

Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions

C. VANDER WILLIGEN, H. W. SHERWIN AND N. W. PAMMENTER*

School of Life and Environmental Sciences, George Campbell Building, University of Natal, Durban 4041, South Africa

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SUMMARY

Five evergreen subtropical tree species growing under identical environmental conditions were investigated to establish which hydraulic properties are genotypically rigid and which show phenotypic plasticity. Maximum xylem-specific conductivity (k_s) correlated well with the anatomical characteristics (conduit diameter and density) for the four angiosperms *Tecomaria capensis*, *Trichilia dregeana*, *Cinnamomum camphora* and *Barringtonia racemosa*; the anatomy of the gymnosperm *Podocarpus latifolius* was not assessed. Huber values (functional xylem cross-sectional area : leaf area) varied inversely with k_s among species. Maximum leaf-specific conductivity was similar in the five unrelated species. Vulnerability of xylem to cavitation differed between species, as did the relationship between transpiration and water potential. Models of these parameters and isolated midday readings confirm that these trees operate at similar maximum leaf-specific conductivity (k_l) values. The data are consistent with the hypothesis that conductivity characteristics (k_l , k_s) are influenced by environment, whereas vulnerability to cavitation is genetically determined.

Key words: hydraulic architecture, hydraulic conductivity, embolism, cavitation, vulnerability curve, water relations, transpiration, xylem.

INTRODUCTION

It is vital for terrestrial plants to transport water from their roots to their leaves to meet the demand for transpiration and solute transport. The techniques to quantify and characterize water transport in plants have been refined considerably since the work of Zimmermann (1983) generated further interest in this subject. Although some theory is still debated (Canny, 1995, 1998; Zimmermann *et al.*, 1995; Milburn, 1996), there is general agreement concerning the principles and mechanisms of long-distance transport of water through plants. The xylem tissues of plants vary in their ability to conduct water, and environmental factors such as nutrients (Radin & Matthews, 1989), light (Schultz & Matthews, 1993) and water availability (Vander Willigen & Pammenter, 1998) have been shown to be important determinants of hydraulic conductivity. However, less is known about factors determining

the vulnerability of xylem to water stress-induced cavitation, although Vander Willigen & Pammenter (1998) suggested this may be determined by genotype rather than habitat.

This paper contributes to the debate concerning the influence of environment vs genotype. These issues could be important with respect to the influence of changing global climate both on the response of currently established, long-lived trees, and on the future distribution of species. We report on the relationships among xylem anatomy, hydraulic conductivity, leaf water status, transpiration rate, and the vulnerability of xylem to cavitation of five unrelated tropical/subtropical evergreen woody species native to different habitats, but grown under identical environmental conditions.

MATERIALS AND METHODS

All the plants were growing under the same conditions in an irrigated, domestic garden. Their natural habitats range from rocky outcrops to swamp

*Author for correspondence (fax +27 31 260 2029; e-mail pammente@biology.und.ac.za).

forests. Of the five species one, *Podocarpus latifolius* (Thunb.) R. Br. (Podocarpaceae), was a gymnosperm and the others were angiosperms. These trees are large (up to 30 m in height), slow-growing, and occur in evergreen forests (Coates Palgrave, 1984). The four angiosperms selected were *Tecomaria capensis* (Thunb.) Spach (Bignoniaceae), a shrub growing up to 4 m which occurs naturally at the margins of evergreen forests, bush or scrub, along stream banks and rocky outcrops; *Cinnamomum camphora* (Linn.) Nees et Eberm. (Lauraceae), a tree usually 15–20 m, native to East and South-East Asia and Australia but naturalized in the mesic subtropical areas of southern Africa (Immelman *et al.*, 1973); *Trichilia dregeana* Sond. (Meliaceae), a very large, slow growing tree > 30 m in height, naturally occurring in evergreen forests; *Barringtonia racemosa* (L.) Spreng. (Lecythidaceae), usually a medium sized, fast-growing tree of 8–12 m, occurring naturally along the banks of rivers and in freshwater swamps (Coates Palgrave, 1984).

Studies were undertaken on three individual plants of two species: *T. capensis* and *T. dregeana*. Measurements on several twigs from replicate plants of these species revealed no statistical differences between plants within a species (data not shown). Only single plants of the other species were available.

