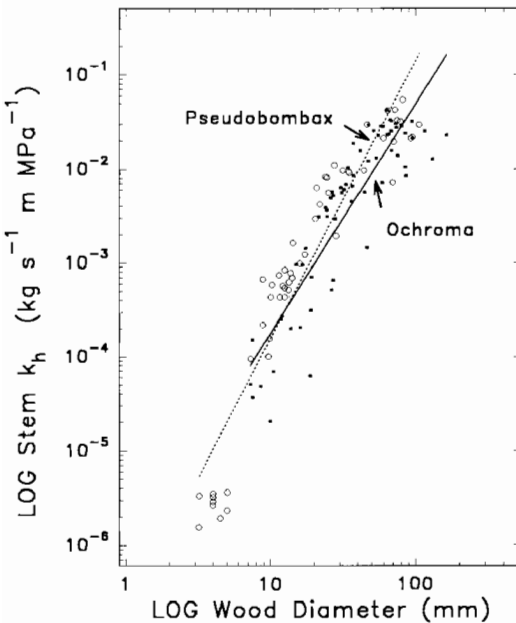


Figure 2. Log-log plot of measured hydraulic conductivity of *Pseudobombax* (O) and *Ochroma* (■) stems per unit pressure gradient ( $k_h$ ) versus diameter of the stem (excluding bark). First order polynomial regressions line are solid for *Ochroma* ( $\log k_h = -6.19 + 2.44\log(\text{Dia})$ ,  $r^2 = 0.8$ ) and dashed for *Pseudobombax* ( $\log k_h = -6.75 + 2.95\log(\text{Dia})$ ,  $r^2 = 0.88$ ).

for *Ochroma* ( $n = 65$ ,  $r^2 = 0.80$ ) and  $Y = 2.953X - 6.758$  for *Pseudobombax* ( $n = 53$ ,  $r^2 = 0.88$ ). Stem cross section is proportional to the diameter squared. So if  $k_s$  is constant, the slope of the regression should be 2.0 (Tyree 1988). The slopes were significantly different and about 2.44 and 2.95 for *Ochroma* and *Pseudobombax*, respectively, indicating that the average conduit diameter or the number of conduits per unit cross section, or both, increased with increasing stem diameter ( $F = 5.52$ ,  $df = 1114$ ,  $P < 0.02$ ).

Leaf specific conductivity ( $k_L$ ) is a useful measure of the hydraulic sufficiency of the stem in supplying water to the leaves. The values of  $k_L$  in Figure 3 were derived from the tree hydraulic maps and computed hydraulic conductivity values from Figure 2. The values included are for the entire tree excluding the petioles, which were analyzed separately from a subsample of branches. The  $k_L$  increased with stem diameter. Larger differences were found in stems less than 15 mm in diameter that corresponded to the leaf-bearing stems. The average  $k_L$  values of leaf-bearing stems of *Ochroma* were 2.3 times higher than those of *Pseudobombax* ( $11.40 \times 10^{-4}$  and  $5.15 \times 10^{-4} \text{ kg s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$ , respectively). On the other hand, the  $k_L$  values of the base of the tree (bole) of *Pseudobombax* were 5.5 times higher than those of *Ochroma*. In both species, the values of  $k_L$  for tree bases (272 and 185 mm in

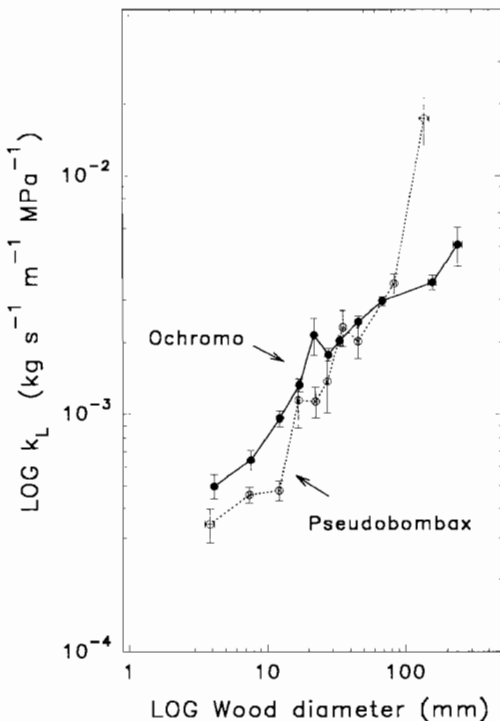


Figure 3. Log-log plot of leaf specific conductivity ( $k_L$ ) versus stem diameter (excluding bark) for *Ochroma* (●) and *Pseudobombax* (○). Values represent the mean  $k_L$  of stem segments for each size class (5 cm range). All values were calculated from the hydraulic map data and  $k_h$  values in Figure 2. Error bars = 1 SEM.



diameter for *Ochroma* and *Pseudobombax*, respectively) were 6 to 70 times higher than for leaf-bearing stems.

Table 1 shows the hydraulic architecture data for petioles and leaf-bearing stems, considered the bottleneck of water flow through trees (Zimmermann 1983). All hydraulic architecture parameters, with the exception of HVs, were lower for petioles than for leaf-bearing stems in both species. The values of  $k_L$  for petioles and leaf-bearing stems of *Ochroma* were 3.4 and 2.3 times higher, respectively, than those for *Pseudobombax*. These differences were accounted for by the higher HVs and  $k_s$ 's of petioles and leaf-bearing stems of *Ochroma*. This follows because  $k_L = k_s(\text{HV})$ . The leaf area supported by leaf-bearing stems and petioles of each species was similar.

