

# Water Relations and Hydraulic Architecture of a Tropical Tree (*Schefflera morototoni*)<sup>1</sup>

## Data, Models, and a Comparison with Two Temperate Species (*Acer saccharum* and *Thuja occidentalis*)

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### ABSTRACT

The water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*) and of two temperate species (*Acer saccharum* and *Thuja occidentalis*) are reported. Among the water relations parameters measured were leaf and stem water storage capacity, leaf water potential, transpiration, and vulnerability of stems to cavitation and loss of hydraulic conductivity by embolisms. Among the hydraulic architecture parameters measured were hydraulic conductivity per unit pressure gradient, specific conductivity, leaf-specific conductivity, and Huber value. In terms of vulnerability of stems to cavitation, stem and leaf capacitances, and leaf-specific conductivity, all three species followed the same sequence: *Schefflera* > *Acer* > *Thuja*. It is argued here that the high stem capacitance and high leaf-specific conductivity of *Schefflera* are necessary to compensate for its high vulnerability to cavitation. Extractable water storage per unit leaf area in *Schefflera* stems is >100 times that of *Acer* and may permit the species to survive unusually long, dry seasons in Panama. Although *Schefflera* frequently grows >20 meters, the biggest resistance to water flow in the shoots resides in the leaves.

We have begun a study of the comparative physiology of large (dominant and co-dominant) canopy trees on the Barro Colorado National Monument, Central Panama. The study site is classified as a tropical moist-forest ecosystem (Holdridge Life Zone system, ref. 8). Trees at this site experience an 8-month wet season and 4-month dry season. Most species of large trees (80–90%) are evergreen; the remainder are leafless for all or at least part of the dry season. We hope that a study of the comparative water relations, hydraulic architecture, and vulnerability to embolism will provide insights into the advantages, necessities, and/or cost benefits of the different

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phenological strategies for surviving in a seasonally dry rainforest.

For example, Goldstein *et al.* (7) studied two evergreen and two deciduous species in the savanna of Venezuela. They reported that the stems of evergreen species had higher LSCs<sup>2</sup> than the deciduous species. Higher LSCs mean that the evergreen species can sustain the same transpiration flux density,  $E$ , from leaves as the deciduous species with a smaller xylem  $dP/dx$  in the stems. Other relevant features that may differ between evergreen and deciduous species are: (a) HV, the sapwood cross-sectional area per unit leaf area fed by the stem; (b)  $k_s$ , which is a measure of porosity of xylem conduits (vessels or tracheids) and chiefly reflected in conduit size and number per unit area; (c) water storage capacity of stems and leaves; (d) vulnerability of xylem to cavitation; and (e) root architecture. These factors are not all independent, e.g. LSC mathematically is the product of  $HV \times k_s$ , and a high vulnerability to cavitation can be compensated for by favorable root and shoot architectures.

*Schefflera morototoni* (formerly *Didymopanax morototoni*), Aralaceae, is an evergreen species that is an early colonizer of gaps. As a juvenile tree, it grows rapidly to a height of 10 to 18 m without branching. The leaves are palmately compound with 10 to 12 leaflets. In juveniles, leaflets can be 20 to 60 cm long and 10 to 20 cm wide; the leaflets are attached by short petiolules to the top of a petiole 0.5 to 1 m long and 5 to 10 mm diameter. Trees 10 to 18 m tall have boles (trunks) 10 to 20 cm diameter at breast height; at this size the terminal apex is replaced by a flower bud. While fruiting, two new shoot apices form, and the tree branches dichotomously. Most years thereafter, the tree forms more or less synchronous terminal inflorescences and each branch forks; however, the pattern of stem junction scars indicates that both branches survive only once every 3 to 4 years. The leaflets and petioles in an adult tree are one-half to one-third the size found in juveniles. The smallest stems bearing petioles are 1.5 to 3 cm in diameter in

<sup>2</sup> Abbreviations: LSC, leaf specific conductivity of stems;  $dP/dx$ , pressure gradient;  $\Delta P$ , pressure difference;  $\Psi_P$ , xylem pressure potential;  $E$ , evaporative flux density from leaves;  $k_h$ , hydraulic conductivity of stems;  $k_s$ , specific conductivity of stems; HV, Huber value;  $\Psi$ , water potential;  $\Psi$  leaf, soil, stem, wood, petiolule, etc. water potential.

adult trees. We thought that *S. morototoni* might be an excellent candidate for modeling of water flow through single large trees because: (a) models for large trees can be simplified by making use of the more or less symmetrical dichotomous branching pattern of the tree; and (b) the trees can be mapped in great detail while taking account of only a few stem segments because the stems are large in diameter and few in number.

## MATERIALS AND METHODS

### Plant Material and Sites

Studies on *Schefflera morototoni* (Aublet) Maguire, Steyermark, Frodin were conducted from October to December 1989 and 1990 (wet season) and February to March 1990 (dry season). All plant material was collected from juvenile and young adult trees in a man-made clearing on Gigante Peninsula, Barro Colorado National Monument (9° 7.5' N, 79° 52' W). The soil type has been classified (2) as Frioles clay, which is characterized by its red color (slightly brownish in the uppermost 5 cm) and by being well-drained, well-aerated, slightly acid to alkaline, and friable when wet. Soils were derived by decomposition of Bohio sandstones and conglomerates (10). The typical daily minimum and maximum temperatures are 21° and 32°C with about a 2°C annual variation in monthly median temperature. Average precipitation in the wet season (mid-April to mid-December) is 2400 mm, and in the dry season (mid-December to mid-April) is 200 mm with typically 30 mm/month in January, February, and March. RH of the air reaches a mean midday low of 68 to 72% at 40 m height in the dry season (21);  $\Psi_{\text{soil}}$  never falls below -0.01 MPa in the rainy season. By the end of the dry season,  $\Psi_{\text{soil}}$  reaches a minimum of -1 MPa at a depth of 0.25 m (measured at another study site 4 km away, monitored 1986-1988 [22]). At better drained sites on Barro Colorado Island,  $\Psi_{\text{soil}}$  as low as -2 MPa has been reported (1).

Studies on *Acer saccharum* Marsh. were completed in the summers of 1986 through 1988. Stems were collected from saplings 3 to 5 m tall and 3 to 8 years old (from the Vermont State Tree Nursery, Essex Junction, VT, 44° 30' N, 73° 07' W) and from adult trees >9 m tall 30 to 100 years old (from the Proctor Maple Research Center, Underhill Center, VT, 44° 32' N, 72° 52' W). The soil types were loamy sand at the Essex Junction site and stony silt loam at the Underhill Center site. The average annual precipitation at the Essex Junction site is 855 mm, with 407 mm occurring in the growth season (late May to early October). Precipitation rates are less well documented at the Underhill Center site; on the basis of a few years of records collected at the Proctor Maple Research Center, the annual precipitation is approximately 1600 mm, with approximately 800 mm in the growing season. Daily average minimum and maximum temperatures are 15° and 27°C, respectively, in July and 7° and 14°C, respectively, in May and October. RH of the air measured at 1.5 m above the ground is 20 to 60% on most sunny days from June to September.  $\Psi_{\text{soil}}$  rarely falls below -0.1 MPa at a depth of 0.3 m in summer (unpublished records collected by the Proctor Maple Research Center over a 20-year period).