Anatomical measurements

Cross-sections were taken from fresh 1–2-yr-old twigs of all five species and viewed with a Jeol 520 scanning electron microscope (Jeol, Tokyo, Japan). The measurements of mean conduit diameters, conduit densities and conduit diameter distributions were done on individual micrographs from each of 20 different branches for all five species.

Vessel length distributions were measured for the four angiosperm species. The method used was modified from Zimmermann & Jeje (1981). An inert, carmine pigment, Colanyl (Hoechst) was used instead of latex paint. Pigment particles between 0.75 and 3 µm were used. *Podocarpus latifolius*, being a gymnosperm, has only short tracheids and no vessels. The twigs of *T. capensis*, *C. camphora*, *T. dregeana* and *B. racemosa* were all cut early in the morning on cool, overcast days. The twigs were flushed with degassed, de-ionized water at 200 kPa for 20 min to remove any embolisms. The pigment suspension was then allowed to flow through the twigs at 2 kPa until flow stopped. This allowed the vessels to become packed with these coloured particles. The pigment-filled twigs were then cut into 1 cm portions and the excess pigment suspension was blotted away. The number of pigment-filled vessels in each section was counted using a dissection microscope at × 40 magnification. Vessel length distribution was calculated according to Zimmermann & Jeje's (1981) adaptation of the work of Skene & Balodis (1968).

Hydraulic properties

Hydraulic vulnerability curves were constructed for branches from all the species, excluding *C. camphora*, according to the methods of Sperry *et al.* (1988), expressing the percentage loss of hydraulic conductivity as a function of water potential. An excised branch was allowed to dehydrate over a period of 3–4 d. During dehydration the branch was repeatedly sealed in a large plastic bag to allow the water to equilibrate among the tissues. The twig water potential was then measured using a Scholander pressure bomb, a branch segment excised under water and its hydraulic conductivity measured. To verify these data, isolated measurements of water potential and hydraulic conductivity were taken on branches excised at midday.

The hydraulic conductivity (k_h) was calculated by measuring the mass flow of water passing through a branch segment connected to a constant pressure reservoir (2 kPa). It was ensured that all branch segments were longer than the longest xylem vessel (Fig. 1). Maximum hydraulic conductivity (k_{max}) was subsequently measured after flushing the branch segment at a pressure of *c.* 200 kPa for 20 min. A solution of 0.01 M HCl with filtered (0.22 µm membrane filter), degassed, distilled water was used throughout. These experiments were undertaken on Strahler second-order branches (McMahon, 1975), except for *B. racemosa* for which first-order branches had to be used. The percentage loss in conductivity (PLC) was then calculated as $PLC = 100(k_{max} - k_h)/k_{max}$.

The data from the vulnerability curves were fitted to the exponential sigmoidal equation:

$$PLC = 100 / \{1 + \exp[a(\psi - b)]\} \quad \text{Eqn 1}$$

(ψ is the water potential and a and b are constants (Pammenter & Vander Willigen, 1998)). The coefficient a determines the slope of the vulnerability curve, whereas b is equivalent to the water potential at which 50% of the conductivity is lost. The coefficients of this equation were determined by regression analysis after transforming the equation to the linear form: $\log_e(100/PLC - 1) = a\psi - ab$. Comparisons among species were conducted using ANOVA and Scheffe's multiple range test on replicate estimates of the coefficients.

For all five species, the functional xylem cross-sectional area was stained (0.05% safranin dye perfusion) and measured after all the embolisms had been removed from the branch segment. The leaf area distal to the branch segment was also measured. The maximum hydraulic conductivity data were then expressed as xylem-specific conductivity (k_s) and leaf-specific conductivity (k_l). The Huber values (functional xylem cross-sectional area:leaf area) were also calculated.