#### Water uptake flux density

Transpirational flux densities for representative sunny days during the onset of the dry season (upper panels) and during the middle of the rainy season (lower panels) are shown in Figure 4 for both *Ochroma* and *Pseudobombax*. The maximum flux density during both days was always higher for *Ochroma* ( $7.28 \times 10^{-4}$  and  $7.36 \times 10^{-4} \text{ kg m}^{-2} \text{ s}^{-1}$  during the dry and wet season, respectively) than for *Pseudobombax* ( $4.8 \times 10^{-4}$  and  $6.2 \times 10^{-4} \text{ kg m}^{-2} \text{ s}^{-1}$  during the dry and wet season, respectively). In the middle of the dry season, maximum flux density for *Ochroma* (around  $9 \times 10^{-4} \text{ kg m}^{-2} \text{ s}^{-1}$ ) was higher than that observed during any other period of the year (data not shown).

Diurnal courses of  $\Psi_{\text{leaf}}$  in excised branches were measured and the midday values were very similar for the two species on both days (Figure 4, small panels).

#### Leaf tissue characteristics and stem capacitances

Leaf capacitance ( $Q_{\text{leaf}}$ ) at a given  $\Psi_{\text{leaf}}$  was calculated as the inverse slope of the

Table 1. Hydraulic architecture data for petioles and leaf-bearing stems of *Ochroma* and *Pseudobombax* from the hydraulic maps. The petioles were collected from large representative branches of different trees ( $n = 4$ ). The values are the mean and 1 SEM (in parenthesis). The values next to the species name are the maximum path length from the base of the tree to the apex of the tallest stem (m) and the total leaf area supported by each tree ( $\text{m}^2$ ).<sup>1</sup>

	<i>Ochroma</i> 12.2 m, 83.02 m <sup>2</sup>		<i>Pseudobombax</i> 13.8 m, 22.96 m <sup>2</sup>	
	Petioles	Leaf-bearing stems	Petioles	Leaf-bearing stems
$n$	261	329	223	87
Diameter (mm)	4.24 (0.16)	9.12 (0.20)	3.55 (0.09)	8.09 (0.32)
Leaf area (m <sup>2</sup> )	0.034 (0.005)	0.25 (0.01)	0.029 (0.002)	0.26 (0.02)
$k_h \times 10^5$ (kg s <sup>-1</sup> m <sup>-1</sup> MPa <sup>-1</sup> )	2.35 (0.23)	18.23 (0.96)	0.78 (0.06)	12.22 (1.99)
$k_s$ (kg s <sup>-1</sup> m <sup>-1</sup> MPa <sup>-1</sup> )	1.53 (0.02)	2.11 (0.02)	0.74 (0.02)	1.62 (0.06)
HV $\times 10^4$	5.91 (0.62)	3.74 (0.23)	3.61 (0.10)	3.28 (0.25)
$k_L \times 10^4$ (kg s <sup>-1</sup> m <sup>-1</sup> MPa <sup>-1</sup> )	9.08 (1.05)	11.4 (0.54)	2.64 (0.06)	5.15 (0.51)

<sup>1</sup> Abbreviations:  $n$ , number of petioles and leaf-bearing stems;  $k_h$ , hydraulic conductivity;  $k_s$ , specific conductivity; HV, Huber value;  $k_L$ , leaf specific conductivity.

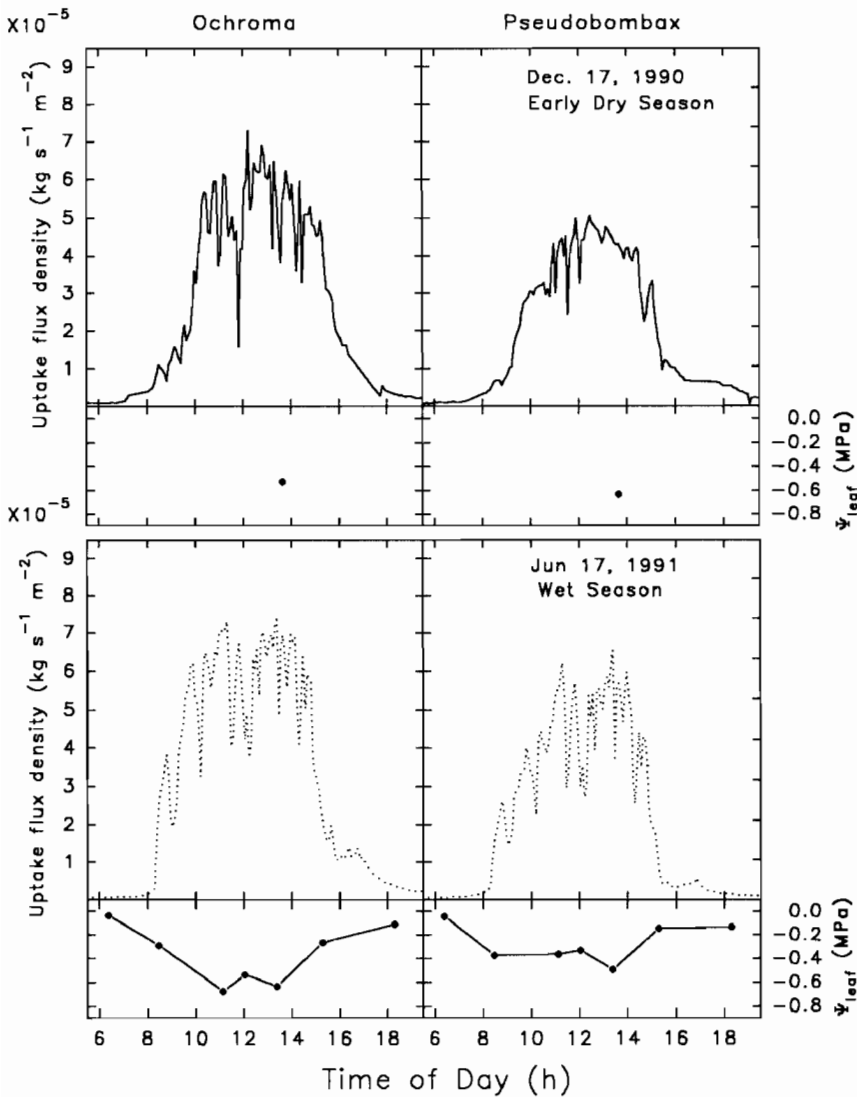


Figure 4. Diurnal water uptake flux density (large panels) and  $\Psi_{\text{leaf}}$  (small panels) measured during the early dry season (December 17, 1990) and wet season (June 17, 1991) for *Ochroma* and *Pseudobombax* branches.