### Water Use and Capacitances

*Acer* stems were collected using pole pruners. *Schefflera* stems were cut using rope-driven saw chains. Monofilament (10-lb test) fishing line was attached to 30-g fishing weights and shot over stems using a sling-shot. The 10-lb test line was used to haul up a 100-lb test fishing line and this, in turn, was used to haul up ropes to which was attached a length of saw chain. Branches were collected in early morning or during rain storms, recut under water in Gatun Lake as soon as possible, and brought back to the laboratory.

Diurnal time courses of water use were measured on excised shoots using a computer-controlled potometer. Shoots bearing 0.5 to 2 m<sup>2</sup> of leaves were connected to a water-filled plastic pipe. Water was delivered through the pipe to the shoot from a 2-L container resting on a digital balance (range, 5 kg; readability  $\pm 1 \times 10^{-5}$  kg). A computer recorded the rate of water uptake by reading the balance weight through a serial port at programmed time intervals (usually every 150 s). Corrections for buoyancy of the pipe in the water container and for evaporation from the container were measured and used (although both were negligible compared with water uptake rate of the shoots during daylight hours).

In some later experiments, we also used a data logger (Datataker<sup>3</sup> model DT100; ZI-TECH Institute Corp., Mountain View, CA) to record micrometeorological data, e.g. net radiation (using a net radiometer; Micromet Institute, Bothell, WA), leaf temperature using 4 T-type thermocouples and methods described in (19), and air temperature and humidity using a forced air wet bulb-dry bulb hygrometer (custom built).

Pressure-volume curves were measured on excised *A. saccharum* leaves using a bench-top dehydration procedure. Excised leaves were dried and periodically weighed before and after their  $\Psi$  were measured using a Scholander-Hammel pressure bomb. Leaf area was measured at the start of each dehydration experiment. Osmotic potential and turgor potentials were calculated in the standard way (16). This method did not work on *S. morototoni* leaves. When leaves were excised at the petioles or petiolules, the vessels plugged with a clear latex-like substance preventing the determination of the balance point in a pressure bomb about 30 min after excision. Therefore, "population" pressure-volume curves were collected by dehydrating whole stems with leaves attached. Periodically, leaves were removed and measurements were made of balance pressure, leaf area, fresh weight, and dry weight. Pressure-volume curves were plotted initially as water content (fresh weight - dry weight) per unit leaf area or per unit dry weight versus balance pressure to get a value for water content at full hydration. Then water deficits could be calculated for the other leaves by difference.

Water storage capacitance of excised *Schefflera* stem segments was measured as described elsewhere for *Acer* stems (20). In brief, excised stems were fitted with ultrasonic acoustic emission transducers (to detect cavitation events) and with stem hygrometers (to measure  $\Psi_{\text{stem}}$ ), and the stems were

<sup>3</sup> The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

slowly dehydrated in air over a period of 2 to 6 d while periodically recording water loss gravimetrically, cumulative acoustic emissions, and  $\Psi_{\text{stem}}$ .

The stem water capacitances and the pressure-volume curves allowed us to estimate likely contribution of stored water to transpiration by leaves and stems in large trees.

### Hydraulic Architecture Data

A number of parameters were collected describing the hydraulic architecture of the study trees. These included: (a)  $k_h = w/(dP/dx)$ , where  $w$  is the mass flow rate ( $\text{kg s}^{-1}$ ) induced in a stem segment by  $dP/dx$  in  $\text{MPa m}^{-1}$ ; (b)  $\text{LSC} = k_h/A_L$ , where  $A_L$  is the leaf area in  $\text{m}^2$  feed by the stem segment; (c)  $k_s = k_h/A_w$ , where  $A_w$  is the sapwood cross-sectional area; and (d)  $\text{HV} = A_w/A_L$ . All measurements were made on stem segments longer than most vessels. Vessel lengths were measured in *Schefflera* stems using the paint perfusion technique (3, 25); 90% of the vessels were found to be under 300 mm long, and 95% were less than 400 mm long so the minimum stem-segment length used in most measurements was >400 mm whenever possible.

Stem segments 25 to 40 cm long were cut from selected shoots while fully immersed in water and a record kept of their diameter (excluding bark) and diameter of pith (*Schefflera*). Leaf area attached to or downstream from the excised segment was measured with a model Li-3100 leaf area meter (Li-Cor, Lincoln, NE). Initial conductivities of stems less than 20 mm diameter (*Acer* only) were measured in a conductivity apparatus described elsewhere (11). Segments >20 mm diameter were fitted at the basal end with a length of rubber tubing cut from appropriately sized bicycle or automobile tire inner tubes. The rubber tubes were kept filled with water while the stems were held in a vertical position, and the rate of water flow through the segments was measured gravimetrically by weighing a receiving reservoir at measured time intervals. The hydraulic conductivity was computed from mass flow rate ( $\text{kg s}^{-1}$ ) divided by pressure gradient ( $\text{MPa m}^{-1}$ ) estimated from the gravitational potential gradient. After hydraulic conductivity measurements, the segments were perfused with a 0.02% (w/v) solution of safranin O dye. After dye perfusion, a 2- to 4-mm-thick disc was cut from the midpoint of the segment and the area of stained sapwood measured using a bit pad and commercial software (Sigma-Scan; Jandel Scientific, Corte Madera, CA).

Relative resistance to water flow of petiolules, petioles, petiole-to-stem junctions, and terminal stems was measured on *Schefflera* shoots using the potometer described above. Leaf blades were excised at the distal ends of petiolules, and the whole shoot immersed in a water bath at a known height below the source container of the potometer. The difference in height gave the  $\Delta P$  between the base of the stem and the cut tips, and immersion in the bath assured that  $\Delta P$  was the same for all tips. The  $\Delta P$  divided by the flow rate gave the total resistance to water flow in the shoot (less leaves). These measurements were repeated after cutting off various structures, *i.e.*: (a) all petiolules cut at the distal end of the petioles; (b) all petioles cut at the base of each petiole; (c) the section of distal stem bearing petiole junctions; and (d) various por-

tions of the remaining stem. The change in resistance after cutting off each structure gave the resistance of that structure.