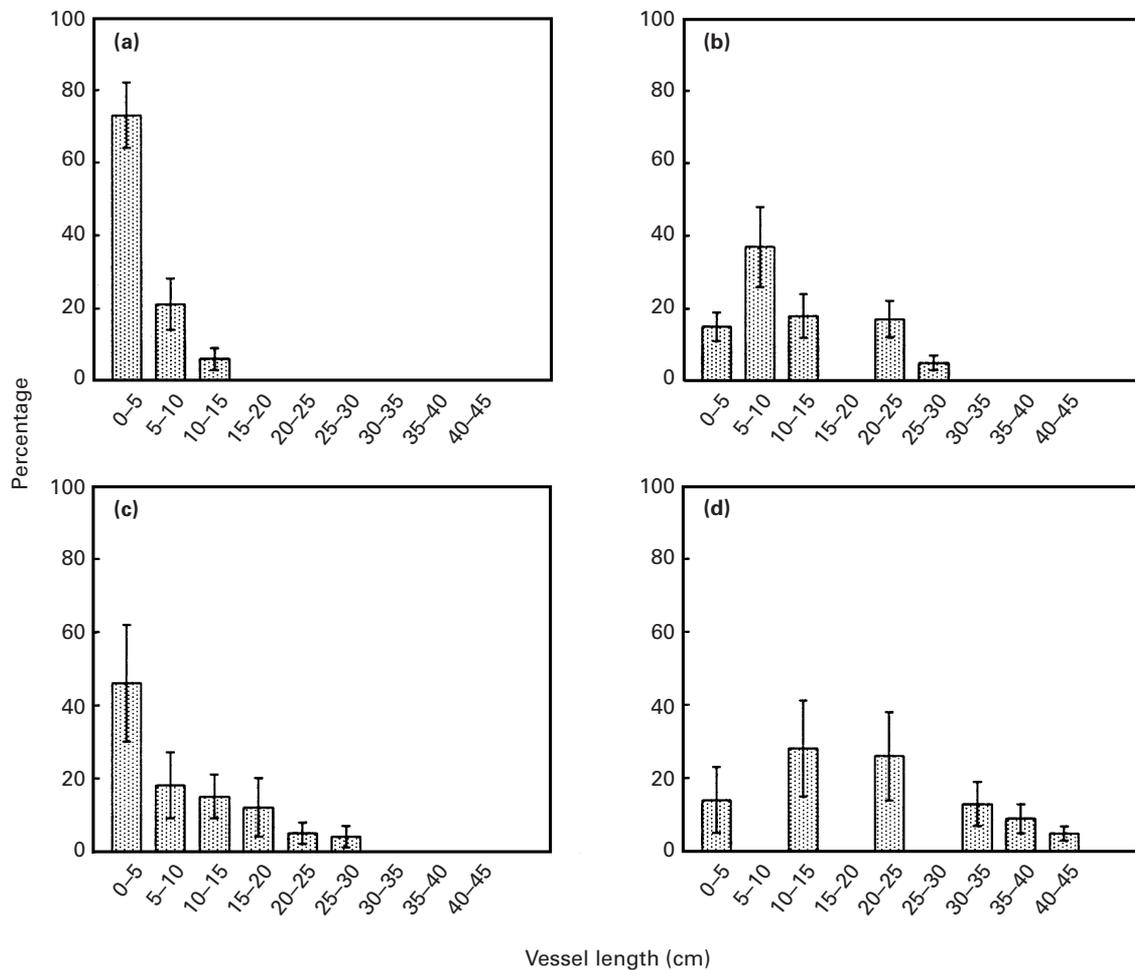


Fig. 1. Distribution of vessel lengths in the twigs of four subtropical, evergreen, angiosperm, woody species: (a) *Tecomaria capensis*, (b) *Cinnamomum camphora*, (c) *Trichilia dregeana*, (d) *Barringtonia racemosa*. The vertical lines represent 1 SD ($n = 6$).

Ultrasonic acoustic emissions

Although maximum hydraulic conductivity of *C. camphora* was measured, it was not possible to measure the vulnerability to cavitation using the air-dehydration hydraulic method because of xylem refilling during measurements. Xylem cavitations were thus detected using ultrasonic acoustic emissions. An 8313 Bruer and Kjaer transducer (Bruer & Kjaer, Naerum, Denmark) was attached to a second-order branch using a setup similar to that described by Sandford & Grace (1985). The threshold was set at 310 mV where the background noise was < 0.5 emissions per minute. The bark under the sensor was removed and the exposed wood was coated with a gel to prevent dehydration and improve the contact between sensor and the xylem. L-51 leaf hygrometers (Wescor, Logan, UT, USA) were attached to three leaves nearest to the sensor. As the branch dehydrated, water potential was regularly measured using the dew point method with a H33T microvoltmeter (Wescor). For each recording, the mean water potential value from three hygrometers was calculated and the corresponding