curve in Figure 5. The results presented are for one representative leaf of each species. The initial  $Q_{\text{leaf}}$  was lower for *Ochroma* ( $0.003 \text{ kg m}^{-2} \text{ MPa}^{-1}$ ) than for *Pseudobombax* ( $0.008 \text{ kg m}^{-2} \text{ MPa}^{-1}$ ). Leaf tissue characteristics derived from the pressure-volume curves are presented in Table 2. The osmotic potentials at full turgor ( $\Psi_{\pi}^{100}$ ) and at turgor loss point ( $\Psi_{\pi}^{\text{tlp}}$ ) were  $-1.37$  and  $-1.60$  MPa for *Ochroma*, respectively, and  $-0.91$  and  $-1.28$  MPa for *Pseudobombax*, respectively. The mean maximum cell wall elastic modulus ( $\epsilon$ ) was lower for *Pseudobombax* (12.8 MPa) than for *Ochroma* (25.7 MPa); these values in combination with differences in

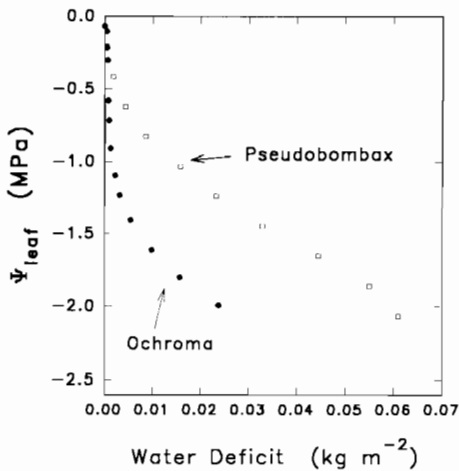


Figure 5. Leaf water potential isotherms from pressure–volume curves for *Ochroma* (●) and *Pseudobombax* (○), generated by plotting  $\Psi_{\text{leaf}}$  versus water loss in  $\text{kg m}^{-2}$  of leaf area. Values presented from one representative leaf.

Table 2. Leaf tissue characteristics from pressure–volume curves for *Ochroma* and *Pseudobombax*. Data were collected on fully expanded leaves during the first week of April 1991. The column headings are osmotic potential at full turgor ( $\Psi_{\pi}^{100}$ ) and at turgor loss point ( $\Psi_{\pi}^{\text{tlp}}$ ), relative water content at turgor loss point ( $\text{RWC}^{\text{tlp}}$ ), and tissue elastic modulus ( $\epsilon$ ). Values are the mean and 1 SEM (in parenthesis),  $n = 3$  and 6 for *Ochroma* and *Pseudobombax*, respectively.

Species	$\Psi_{\pi}^{100}$ (MPa)	$\Psi_{\pi}^{\text{tlp}}$ (MPa)	$\text{RWC}^{\text{tlp}}$	$\epsilon$ (MPa)
<i>Ochroma</i>	-1.37 (0.03)	-1.60 (0.03)	0.95 ( $6.3 \times 10^{-4}$ )	25.74 (1.01)
<i>Pseudobombax</i>	-0.91 (0.01)	-1.28 (0.02)	0.87 ( $3.5 \times 10^{-3}$ )	12.80 (0.76)

relative water content at turgor loss point ( $\text{RWC}^{\text{tlp}} = 0.87$  and  $0.95$  for *Pseudobombax* and *Ochroma*, respectively) suggest that the tissue of *Pseudobombax* is more elastic.

Diurnal variations in  $\Psi_{\text{leaf}}$  were measured from several trees 12 to 18 m tall and are presented in Figure 6. The difference in  $\Psi_{\text{leaf}}$  between predawn and midday was larger for *Ochroma* than for *Pseudobombax* ( $-0.87$  MPa versus  $-0.28$  MPa).

The stem dehydration isotherms (Figure 7, upper panels) followed the three phases of dehydration (capillary, elastic and cavitation water storage) described by Tyree and Yang (1990) for stems of *Thuja*, *Tsuga* and *Acer*. There was an increase in stem capacitance ( $Q_{\text{stem}}$ ) with a decrease in  $\Psi$  and this was associated with an increase in cavitation events, as detected acoustically (Figure 7, bottom panels). The dry season  $Q_{\text{stem}}$  values for a range of  $\Psi$  from  $-0.15$  to  $-1.0$  MPa were slightly different for *Ochroma* and *Pseudobombax* ( $0.062$  and  $0.078 \text{ kg l}^{-1} \text{ MPa}^{-1}$ , respectively). Larger differences of  $Q_{\text{stem}}$  for the same range of  $\Psi$  were found in the rehydrated stems ( $0.134$  and  $0.047 \text{ kg l}^{-1} \text{ MPa}^{-1}$  for *Ochroma* and *Pseudobombax*, respectively).