Data for a hydraulic map for selected shoots and for one large tree of each species were collected as described previously (11). These data included: (a) segment number of each segment and the number of the segment connected to its base; (b) segment diameter (without bark); (c) segment length; and (d) the area of leaves attached to the segment. A 20-m *S. morototoni* tree could be mapped adequately with 153 segments, whereas the 10-m *A. saccharum* tree required about 3000 segments. These data were used in simulation models of the dynamics of water flow in the mapped trees as done by Tyree (12) in a single *Thuja occidentalis* tree.

### Vulnerability Curves

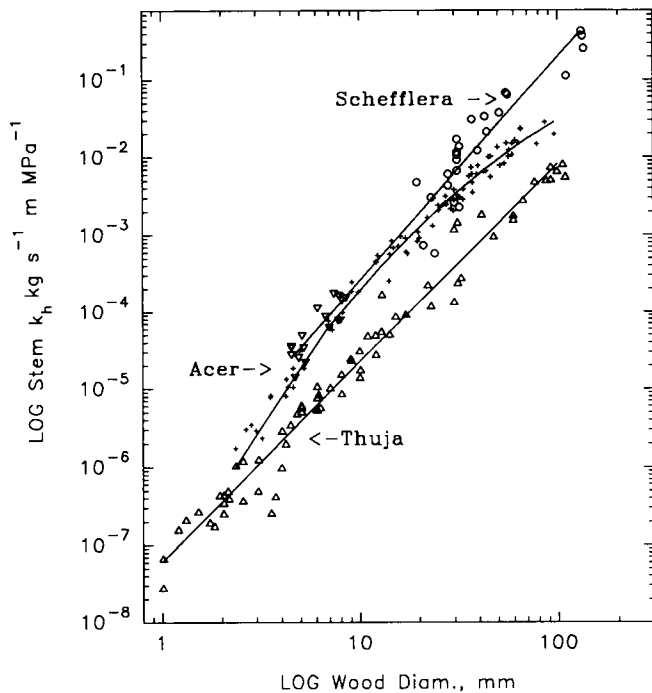
Vulnerability curves provide information on how negative xylem pressure potentials, caused by drought, reduce the hydraulic conductivity of stems. Vulnerability curves were measured by dehydrating replicate shoots and measuring the effect of water stress on loss of hydraulic conductivity by cavitation, which causes interruption of flow in cavitating conduits by air blockage (embolisms [17]). Vulnerability curves have been measured previously on *Acer* stems from 6- to 20-mm diameter (11). But these measurements were repeated in a similar way on *Acer* stems 1.5 to 6 mm in diameter and on the smallest leaf-bearing stems of *Schefflera* 15 to 30 mm diameter. Because flow rates were so small through the *Acer* stems, hydraulic conductivity had to be measured with  $\Delta P$  of about 0.2 MPa, *i.e.* the same pressure used to "flush" stems to dissolve air bubbles. The conductivity apparatus was redesigned to use miniature stopcocks and small diameter tubing (2–5 mm i.d.).

## RESULTS

For comparative purposes, data on *A. saccharum* and *S. morototoni* will be contrasted with data on *T. occidentalis* (L.) Carr. published elsewhere (12, 15).

The diameter of stems bearing leaves, *i.e.* stem with leaf vascular insertions, differed substantially. Over 50% of the scale leaves of *Thuja* were attached to stems  $\leq 2$  mm diameter, whereas in *Acer* and *Schefflera* the wood diameter bearing >50% of the leaves was  $\leq 4$  and 23 mm, respectively.

The hydraulic conductivity of stems,  $k_h$ , versus wood diameter are shown in Figure 1. The smallest leaf-bearing stems of *Schefflera* had  $k_h$ s close to those of *Acer* of the same diameter. *Schefflera* petioles also had  $k_h$ s close to those of *Acer* stems of the same diameter. However,  $k_h$  of larger stems (20- to 30-mm diameter) were 3 to 10 times larger in *Schefflera* than in *Acer*. *Thuja* had  $k_h$ s 10 to 20 times lower than the other two species for stems of the same diameter. Since the functional xylem comprised >80% of the wood in all stems measured in Figure 1,  $k_s$  can be calculated approximately for any given wood diameter,  $d$ , by dividing  $k_h$  by  $\pi d^2/4$ . In all species,  $k_s$  increased with wood diameter. This can be deduced from the slope of the log-log plot in Figure 1. If  $k_s$  were constant, then the slope should be 2.0. The slopes were about 2.5, 2.6, and 2.8 for *Thuja*, *Acer*, and *Schefflera*, respectively. A slope >2 indicated that the average conduit diameter and/



**Figure 1.** Log hydraulic conductivity (ordinate) of stems per unit stem length,  $k_h$ , plotted versus log diameter of the stem (excluding bark, abscissa).  $\Delta$ , *Thuja*; +, *Acer*;  $\circ$  and  $\nabla$ , *Schefflera* stems and petioles, respectively.

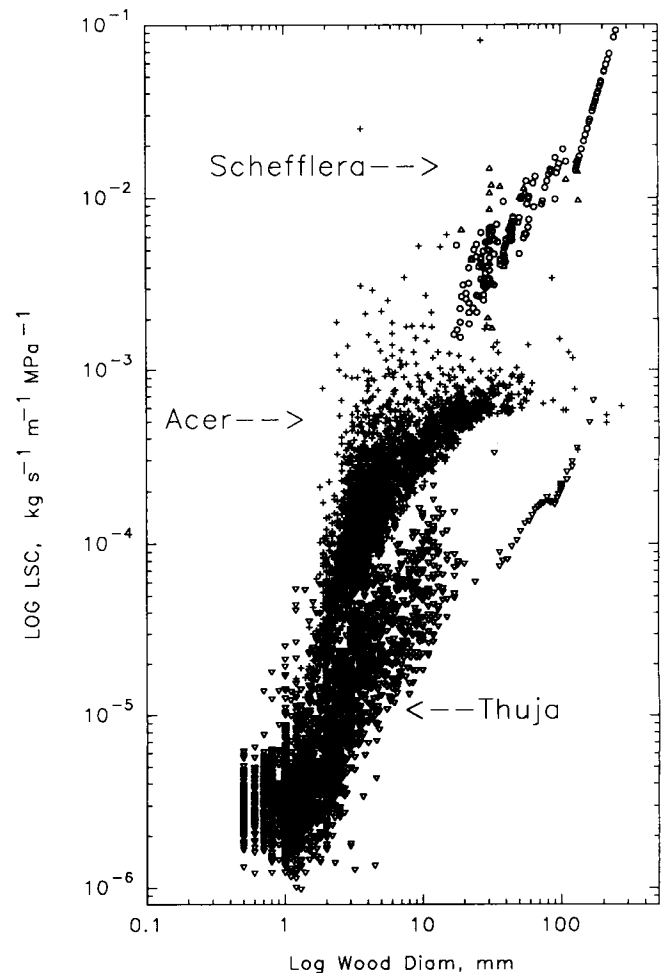
or the number of conduits per unit area increased with increasing wood diameter.