number of accumulated acoustic emissions noted. To allow for rapid equilibration, each hygrometer was attached to the area in which the adaxial leaf surface had been lightly abraded with Al_2O_3 (0.3 μm particle size) as suggested by Savage *et al.* (1984). During the equilibration period the entire branch was covered in a plastic bag and the cut end immersed in water. The data were fitted to Eqn 1, replacing PLC with percentage maximum acoustic emissions.

Transpiration versus water potential measurements

Measurements of transpiration rate and water potential were taken from just after dawn until midday on three consecutive, clear summer days. Transpiration rates were measured using an MCS 301 null balance porometer (MC Systems, Cape Town, South Africa). Changes in water potential were measured with increasing transpiration rate only, to avoid any possible hysteresis effects. Water potentials were measured using a Scholander pressure chamber on individual leaves (in the case of the large-leaved *T. dregeana* and *B. racemosa*) or twigs (the other

species), from which transpiration measurements were taken.

RESULTS

Anatomical measurements

The xylem anatomy of the four angiosperm species was diffuse porous. The mean conduit diameters and densities of the five species are given in Table 1, and their diameter distributions in Fig. 2. *Podocarpus*

latifolius, having only tracheids, had the narrowest conduits. Among the angiosperm species, mean conduit diameter increased from the scrub species *T. capensis* through the forest species *C. camphora* and *T. dregeana*, with the swamp forest species *B. racemosa* having the largest conduits. All mean conduit diameters were significantly different from each other. Although the relationship was not linear, as conduit diameter increased conduit densities decreased.

The distributions of vessel lengths in the four

Table 1. Diameters and densities of xylem conduits of five subtropical evergreen woody species growing under identical conditions

Species	Mean conduit diameter (μm)	Conduit density (mm^{-2})
<i>Podocarpus latifolius</i>	$7.3 \pm 1.1^{\text{a}}$	$9087 \pm 2060^{\text{a}}$
<i>Tecomaria capensis</i>	$12.7 \pm 1.5^{\text{b}}$	$916 \pm 176^{\text{b}}$
<i>Cinnamomum camphora</i>	$19.5 \pm 2.2^{\text{c}}$	$271 \pm 69^{\text{c}}$
<i>Trichilia dregeana</i>	$28 \pm 3^{\text{d}}$	$160 \pm 43^{\text{c}}$
<i>Barringtonia racemosa</i>	$30 \pm 2^{\text{e}}$	$2698 \pm 76^{\text{c}}$

Values with different letters are significantly different (Scheffe's multiple range tests $P < 0.05$).