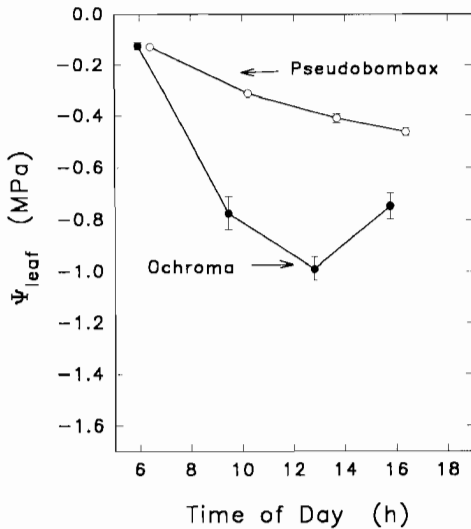


Figure 6. Diurnal course of  $\Psi_{\text{leaf}}$  for *Ochroma* (●) and *Pseudobombax* (○) trees. Measurements were taken on April 4, 1991, during a clear and sunny day on fully expanded leaves. Data points represent the mean of five values. Error bars = 1 SEM.

#### *Leaf stomatal conductance versus leaf-to-air vapor pressure difference ( $\Delta W$ )*

Figure 8 shows the response of leaf stomatal conductance to variations in  $\Delta W$  for different values of  $\Psi_{\text{leaf}}$ . *Ochroma* had light-saturated stomatal conductances that were 6 to 10 times higher than those for *Pseudobombax* for the same range of  $\Psi_{\text{leaf}}$  ( $\approx -0.2$  MPa) and  $\Delta W$  values. Both species showed a reduction in stomatal conductance with increasing  $\Delta W$ , indicating the presence of stomatal control. However, there was no evidence of complete stomatal closure at either high  $\Delta W$  or low  $\Psi_{\text{leaf}}$ .

#### *Vulnerability curves*

The relationship between  $\Psi$  and the percentage loss in hydraulic conductivity (PLC), as a result of the formation of embolisms, for leaf-bearing stems of *Ochroma* and *Pseudobombax* is shown in Figure 9. The two species showed similar vulnerability to embolism. Stems of both species lost 50% of their conductivity at  $\Psi \approx -0.95$  MPa. The vulnerability curve of *Schefflera morototoni*, Aralaceae, an evergreen tropical canopy tree, is included only for comparison (Tyree et al. 1991).

## Discussion

The vulnerability of xylem to water-stress-induced embolism was remarkably similar for *Ochroma* and *Pseudobombax* and was higher than that for most tree species growing in the temperate forest where water is not limiting (Tyree and Ewers 1991). Nevertheless, it seems to be consistent with previous values reported for another tropical evergreen species, *Schefflera morototoni* (Figure 9). The high vulnerability to embolism of tropical evergreen and deciduous tree species is comparable only

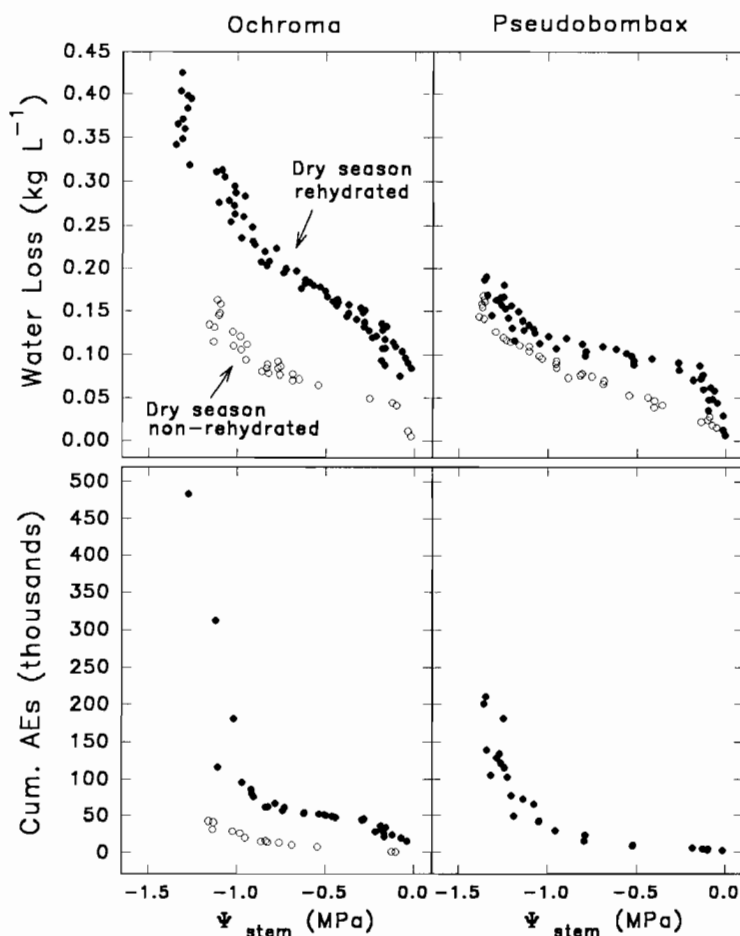


Figure 7. Dehydration isotherms of stems of *Ochroma* and *Pseudobombax*. Values presented are water loss versus  $\Psi_{\text{stem}}$  for rehydrated (●) and non-rehydrated (○) stems collected during the dry season (upper panels) and cumulative acoustic emissions versus  $\Psi_{\text{stem}}$  (lower panels).

with the vulnerability reported for *Populus deltoides* growing in Canada and the northern United States (Tyree et al. 1992, Tyree et al. in preparation).