There were large differences in LSC ranging over 5 orders of magnitude. The LSCs in Figure 2 were calculated from the hydraulic maps collected for each species. The trees were cut into 4100, 2900, and 153 segments for single trees of *Thuja*, *Acer*, and *Schefflera*, respectively. The data sets are too large to reproduce here, but will be provided to anyone wishing to send a 360K or 720K IBM-compatible floppy disk to M. T. Tyree. The regression lines in Figure 1 were used to assign  $k_h$  values to each stem segment in the data sets, and LSCs were calculated by dividing  $k_h$  by leaf area fed by the segment that could be calculated from the data sets. Estimates of LSC calculated in this way were not as accurate as direct measurements of LSC, but we have found that directly measured LSCs agreed with those in Figure 2. The directly measured values tend to have a slightly larger variance in LSC at any given wood diameter. The leaf-bearing stems of *Thuja*, *Acer*, and *Schefflera* had LSCs of  $5 \times 10^{-6}$ ,  $1 \times 10^{-4}$ , and  $3 \times 10^{-2}$   $\text{kg m s}^{-1} \text{MPa}^{-1}$ . The LSCs of *Schefflera* stems bearing leaves are 2 to 20 times higher than comparable stems in a wide range of dicot lianas, trees, and shrubs (4). The LSC of 10 *Schefflera* petioles was  $5 \times 10^{-4} \pm 1 \times 10^{-4}$   $\text{kg m s}^{-1} \text{MPa}^{-1}$ . LSCs of the major stems (boles) differ by comparable orders of magnitude in these species.

The higher LSC values in *Schefflera* versus *Acer* and *Thuja* were in part due to larger HVs, i.e. *Schefflera* produced more stem cross-sectional area per unit leaf area than the other species. Huber values for *Schefflera* ranged from 2 to  $20 \times 10^{-4}$   $\text{m}^2$  of stem cross-sectional area per  $\text{m}^2$  of leaf area fed

for small stems and large stems, respectively. In comparison, HVs for *Acer* ranged from 1 to  $2 \times 10^{-4}$  and for *Thuja* from 0.2 to  $2 \times 10^{-4}$ . The rest of the difference in LSC values was due to differences in  $k_s$  since  $\text{LSC} = \text{HV} \times k_s$ .

The relative contribution of petioles and petioles to the resistance of shoots to water flow was substantial. Two shoots used in the potometer were harvested after 1 or 3 d, and the resistances of various structural components were measured and reported in Table I. The shoots slowly plug, probably because of microbial growth at the base of the shoots, causing a substantial increase in overall resistance from about 700 to 10,000  $\text{MPa s kg}^{-1}$ . This natural plugging of stems was fortunate in our view because it permitted us to measure water use by leaves at different  $\Psi$  in the course of 3- to 4-d experiments. We found it possible to induce plugging on the first day by injecting India ink (carbon black) into the water supply. On 1-d-old samples, the combined resistance of the petioles + petiole junctions was still half that of the whole shoot (less leaves). Typical midday (1000–1400 h)



**Figure 2.** Log leaf specific conductivity (ordinate) versus log wood diameter (excluding bark, abscissa). Most values were calculated from hydraulic map data and the  $k_h$  values in Figure 1.  $\nabla$ , *Thuja*; +, *Acer*; and  $\circ$ , *Schefflera*.  $\Delta$  for *Schefflera* are directly measured LSC values.

**Table 1.** Relative Resistances of Structures of *Schefflera* Shoots Measured after 1 or 3 d on the Potometer

Errors reported were computed from SD of five measured flow rates used to calculate resistances. R is the total resistance of the shoots excluding leaves; E is measured during sunny periods in the wet season;  $\Delta P$  is the pressure drop =  $-E \times R \times \text{leaf area}$ ,  $\Psi_{\text{leaf}}$  is measured with a pressure bomb.

Parameter	1 d	3 d
R (MPa s kg <sup>-1</sup> )	659 ± 9	10,300 ± 400
Stem length (m)	1.02	0.32
Leaf area (m <sup>2</sup> )	1.3934	0.8819
Midday E (kg s <sup>-1</sup> m <sup>-2</sup> )	6 × 10 <sup>-5</sup>	5 × 10 <sup>-5</sup>
Computed $\Delta P$ (MPa)	-0.06	-0.45
Measured $\Psi_{\text{leaf}}$ (MPa)	-0.5--0.8	-0.8--1.2
% resistances of		
Petiolules	17.5 ± 2.1	4.5 ± 5.1
Petioles	20.6 ± 2.4	1.1 ± 4.8
Petiole-stem junction	17.5 ± 3.0	0.1 ± 4.2
Stems	50.4 ± 2.5	89.6 ± 4.1

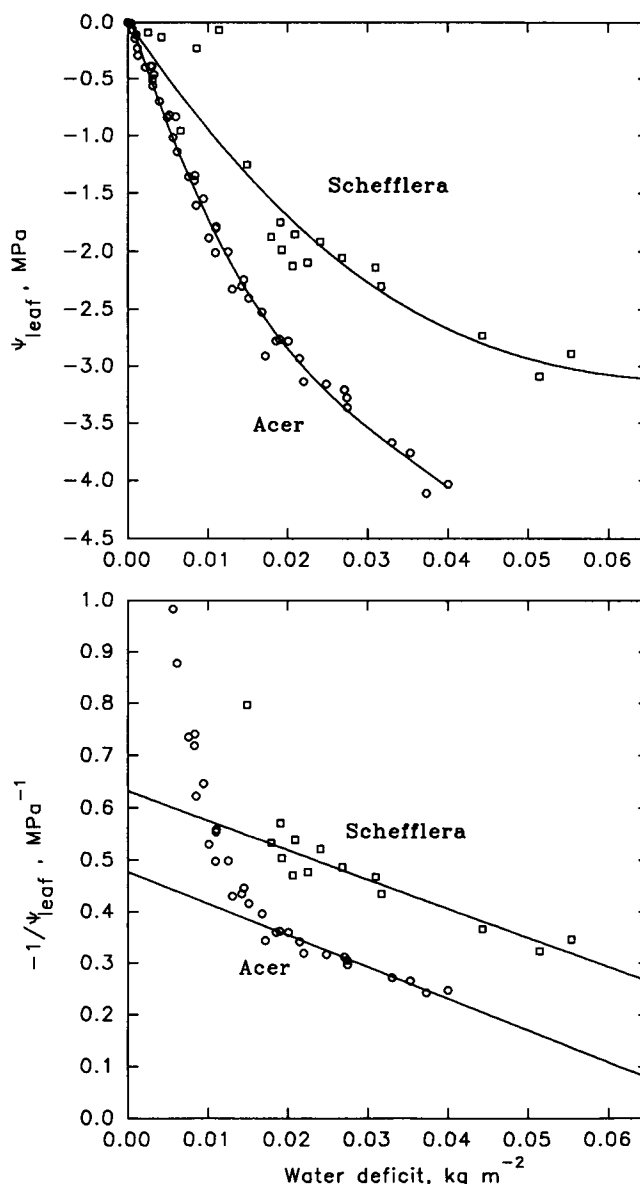
water use flux densities also are reported together with computed  $\Psi$  drops in the shoots (less leaves) and the range of  $\Psi_{\text{leaf}}$  measured during the midday hours. Since  $\Psi_{\text{leaf}}$  was generally 0.6 MPa more negative than the computed drop in  $\Psi$  across the whole shoot, we concluded that the leaves had a substantial resistance to water flow in *Schefflera*.