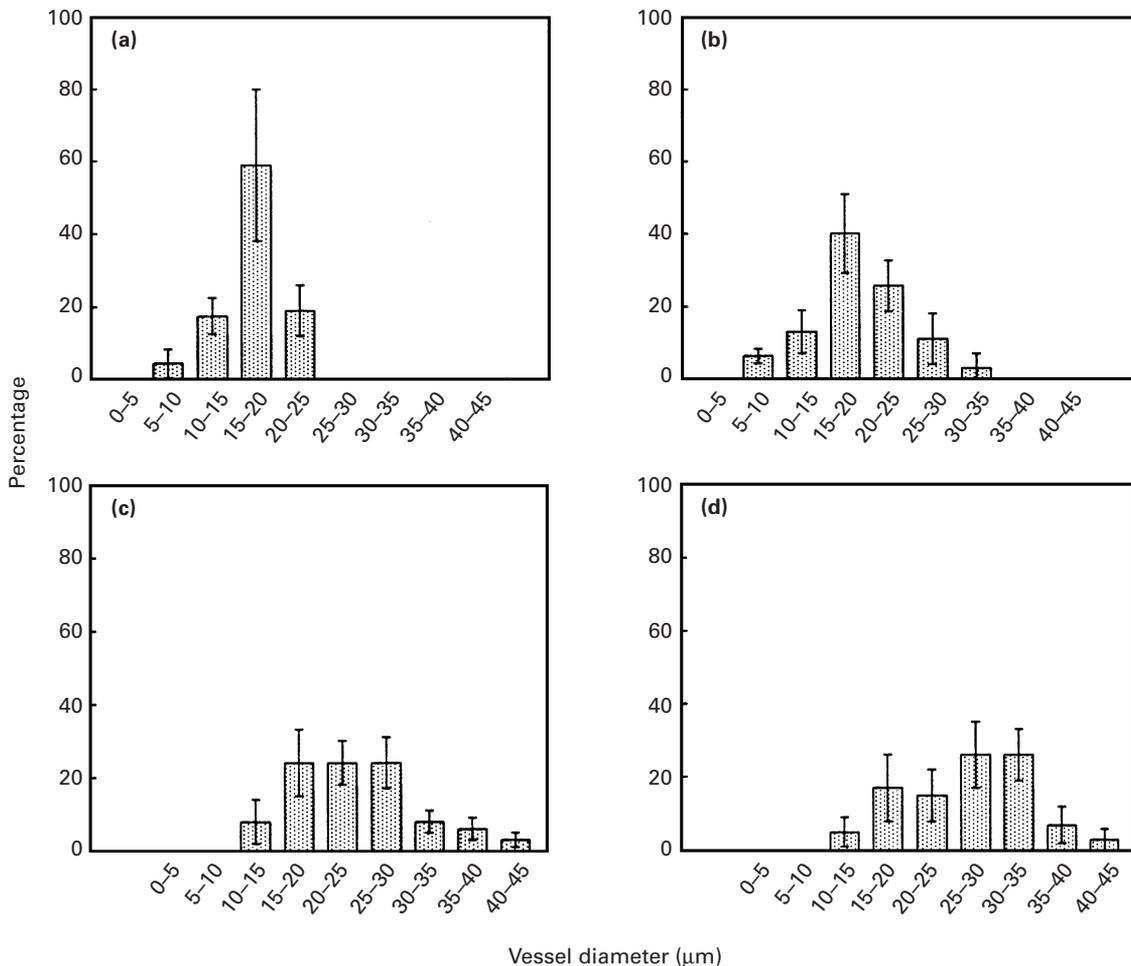


Fig. 2. Distribution of vessel diameters in twigs of four subtropical, evergreen, angiosperm, woody species: (a) *Tecomaria capensis*, (b) *Cinnamomum camphora*, (c) *Trichilia dregeana*, (d) *Barringtonia racemosa*. The vertical lines represent 1 SD ($n = 20$).