The hydraulic architecture of *Ochroma* appeared to be more efficient in supplying water to the leaves (higher  $k_L$ ) than that of *Pseudobombax* (Table 1, Figure 3). However, the differences were small and found only in the leaf-bearing stems and petioles, which are considered the bottleneck of water transport (Zimmermann 1983), but not in stems larger than 15 mm (main branches and bole, Figure 3). Goldstein et al. (1989) reported large differences in leaf specific conductivity for leaf-bearing stems ( $\approx 11$  mm in diameter) of tropical evergreen and deciduous savanna species ranging from  $20.8$  to  $6.56 \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$  and  $1.21$  to  $2.79 \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$ , respectively. However, they did not take into account the entire hydraulic architecture of the species. Their work suggests that the more efficient hydraulic

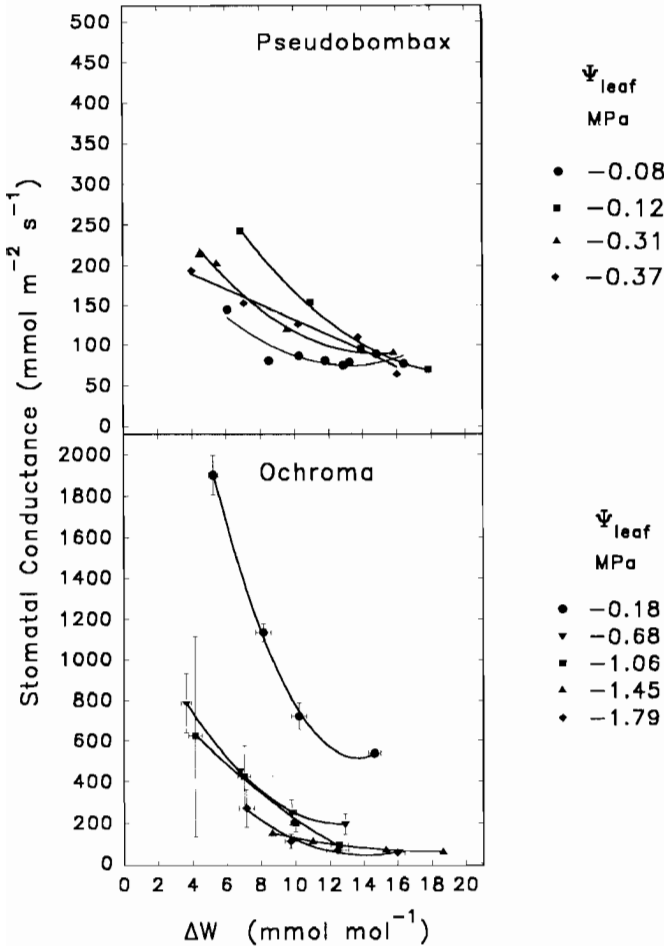


Figure 8. Leaf stomatal conductance response to leaf-to-air vapor pressure difference at different values of  $\Psi_{\text{leaf}}$  for *Pseudobombax* (upper panel) and *Ochroma* (lower panel). Values represent the mean of two values for *Ochroma*. Error bars = 1 SEM.

architecture of the evergreen trees allows them to maintain their leaves at a more favorable water balance (less negative  $\Psi$ ) than the deciduous trees during periods of higher evaporative demand. Here, we used the data from the hydraulic architecture map to evaluate the impact of  $k_L$  on the profile of stem  $\Psi_{xP}$  versus the path length of the tree during steady-state evaporation (Figure 10). We also included the results for another tropical evergreen species, *Schefflera morototoni*, previously reported by Tyree et al. (1991). Every leaf was allowed to have the same evaporative flux density ( $E$ ) at steady-state evaporation measured during the onset of the dry season (i.e., December; see Table 3 and Figure 4), and the profiles of stem  $\Psi_{xP}$  were calculated from the base of the tree to some representative leaf-bearing stems. The low  $k_L$  values of terminal branches in the evergreen and deciduous species caused steep declines in  $\Psi_{xP}$  with increased distance through the minor stems. The gradient in  $\Psi_{xP}$  needed

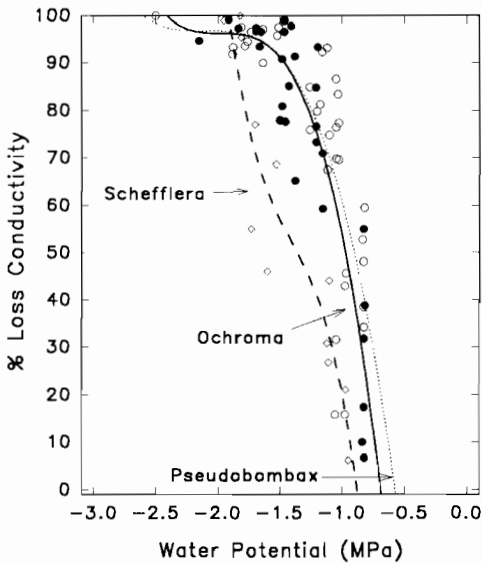


Figure 9. Vulnerability curves for *Ochroma* (●), *Pseudobombax* (○) and *Schefflera* (◇) stems. Curves indicate the  $\Psi$  required to induce a given percent loss of hydraulic conductivity. The curve for *Schefflera* is presented for comparison and was originally reported by Tyree et al. (1991). Each point represents a separate stem. Lines are the result of third order polynomial regression.