Leaf water potential isotherms from pressure-volume curves are reproduced in Figure 3. The results from *Acer* are for five leaves repeatedly weighted and measured in the pressure bomb (Fig. 3, open circles) for reasons given in "Materials and Methods." The upper curves in Figure 3 were used to calculate leaf capacitances, and regression lines of the third-order polynomials were used to provide information on leaf water storage capacity in models of the dynamics of water flow in the trees. The initial capacitances were larger in *Schefflera*, 0.0105 kg MPa<sup>-1</sup> m<sup>-2</sup> of leaf area versus 0.00506 in *Acer*. Solute potentials at full hydration and at the turgor loss point were -2.17 and -2.78 MPa, respectively, in *Acer* and -1.56 and -1.82 MPa, respectively, in *Schefflera* (see lower graph in Fig. 3). The solute potentials at full hydration and at the turgor loss point were rather low in *Acer* compared with that reported in other studies (14) where the values were -1.5 and -1.9 MPa, respectively. The later values correspond closely with the  $\Psi_{\text{leaf}}$  for stomatal closure in *Acer* leaves collected from the same sites in Vermont (S. Yang, personal communication) so bench-top dehydration may underestimate leaf solute potentials in *Acer* and perhaps in *Schefflera*.

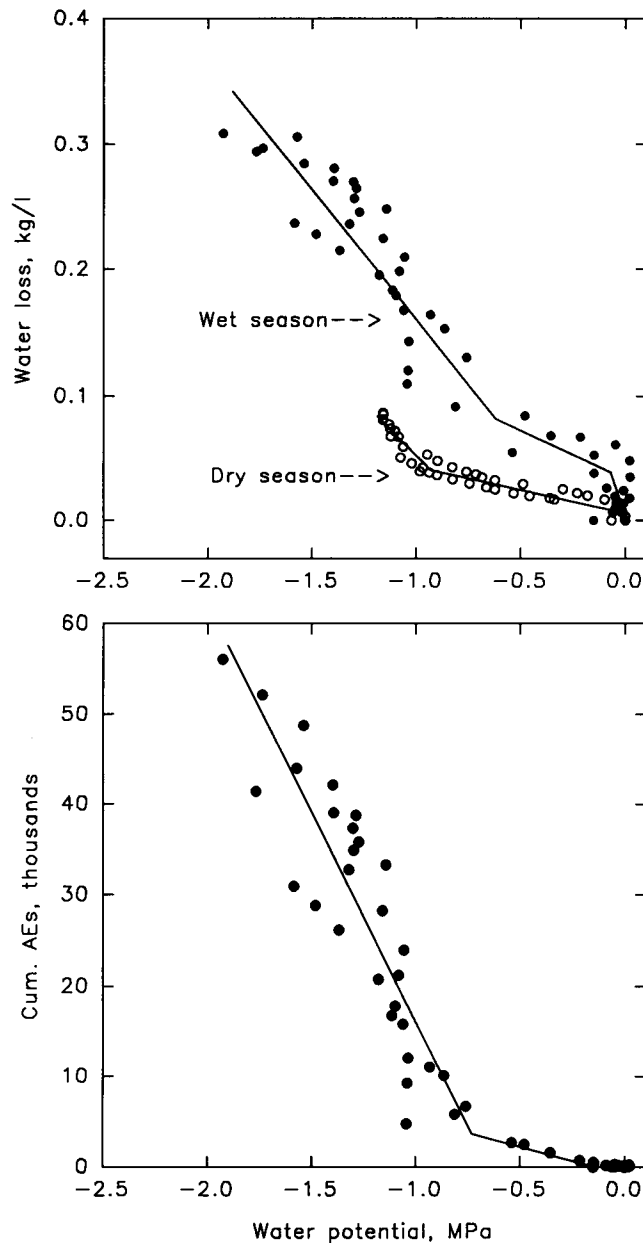
Stem capacitances of *Schefflera* were evaluated from data in Figure 4. Stem capacitance was found to increase with decreasing water potential, and this correlated with an increase in cavitation events detected acoustically. This pattern is similar to that reported by Tyree and Yang (20) for *Acer*, *Thuja*, and *Tsuga*. Stem capacitances for  $\Psi$  from -0.2 to -1.0 MPa were higher in *Schefflera* (0.03 and 0.2 kg L<sup>-1</sup> MPa in dry season and wet season, respectively) than reported for *Acer* and *Thuja* (0.020 and 0.017 kg L<sup>-1</sup> MPa<sup>-1</sup>, respectively

[20]). The lower stem capacitance of *Schefflera* measured on samples collected in March (dry season) compared with samples collected in November (wet season) may be due to a progressive loss of water content as  $\Psi_{\text{soil}}$  declined. Stem samples were kept in water for a few hours before the start of the dehydration, and this did return the stems to  $\Psi = 0$ , but apparently was not enough to dissolve air bubbles to cause full rehydration. Previous reports suggest that full rehydration takes days (20).