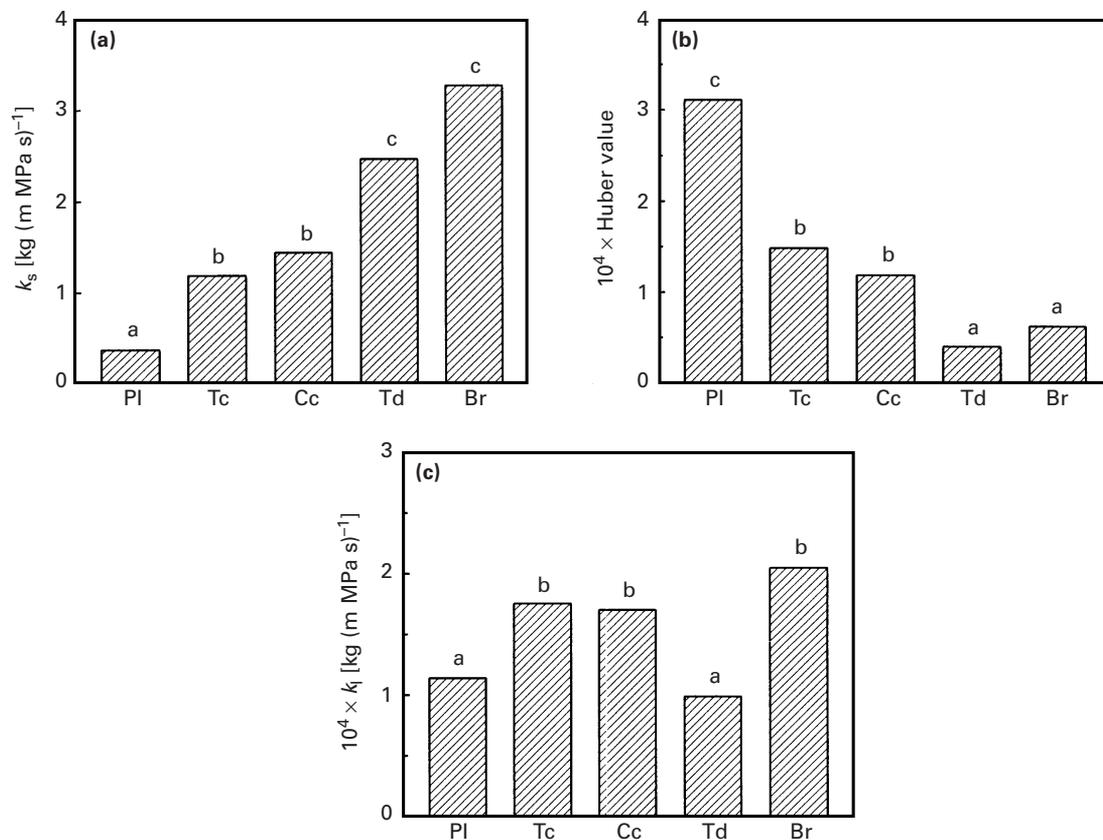


Fig. 3. (a) Maximum xylem-specific conductivity; (b) Huber values; and (c) maximum leaf-specific conductivity of branches from five subtropical, evergreen, woody species. Letters represent mean separation by Scheffe's multiple range test ($P < 0.05$, $n = 10\text{--}16$). PI, *Podocarpus latifolius*; Tc, *Tecomaria capensis*; Cc, *Cinnamomum camphora*; Td, *Trichilia dregeana*; Br, *Barringtonia racemosa*.

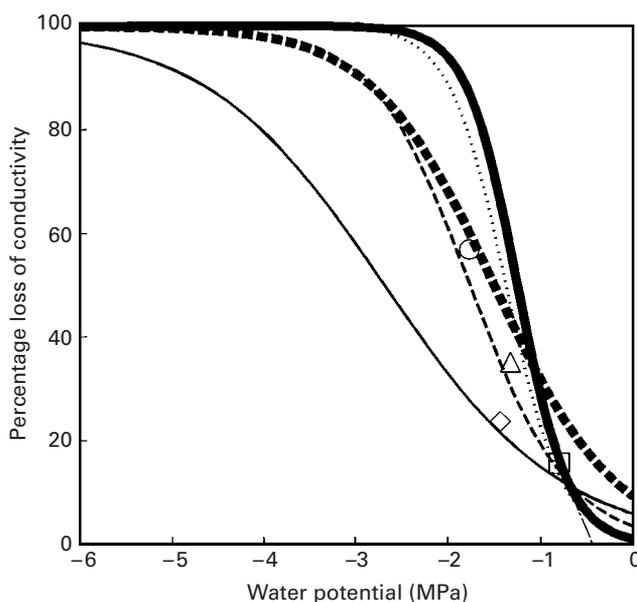


Fig. 4. Vulnerability of xylem to cavitation in branches from five subtropical, evergreen, woody species. Data were fitted to an exponential sigmoidal equation (Eqn 1): *Podocarpus latifolius* (circle, bold dashed line); *Tecomaria capensis* (triangle, fine dashed line); *Cinnamomum camphora* (bold unbroken line); *Trichilia dregeana* (diamond, fine unbroken line); *Barringtonia racemosa* (square, dotted line). Symbols indicate measured midday water potential and conductivity readings.

angiosperm species are shown in Fig. 1. There was considerable variation in these data as shown by the large standard deviations. The tracheids of *P. latifolius* were short compared with the vessels of the angiosperms, and length distribution was not investigated. The longest vessels of *T. capensis* were < 15 cm, with the majority of the vessels (73%) in the shortest vessel class of 0–5 cm (Fig. 1). *Cinnamomum camphora* appeared to have four distinct vessel length classes, possibly in a bimodal distribution. Most vessels were < 15 cm long, but 22% were > 20 cm, with no vessels being between 15 and 20 cm long. Vessel length distribution in *T. dregeana* showed a pattern similar to that of *T. capensis*, but with some vessels up to 30 cm long. The vessel length distribution of *B. racemosa* was also irregular, this swamp forest species having the longest with approx. 29% between 30 and 45 cm, although most were within the 10–15 and 20–25 cm classes (Fig. 2). Although not marked, there was a trend of increasing diameter with increasing vessel length (compare Figs 1 and 2).