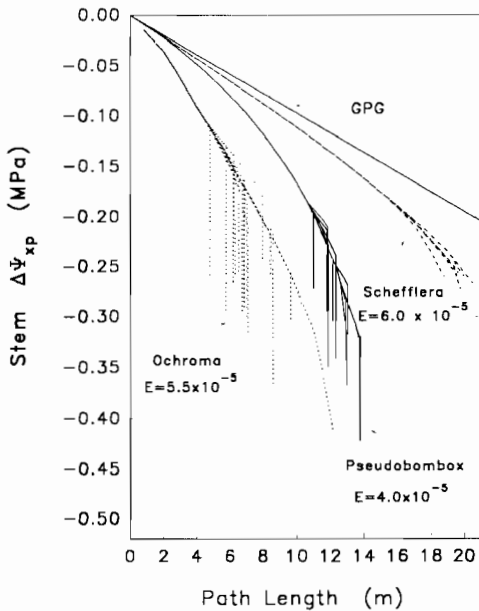


Figure 10. Profiles of xylem pressure potential ( $\Psi_{xp}$  in MPa) of stems of *Ochroma* (dots) and *Pseudobombax* (solid line) versus the path length (distance in m) water must travel from the base of the tree to the leaf-bearing stems. All values include the gravitational potential gradient (GPG). Curves are calculated from the hydraulic maps and average midday evaporative flux density ( $E$  in  $\text{kg s}^{-1} \text{m}^{-2}$ ) measured early in the dry season.

to supply water to the more distal leaf-bearing stems was similar for *Ochroma* (33.4 kPa m<sup>-1</sup>) and *Pseudobombax* (24.2 kPa m<sup>-1</sup>) and was much smaller for *Schefflera* (12.5 kPa m<sup>-1</sup>). But *E* was 8 and 30% lower for *Ochroma* and *Pseudobombax*, respectively, compared to that for *Schefflera* during the early dry season (Figure 11 and Figure 5 in Tyree et al. 1991). However, we found a discrepancy between the calculated drop in  $\Psi_{xP}$  and the values measured in the field (Figure 6) for *Pseudobombax*. This difference may be explained by either an over-estimation of the *E* values measured with the potometer or by an error in the measurements of  $\Psi_{xP}$  ( $\approx \Psi_{leaf}$ ) in the field. Also, we evaluated only the drop of  $\Psi_{xP}$  from the base of the tree to the leaf-bearing stems and we expect to find even larger drops in  $\Psi_{xP}$  when the hydraulic resistances from the roots and petioles are included.

The results shown in Figure 10 are in accordance with the segmentation hypothesis proposed by Zimmermann (1983). He suggested that *k<sub>L</sub>* declines toward terminal stems and that this decline helps to confine cavitation and embolism to more expendable minor branches. If this is the case, there could be strong hydraulic segmentation causing a very rapid decline of  $\Psi_{xP}$  in petioles, leading to leaf dieback. This induced dieback could be a strategy for avoiding excessive embolism formation and protecting the more essential parts of the tree, such as the leaf-bearing stems and

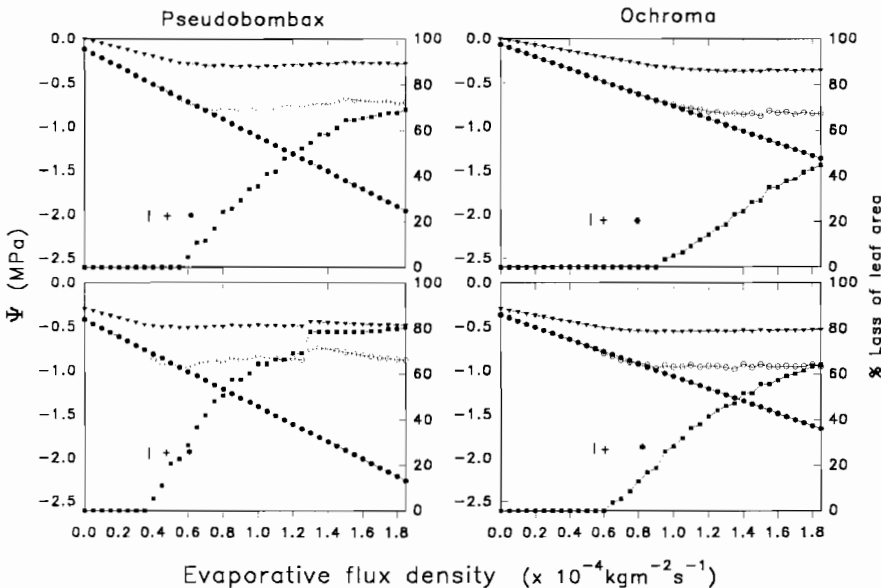


Figure 11. Runaway embolism cycle model of *Pseudobombax* and *Ochroma* for different values of soil water potential: 0 MPa (upper panels) and -0.3 MPa (lower panels). Values shown are  $\Psi$  at the base of the tree ( $\blacktriangledown$ ), the average  $\Psi$  of all leaf-bearing stems assuming no embolism ( $\bullet$ ) or if embolism occurred ( $\circ$ ), and the percent loss of leaf area ( $\blacksquare$ ). The symbols |, + and \* represent the maximum values of evaporative flux density (*E*) measured for both species in July, December, and March, respectively (see Table 3). The *E*\* value for *Pseudobombax* is hypothetical based on what it might be if leaves were retained and the ratio of *E* between *Ochroma* and *Pseudobombax* maintained (see Table 3). Root resistance was set to a constant value of 100% of the total shoot resistance (21 and 105 MPa s kg<sup>-1</sup> for *Ochroma* and *Pseudobombax*, respectively).



main branches. However, for the hydraulic segmentation to be effective, it is necessary that  $E$  remains high and constant during the periods when  $\Psi$  in the leaf-bearing stems, petioles and leaves is low enough to induce cavitations and embolisms. Under these conditions, the drop in  $\Psi_{xP}$  between the petioles or leaves and the leaf-bearing stems might be large enough to confine embolisms to the distal organs (Tyree et al. in preparation). But this situation is unlikely to occur because plants usually reduce transpiration through stomatal closure when their  $\Psi$  reaches very negative values (Hsiao 1973, Ludlow 1980). Nevertheless, recent evidence presented by Sperry and Pockman (1993) and Sperry et al. (1993) for *Betula occidentalis*, suggests that in some cases, stomatal regulation is not sufficient to prevent runaway embolism.