Dry season transpiration flux densities for *Schefflera* are shown in Figure 5A for a representative sunny day. Wet season transpiration rates during sunny periods reached sim-



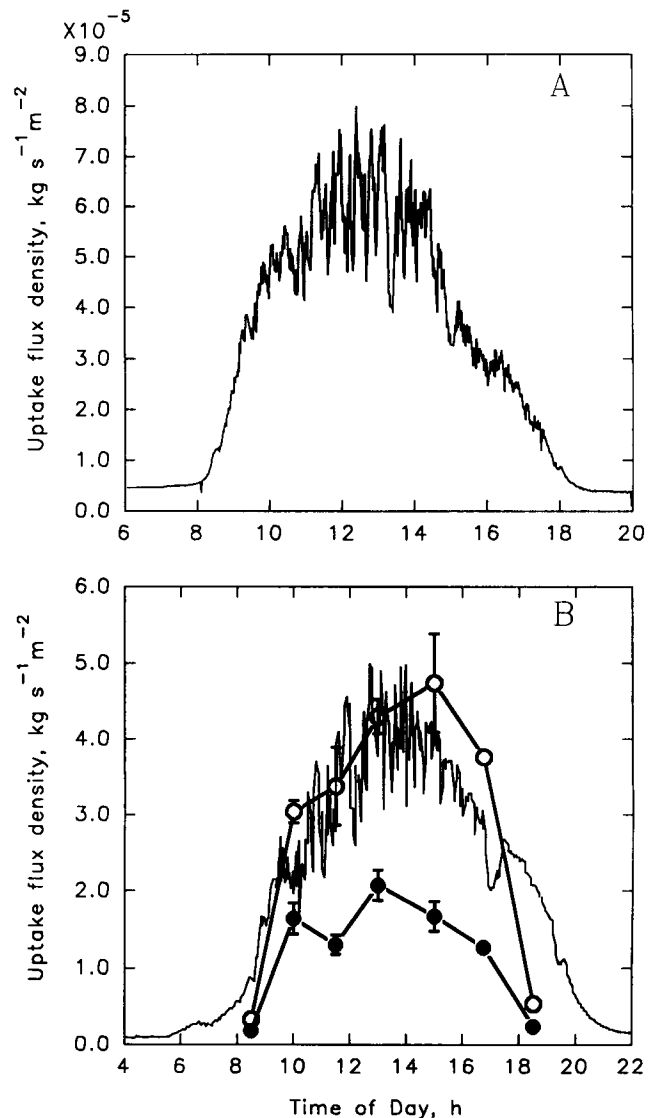
**Figure 3.**  $\Psi$  Isotherms for *Schefflera* ( $\square$ ) and *Acer* ( $\circ$ ). Upper graph is  $\Psi$  versus water deficit in kg m<sup>-2</sup> of leaf area. Lower graph is the "pressure-volume" curve. *Acer* data represent the result for five leaves combined, whereas each point for the *Schefflera* data is a separate leaf.



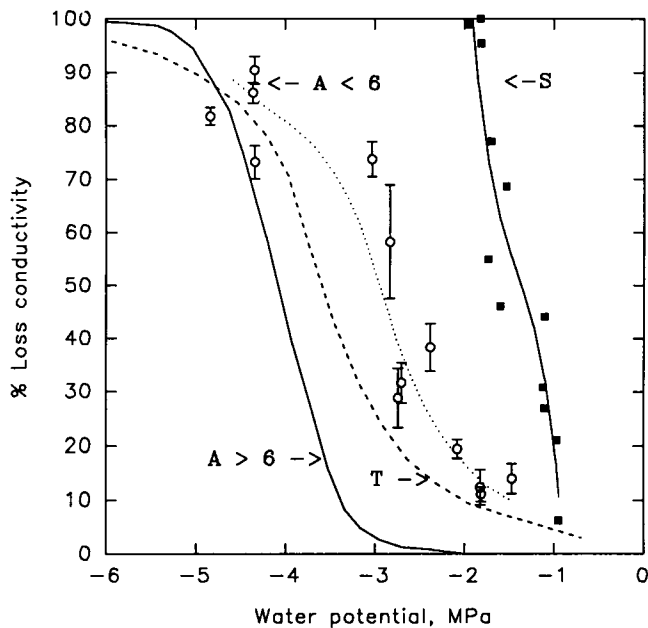
**Figure 4.** Upper graph is  $\Psi$  isotherms for the dehydration of *Schefflera* stems collected in wet (●) and dry (○) seasons. Lower graph is cumulative acoustic emissions versus  $\Psi$  for wet season stems.

ilar peak rates (data not shown), and variation in rate was strongly correlated with variation in net radiation. Comparable data for a sunny summer day for *Acer* are shown in Figure 5B. These curves were used in simulation models to calculate the dynamics of water flow through these species using the hydraulic map data.

Vulnerability curves for leaf-bearing stems of *Schefflera* and *Acer* are shown in Figure 6. Leaf-bearing stems of *Acer* were more vulnerable than larger stems; stems >6 mm diameter lost 50% of their conductivity at a  $\Psi$  of -4.1 MPa versus -3.0 MPa in leaf-bearing stems <6 mm diameter. *Schefflera* stems were much more vulnerable than *Acer*, losing 50% of



**Figure 5.** Upper graph is the water uptake flux density measured during the dry season for *Schefflera* stems. Wet season rates had comparable flux densities during midday sunny intervals, but were less during cloudy or rainy periods. The lower graph is the water uptake flux density for *Acer* on a typical sunny summer day in July 1990. The values plotted as lines without symbols are values measured on excised branches using the potometer. Values plotted with circles and error bars are flux densities measured by a Li-Cor 1600 steady state porometer measured on an intact *Acer* tree in July 1988; values are plotted for sun (○) and shade (●) leaves. Error bars are the SE ( $n = 5$ ).



**Figure 6.** Vulnerability curves plotted as percentage loss hydraulic conductance versus  $\Psi$  required to induce the loss.  $A > 6$ , a curve for *Acer* published elsewhere (17) for stems  $>6$  mm diameter.  $A < 6$ , means  $\pm$  SE of 10 stems less than 6 mm diameter bearing leaves from this study. T, a curve for *Thuja* published elsewhere (18). S, curve for *Schefflera* from this study; each point represent a separate stem. The line is a second order polynomial fit of the data.

their conductivity at  $\Psi$  of  $-1.5$  MPa. The vulnerability of *Schefflera* was more than that of any published report for trees (18), although it was similar to that of *Populus deltoides* (S Salleo and MA LoGullo, personal communication and reproduced in our laboratory).