Negative values were obtained from the calculations of vessel length distributions with all four species. This indicated that the vessel length classes of these four species were not randomly arranged throughout the stem (Zimmermann & Jeje, 1981).

Table 2. Coefficients for the sigmoidal equation describing the vulnerability curves for five subtropical evergreen woody species

Species	<i>a</i>	<i>b</i>	<i>R</i> ²
<i>Podocarpus latifolius</i>	1.90 ^b	1.74 ^b	0.92
<i>Tecomaria capensis</i>	1.54 ^c	1.48 ^c	0.92
<i>Trichilia dregeana</i>	1.04 ^d	2.66 ^a	0.94
<i>Cinnamomum camphora</i>	3.69 ^a	1.24 ^c	0.86
<i>Barringtonia racemosa</i>	3.32 ^a	1.36 ^c	0.90

The vulnerability of *Cinnamomum camphora* to cavitation was assessed using acoustic emissions, the hydraulic technique was used for the other species. Values with different letters are significantly different (Scheffe's multiple range tests $P < 0.05$, $n = 5-8$).

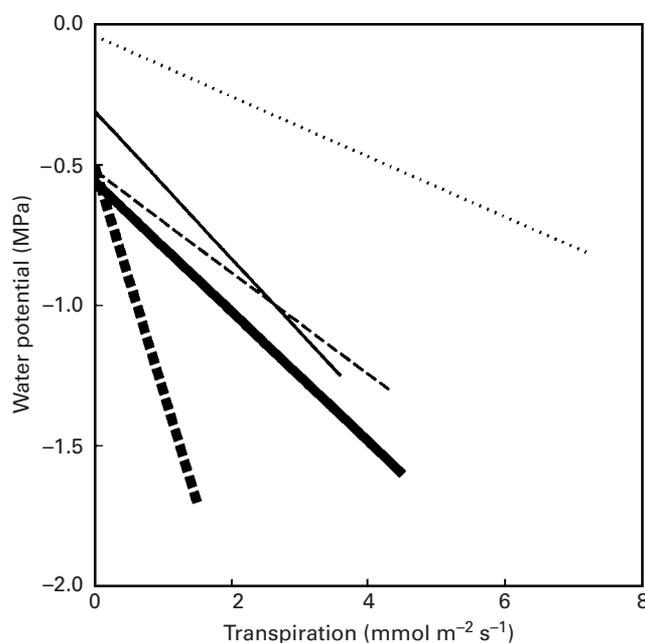


Fig. 5. Fitted regression lines showing the change in leaf water potential with increasing transpiration rate. Measurements were taken on a single specimen of each species on 3 consecutive days from sunrise to noon. Each line is extended to the maximum transpiration rate achieved by each species. The equations of the fitted regression lines are:

Species	<i>y</i>	<i>R</i> ²
<i>Podocarpus latifolius</i> (bold dashed line)	$-0.83x - 0.51$	0.82
<i>Tecomaria capensis</i> (fine dashed line)	$-0.18x - 0.52$	0.90
<i>Cinnamomum camphora</i> (bold unbroken line)	$-0.23x - 0.56$	0.73
<i>Trichilia dregeana</i> (fine unbroken line)	$-0.26x - 0.31$	0.88
<i>Barringtonia racemosa</i> (dotted line)	$-0.04x - 0.33$	0.55

Species names followed by different letters in parenthesis are significantly different (ANOVA, $P < 0.05$, $n = 15$).

Hydraulic properties

There were clear differences in maximum k_s between species (Fig. 3a). The swamp forest species *B.*

racemosa had a k_s three times that of the gymnosperm *P. latifolius*. However, the Huber values (Fig. 3b) followed the reverse trend and consequently there were only minimal differences in the maximum k_1 of the five species (Fig. 3c).