Overall, as noted by Tyree et al. (1991), we cannot predict the entire role of strong hydraulic segmentation without knowledge of the vulnerability of petioles and leaves versus large stems.

The  $k_L$  of leaf-bearing stems of tropical canopy trees is 5 to 200 times higher than that of temperate trees such as *Acer saccharum* and *Thuja occidentalis* (Tyree and Ewers 1991, Tyree et al. 1991). The values of  $k_L$  in tropical species ranged from  $5 \times 10^{-4}$  to  $11 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$  for *Pseudobombax* and *Ochroma*, respectively, and from  $0.05 \times 10^{-4}$  to  $1 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$  for *Thuja* and *Acer*, respectively (Tyree et al. 1991). The higher  $k_L$  values in tropical tree species versus temperate tree species were, in part, due to the larger HVs of the tropical tree species (i.e., *Pseudobombax* and *Ochroma* produced more stem cross-sectional area per unit leaf area than *Thuja* and *Acer*). In comparison, the HVs of leaf-bearing stems for the tropical tree species ranged from  $3 \times 10^{-4}$  to  $4 \times 10^{-4} \text{ m}^2$ , and for the temperate tree species, ranged from  $0.2 \times 10^{-4}$  to  $2 \times 10^{-4} \text{ m}^2$  (Tyree et al. 1991). The remaining difference in  $k_L$  values was due to the differences in  $k_s$ , since  $k_L = \text{HV}(k_s)$ . However, leaves of tropical trees tend to have higher evaporative flux densities ( $E$ ) than temperate trees, so differences in the gradient of  $\Psi_{xP}$  needed to supply water to the more distal leaf-bearing stems are not as large as expected in accounting only for differences in  $k_L$  (Tyree and Ewers 1991).

It seems that tropical tree species show a pattern of highly vulnerable stems with high leaf specific conductivities. This pattern supports ideas about the existence of a trade-off between the safety and efficiency of the xylem found in temperate tree species (Zimmermann 1983, Tyree and Sperry 1989). Both *Pseudobombax* and *Ochroma* risk high vulnerability for higher  $k_L$ .

To test further the ability of *Ochroma* and *Pseudobombax* stems to maintain elevated transpiration rates during periods of high evaporative demand before any dieback occurs, we used the runaway embolism cycle model described by Tyree and Sperry (1988) to model the loss of leaf area and conductivity under conditions of unstable embolism (Figure 11). Root resistance was set to a constant value calculated as a percentage (i.e., 100%) of the total shoot resistance (total average shoot resistance was 42 and 210  $\text{MPa s kg}^{-1}$  for *Ochroma* and *Pseudobombax*, respectively). When the  $\Psi_{\text{soil}}$  was assumed to be at or near saturation (i.e., 0 MPa), the model predicted the initiation of loss of leaf area at  $E$  values higher than those observed at any time of the year for each species (Figure 11 upper panels, and

Table 3). However, when the  $\Psi_{\text{soil}}$  was reduced to  $-0.3$  MPa, the leaf-bearing stems of *Pseudobombax* were predicted to begin to dieback due to the formation of embolisms, leading to an increase in percent loss of leaf area at  $E$  values larger than  $3.5 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$ , whereas the leaf-bearing stems of *Ochroma* started to lose leaf area at  $E$  values higher than  $6.0 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$  (Figure 11, bottom panels). If *Pseudobombax* were to keep its leaves during the dry season and maintain an  $E$  ranging from  $3.5$  to  $6.0 \text{ kg m}^{-2} \text{ s}^{-1}$  (Table 3), this would induce a predicted loss of leaf area of 5 to 30%. The percent loss of leaf area presented in the runaway embolism model is not enough to explain the deciduous behavior of *Pseudobombax* trees. It is possible that the petioles of *Pseudobombax* are even more vulnerable to embolism than the leaf-bearing stems, but more work is required to test this hypothesis.

Nevertheless, the biggest unknown in this model is the contribution of the root resistance to the overall hydraulic architecture and vulnerability to embolism. To estimate the effect of root resistance, we calculated the  $E$  at which 10% of leaf loss ( $E_{10\%}$ ) occurs based on the runaway embolism cycle model, changing the root resistance or the  $\Psi_{\text{soil}}$  (Table 4). Increasing the root resistance by a factor of 4 from 50 to 200% resulted in a decrease of  $E_{10\%}$  from  $14.0 \times 10^{-5}$  to  $8.0 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$  in *Ochroma* and  $8.0 \times 10^{-5}$  to  $5.0 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$  in *Pseudobombax*. Lowering the  $\Psi_{\text{soil}}$  from  $-0.2$  to  $-0.6$  MPa resulted in even larger changes in  $E_{10\%}$  from  $9.0$  to  $4.5 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$  in *Ochroma* and  $5.0$  to  $2.5 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$  in *Pseudobombax*. The latter values were in the range of  $E$  values measured in excised branches. This analysis showed the importance of including the root water transport properties and soil water availability in the overall hydraulic architecture of trees; work of this kind is lacking in the literature (Tyree and Ewers 1991).

Some authors (Waring and Running 1978, Waring et al. 1979, Tyree and Ewers 1991, Tyree et al. 1991) have suggested that the contribution of water storage from stems and leaves may be important in the seasonal and diurnal water economy of trees. We have evaluated this role in evergreen and deciduous trees under steady-state evaporation conditions (Table 5). Stem capacitance was assigned a constant value of  $0.10$  and  $0.06 \text{ kg l}^{-1} \text{ MPa}^{-1}$  (valid for  $\Psi = -0.15$  to  $-1$  MPa) for *Ochroma* and *Pseudobombax*, respectively. Leaf capacitance was given a value of  $0.003$  and  $0.008 \text{ kg m}^{-2} \text{ MPa}^{-1}$  (valid for  $\Psi = 0$  to  $-1.0$  MPa) for *Ochroma* and *Pseudobombax*,

Table 3. Midday values of evaporative flux density,  $E$ , for March, July, and December, measured with the potometer, and of  $\Psi_{\text{leaf}}$  for April, measured in the field. Values are the mean and the number of observations (in parenthesis).