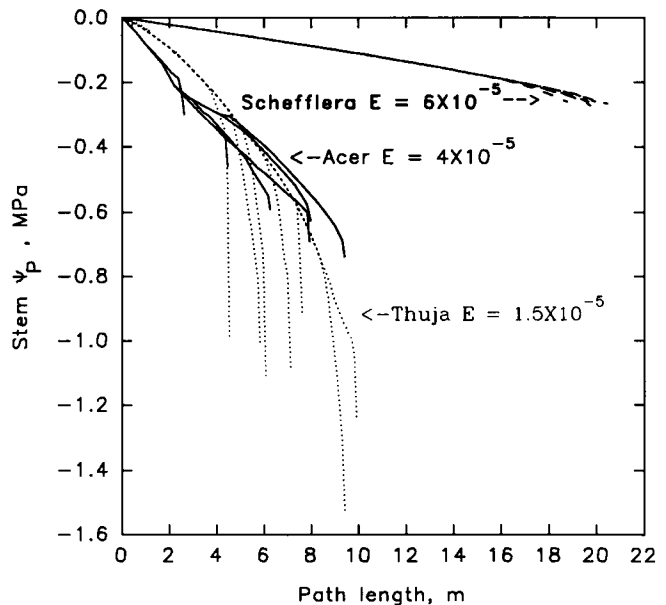
## DISCUSSION

LSC is a useful parameter because it is the proportionality constant relating the average  $E$  to the  $dP/dx$  in a stem needed to supply water to the leaves fed by the stem, i.e.  $E = LSC \cdot dP/dx$ . The lower the LSC, the larger the  $dP/dx$  needs to be to keep up with evaporative flux. The data in the hydraulic maps have been used to illustrate the impact of LSC on the profile of  $\Psi_P$  versus pathlength. Profiles of  $\Psi_P$  were calculated for representative  $E$  values for each species during steady-state evaporation at the same value of  $E$  for all leaves. In Figure 7, we plot  $\Psi_P$  profiles from the base of each tree to a few of the smallest stems bearing leaves; all  $\Psi_P$  values are given as the deviation from  $\Psi_P$  at ground level. The low LSCs in the smallest *Thuja* stems caused a very steep decline in  $\Psi_P$  versus distance through the minor stems. The  $\Psi_P$  profiles in larger stems of *Acer* were about the same as for large stems in *Thuja*; the LSCs of the smallest diameter *Acer* stems had steeper  $\Psi_P$  gradients than did the larger stems, but the effect was not as dramatic as in *Thuja*. LSCs were so large in *Schefflera* that very little drop in  $\Psi_P$  was needed to draw water up to the leaves; the average  $dP/dx$  was  $12.5$  kPa/m over the 20-m height of the stem, i.e. little more than needed to lift water

against the gravitational potential gradient ( $9.8$  kPa/m);  $\Psi_{leaf}$ s are likely to be nearly identical in the crown of *Schefflera* trees, because of their symmetrical growth habit.

Zimmermann (24) introduced the concept of plant segmentation to explain certain patterns in hydraulic and anatomical architecture of trees. In both angiosperms and gymnosperms studied by Zimmermann and others (5, 6, 15, 23), stem LSC decreases with wood diameter and stem junctions tend to have lower LSCs than adjacent internodes. Zimmermann suggested that this property of the hydraulic architecture tended to put the apices of trees under more negative  $\Psi_P$  than large stems. So Zimmermann suggested that xylem embolisms caused by cavitations will be confined to small stems that are expendable while preserving bigger stems that represent a larger investment of biomass. This qualitative proposal has been confirmed by mathematical models of the dynamics of runaway embolism in trees (12, 13).

We believe that Zimmermann's segmentation hypothesis may be generalized by introducing the additional concept of vulnerability segmentation. Hydraulic and anatomical segmentation are of no value to trees if apices are less vulnerable to cavitations than big stems. Also, a pattern of decreasing LSC with decreasing wood diameter is not necessary to predict the confinement of embolisms to apices. Apices always will be at more negative  $\Psi_P$  than large stems even if LSC increases with decreasing wood diameter, because  $\Psi_P$  always must decrease in the direction of water flow. So, as long as the vulnerability of small stems is at least the same as big stems, embolisms will always occur more in small stems. When examining the segmentation hypothesis, it is important to consider both hydraulic and vulnerability segmentation. In



**Figure 7.** Profiles of pressure potential of stems versus distance water must travel from the base of the tree to a stem apex. All values include the gravitational potential gradient required to lift water up the tree. These curves were calculated from the hydraulic maps and representative evaporative flux densities indicated for each species in the graph.

*Thuja* there was a very strong hydraulic segmentation causing a very rapid decline of xylem pressure in minor stems (Fig. 7). We cannot fully predict the role of this in segmentation without a knowledge of the vulnerability of small versus large stems. In *Acer* there was less dramatic hydraulic segmentation than in *Thuja*, but this was compensated for by an increased hydraulic vulnerability of the smallest leaf-bearing stems (Fig. 6). In *Schefflera* there was little hydraulic segmentation in the stems (Fig. 7), but the role of minor stems may be replaced by the long petioles that have LSCs of  $5 \times 10^{-4}$  versus  $300 \times 10^{-4} \text{ kg m s}^{-1} \text{ MPa}^{-1}$  for the smallest stems. Additional hydraulic segmentation is provided by the petiolules, which had a resistance equal to half that of the petioles (Table I, day 1).

*Schefflera* had a larger leaf-water storage capacitance than *Acer* and larger stem capacitance than *Thuja* and *Acer* (20), so the contribution of stored water to diurnal changes in E might be of importance in *Schefflera*. We used our data sets to test a hypothesis about the role of stem and leaf capacitances in the diurnal water economy of trees. Large leaf and water storage capacitance would reduce the maximum rate of water uptake from the roots substantially below the maximum transpiration rate (leaf area  $\times$  E,  $\text{kg s}^{-1}$ ) at midday and spread out the period of water uptake by the roots over more hours in the diurnal cycle. This could reduce the need to allocate carbohydrates to root growth.

To examine the likely contribution of stored water to the water economy of a single *Schefflera* tree, we used dynamic models like those in Tyree (12) to model water flow, storage, and retrieval in stems and leaves. Stem capacitance was assigned a constant value of 0.033 kg per L of stem per MPa (valid from  $\Psi = -0.2$  to  $-1.1$  MPa) and leaf capacitance was given a value of 0.01 kg per  $\text{m}^2$  of leaves per MPa (valid from  $\Psi = 0$  to  $-1.5$  MPa). A simulation was run for a tree starting out at  $E = 0$  and at time zero increasing in a step function to  $E = 1 \times 10^{-4} \text{ kg s}^{-1} \text{ m}^{-2}$  until a steady-state  $\Psi_P$  was reached in every leaf and stem segment. Leaves were separated from leaf-bearing stems by an average petiole + petiolule resistance =  $310 \text{ MPa s kg}^{-1}$ . An arbitrary and small root resistance,  $r = 10 \text{ MPa s kg}^{-1}$ , was assigned. Soil  $\Psi$  was assigned a value of  $-0.1$  MPa. The approach to steady state was evaluated by a fraction,  $F = 1 - (\Psi_P - \Psi_t)/(\Psi_P - \Psi_0)$ , where the subscripts o, s, and t indicate the value at time 0, at steady state, and at time t, respectively. The results are shown in Figure 8. The leaf and base of the bole approach the steady state with approximate half-times of 0.7 and 6 min, respectively. This means that water storage and retrieval can be of little importance to the diurnal water budget of large *Schefflera* trees. The dynamic model discussed below predicted a total diurnal change in water storage of 0.7 kg in stems and 0.2 kg in leaves, which equals 2% and 0.5%, respectively, compared with a daily quantity of water transpired of 40 kg. In comparison, the daily extraction of stored water in leaves and stems of *Thuja* was 5.5% and 16%, respectively, of the daily transpiration (12). Similar calculations on *Acer* predicted that diurnal extraction of stored water from stems and leaves would be 3% and 14%, respectively, of the daily transpiration.