Species	$E$ ( $\times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1}$ )			$\Psi_{\text{leaf}}$ (MPa)
	March	July	December	April
<i>Ochroma</i>	8.4 (48)	6.0 (48)	5.3 (48)	-1.09 (5)
<i>Pseudobombax</i>	6.0 <sup>1</sup>	4.5 (48)	3.8 (48)	-0.46 (5)

<sup>1</sup> *Pseudobombax* trees are leafless during the month of March and evaporative flux density was calculated based on the ratio of  $E$  between the two species for July and December.

Table 4. Effect of changing the  $\Psi_{\text{soil}}$  or root resistance ( $r_r$ ) on the evaporative flux density at which 10% leaf loss ( $E_{10\%}$ ) occurs. The  $E_{10\%}$  values were obtained using the runaway embolism model described by Tyree and Sperry (1988). The  $r_r$  values are expressed as a percentage of the total shoot resistance (42 and 210  $\text{MPa s kg}^{-1}$  for *Ochroma* and *Pseudobombax*, respectively) calculated from the hydraulic maps.

$\Psi_{\text{soil}}$ (MPa)	$r_r$ (%)	$E_{10\%}$ ( $\text{kg m}^{-2} \text{s}^{-1}$ )	
		<i>Ochroma</i>	<i>Pseudobombax</i>
0.0	25	$1.6 \times 10^{-4}$	$9.0 \times 10^{-5}$
0.0	50	$1.4 \times 10^{-4}$	$8.0 \times 10^{-5}$
0.0	75	$1.3 \times 10^{-4}$	$7.5 \times 10^{-5}$
0.0	100	$1.1 \times 10^{-4}$	$6.5 \times 10^{-5}$
0.0	150	$9.5 \times 10^{-5}$	$5.5 \times 10^{-5}$
0.0	200	$8.0 \times 10^{-5}$	$5.0 \times 10^{-5}$
-0.2	100	$9.0 \times 10^{-5}$	$5.0 \times 10^{-5}$
-0.3	100	$8.0 \times 10^{-5}$	$4.5 \times 10^{-5}$
-0.4	100	$6.5 \times 10^{-5}$	$4.0 \times 10^{-5}$
-0.6	100	$4.5 \times 10^{-5}$	$2.5 \times 10^{-5}$

Table 5. Stem and leaf water-storage capacitances ( $Q_{\text{stem}}$  and  $Q_{\text{leaf}}$ ), and the contribution of stored water to the diurnal transpiration of *Ochroma* and *Pseudobombax*. The  $Q_{\text{stem}}$  was measured during the dry season from rehydrated and non-rehydrated stems, and the  $Q_{\text{leaf}}$  was obtained from the pressure-volume curves.

Species	$Q_{\text{leaf}}$ ( $\text{kg m}^{-2} \text{MPa}^{-1}$ )	$Q_{\text{stem}}$ ( $\text{kg l}^{-1} \text{MPa}^{-1}$ )	Extractable water		% $T_{\text{leaf}}^1$	% $T_{\text{stem}}$	$V/A^2$ ( $\text{l m}^{-2}$ )
			Leaf (kg)	Stem (kg)			
<i>Ochroma</i>	0.003	0.06 to 0.13	0.14	15.9	< 1	20	4.96
<i>Pseudobombax</i>	0.008	0.05 to 0.07	0.14	2.5	< 1	18	5.72

<sup>1</sup> % $T$  is the percentage of the total transpiration from predawn to midday (0.95 and 0.67  $\text{kg m}^{-2}$  for *Ochroma* and *Pseudobombax*, respectively) derived from water storage in the leaves and stems based on the  $\Psi_{\text{leaf}}$  and  $\Psi_{\text{stem}}$  differences from predawn to midday, respectively.

<sup>2</sup>  $V/A$  is the stem volume per unit leaf area.

respectively. Root resistance was assigned a value of 50% of the total shoot resistance of every tree (see above). Soil  $\Psi$  was assigned a value of  $-0.004$  MPa. The model predicted a change in water storage from predawn to midday of 15.9 and 2.5 kg in stems of *Ochroma* and *Pseudobombax*, respectively, and 0.14 kg in leaves of both species, compared with a total of 80 and 15 kg of water transpired for *Ochroma* and *Pseudobombax*, respectively. Thus, stem water storage accounts for almost 20% of the total transpired water from predawn to midday for both species, whereas leaf water storage accounts for less than 1%. The similarity in these values may be explained by the similar stem volume per unit leaf area ratio observed in the two species (Table 5). The large contribution of stem water capacitance to the daily transpiration perhaps reduces the water uptake from the roots to the leaves at periods of high evaporative demand, allowing the plant to invest less in the production of roots (Tyree and Ewers 1991).

At this point we cannot conclude that the hydraulic architecture and vulnerability to embolism of tropical trees is the ultimate cause of the phenological patterns observed. But a pattern has emerged where the high vulnerability of xylem to water-stress-induced embolism of these species is associated with a highly efficient hydraulic architecture, independent of the water availability, and the phenological strategies. The high efficiency of the stems will prevent the development of large drops in water potential and thus reduce the formation of embolism in the more valuable parts of the trees, such as the leaf-bearing stems and leaves. The hydraulic architecture also may play an important role in the competitive abilities of these two tropical species by allowing them to maintain high transpiration rates with a small reduction in  $\Psi_{XP}$ , thus ensuring the maintenance of high turgor in the growing and reproductive parts of these trees.

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