The reason for the small contribution of stem and leaf capacitance to diurnal water economy of *Schefflera* probably is related to the high LSCs. Water cannot be extracted from

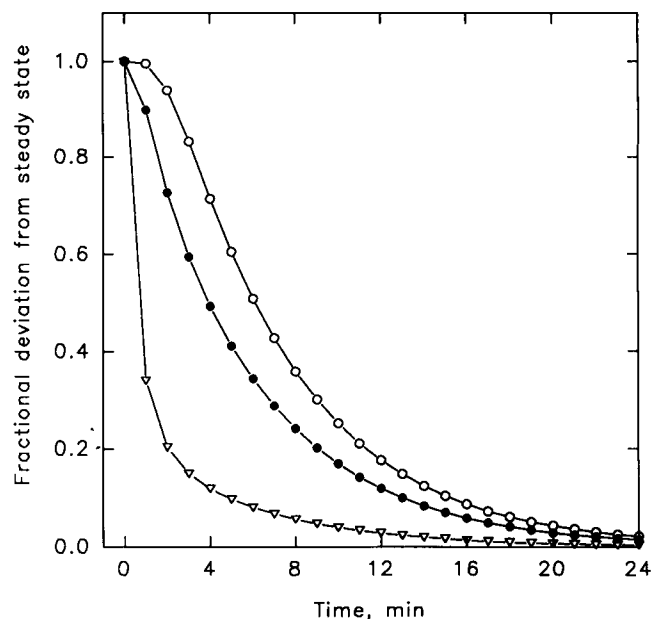


Figure 8. Dynamics of the approach to steady state for *Schefflera* stems.  $\nabla$ , Petiolules;  $\bullet$ , apex of the bole at 15 m height;  $\circ$ , the base of the bole.

stem stores without a decline in stem water potentials. High LSC prevents the stems from attaining a very negative  $\Psi_P$ . The only way the water stores can be tapped is when soil water potentials become very negative.

Therefore, stored water recovered in the last month of the dry season could be of considerable importance to *Schefflera*. Some speculative calculations easily prove this. Let us assume that stomates are closed for most of the day whenever  $\Psi_{\text{soil}}$  falls below  $-0.7$  MPa giving a 24-h average E of  $2 \times 10^{-6} \text{ kg s}^{-1} \text{ m}^{-2} = 5.2 \times 10^{-5} \text{ kg s}^{-1}$  for the whole tree in our model, which has  $26.2 \text{ m}^2$  of leaf area. Let us also assume a stem capacitance of  $0.2 \text{ kg L}^{-1} \text{ MPa}^{-1}$  for  $\Psi_{\text{stem}}$  in the range of  $-0.5$  to  $-2$  MPa; these are appropriate wet season stem capacitances (Fig. 4). Let us also assume that in the dry season the  $\Psi_{\text{soil}}$  falls to  $-1.5$  MPa before rains begin. The total volume of wood in our mapped tree is 462 L, so the total water that could be extracted from the wood is approximately 70 kg for a 0.8-MPa change in  $\Psi_{\text{wood}}$  from  $-0.7$  to  $-1.5$  MPa. This is enough water to sustain a water loss rate of  $5.2 \times 10^{-5} \text{ kg s}^{-1}$  for a total of 16 d without any water extraction from the soil. Of course, the tree will extract some water from the soil, so the relative importance of stored water is difficult to determine. Based on this calculation, we postulate that *Schefflera* is likely to be capable of withstanding more than 2 weeks and perhaps more than a month of drought with leaves remaining at or below the turgor loss point, provided that some water is extracted from the soil to augment that released from the stems. One *Schefflera* root system was excavated, and we found some roots  $>8$  cm in diameter at a depth of 1.2 m, so it is unlikely that stems would ever fall to a  $\Psi$  of  $-2$  MPa, which would cause 100% loss of hydraulic conductivity.

The likely contribution of stored water to the transpiration stream is much less in *Acer* trees when drought takes the



leaves beyond the turgor loss point for weeks. Severe droughts rarely occur in Vermont, but in the extreme southern range of the species, droughts that might take the species beyond the turgor loss point for most of the day are likely to occur at least once every 10 or 20 years. While  $\Psi_{\text{soil}}$  falls from  $-1.8$  to  $-2.8$  MPa, leaves are likely to have closed stomates for most of the day. But calculations similar to those above reveal that water stored in *Acer* stems is enough to provide  $<0.2$  d of transpiration. This is because stem volume per leaf area is less,  $1.33 \text{ l m}^{-2}$  in *Acer* versus  $17.6$  in *Schefflera*, and stem storage capacities for the 1 MPa range beyond the turgor loss point also are less,  $0.02$  versus  $0.2 \text{ kg L}^{-1} \text{ MPa}^{-1}$  for *Acer* and *Schefflera*, respectively ([20] and this paper). This means that the extractable water storage of per unit leaf area in *Schefflera* is  $>100$  times that of *Acer*.

Since stem LSC is so large in *Schefflera*, we can predict a rather modest diurnal variation in  $\Psi_{\text{stem}}$ . We modeled the dynamics of water stress development in stems using the same parameters in the steady state model above except that E was allowed to follow a diurnal time course in Figure 6 (but based on the hourly average rates). The computational methods used were as described by Tyree (12). The diurnal variation in mean  $\Psi$  petiole for all leaves on the tree predicted by the model was 0.2 MPa. The resistances of the roots, stems, and petioles + petioles account for amplitudes of approximately 0.02, 0.16, and 0.02 MPa, respectively. The biggest unknown in this simulation was the root resistance, which was set at an arbitrarily low value. Although stem resistance to water flow was slight, we do have evidence that leaf resistance is very high (Table I), so we can predict much larger diurnal variation in  $\Psi_{\text{leaf}}$ . The only practical way of sampling leaves from  $>20$  m trees is to shoot them down with a shotgun, but at the time of this study the restrictions on civilian access to guns and ammunition in Panama prevented these measurements.

We do not know if the hydraulic architecture of *Schefflera* is a deciding factor in the adaptation of this species to rapid growth rates in gaps. More comparative studies are needed to draw firm conclusions, but tentative conclusions are possible. The high LSC values would permit high transpiration rates and, therefore, maximum photosynthetic rates in the wet and much of the dry season with minimum reduction in  $\Psi_{\text{stem}}$ . From this we conclude that the turgor potential of meristems always will be near the maximum possible level. This will facilitate the rapid growth needed for any gap specialist (9). The high stem volume to leaf area ratios also may permit survival of the tree through the last weeks of severe dry seasons. The high LSC appears necessary to prevent excessive water stress in the stems, which would cause embolism in the highly vulnerable stems.

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