There were notable differences in the vulnerability curves of the species (Fig. 4). The coefficients derived when these data were fitted to Eqn 1 are shown in Table 2. *Cinnamomum camphora* and *B. racemosa* showed the highest vulnerability, with both species losing conductivity over a narrow water potential range and reaching 50% conductivity loss at water potentials close to 1 MPa. *Trichilia dregeana* was the least vulnerable and additionally lost conductivity over a wide range of water potentials.

Transpiration versus water potential

The fitted regression lines of water potential vs transpiration data are shown in Fig. 5. *Barringtonia racemosa* had the most gradual decrease in water potential with increasing rates of transpiration. *Tecomaria capensis*, *C. camphora* and *T. dregeana* operated similarly, with their water potential gradient gradually decreasing as transpiration increases. By contrast, *P. latifolius* showed a sharp decrease in water potential with only a relatively slight increase in transpiration rate.

DISCUSSION

Hydraulic parameters of branches have been shown to vary as a power function of branch diameter (Zotz *et al.*, 1994; Patiño *et al.*, 1995; Tyree & Ewers, 1996), and this relationship was verified in this instance for *T. dregeana* (data not shown). The variation with branch diameter suggests that when comparisons between species or treatments are made they should be between branches of similar diameter. However, as Patiño *et al.* (1995) have pointed out, it may be more meaningful to compare hydraulic properties from branches of the same 'morphological' diameter. Consequently we chose to compare Strahler second-order branches, that is, branches one junction from the terminal twigs. The exception was *B. racemosa*, the leaves of which are arranged in whorls at the tips of the terminal twigs (mean diameter 2.8 cm). We used these branches rather than the second-order branches, which were considerably larger (diameter 4 cm) than those of the other species (diameters 1.1–2.3 cm).

The maximum xylem-specific conductivity of each species (Fig. 3a) correlates well with their vessel diameters (Fig. 2), higher conductivities being associated with larger vessel diameters. This association is already well documented (Zimmermann, 1983; Calkin *et al.*, 1985; Ewers *et al.*, 1989) and is attributed to the Hagen-Poiseuille equation whereby

conductance is related to the fourth power of the conduit radius (Zimmermann, 1983). The pattern of the response of hydraulic conductivities to environmental conditions seems to vary between species. In four *Eucalyptus* clones (Vander Willigen & Pammenter, 1998), *Vitis vinifera* (Schultz & Matthews, 1988; Lovisolo & Schubert, 1998), *Quercus rubra* and *Liriodendron tulipifera* seedlings (Shumway *et al.*, 1993), an increase in water availability was associated with an increase in maximum xylem-specific conductivity. Schultz & Matthews (1988) and Shumway *et al.* (1993) found differences in Huber values which resulted in increases in leaf-specific conductivity with decreasing water availability. Conversely, Lovisolo & Schubert (1998) and Vander Willigen & Pammenter (1998) both found that the Huber values did not change, hence maximum leaf-specific conductivity increased with water availability. Lovisolo & Schubert (1998) found that the decrease in conductivity with decreased water availability was directly related to a reduction in vessel diameter. In the present case, five unrelated species from a range of habitats with very different xylem specific conductivities, when grown under the same conditions, had Huber values such that maximum leaf-specific conductivities were almost identical (the difference between the two statistically different groups in Fig. 3 is negligible compared with the range of leaf-specific conductivities reported in the literature). The variation in response notwithstanding, data are accumulating that indicate that xylem-specific conductivities, or Huber values, or both respond to environmental conditions.

It was originally thought that there was a trade-off between the hydraulic efficiency associated with large conduits and their vulnerability to cavitation (Zimmermann, 1983), but it is now considered that the maximum pit pore size is critical in the vulnerability of the conduits to dysfunction (Tyree & Sperry, 1989). The data presented here show no relationship between conduit size (diameter or length) and vulnerability to cavitation. This provides further evidence suggesting the original trade-off hypothesis is incorrect. The steep slopes of the vulnerability curves for *C. camphora* and *B. racemosa* suggest that the maximum pore sizes are similar among xylem vessels, while the low vulnerability and gradual slope of the curve for *T. dregeana* suggests smaller maximum pore sizes, but a wide range in these sizes among vessels. The values of water potential and conductivity measured on branches excised at midday fell in the experimentally determined vulnerability curves (Fig. 4), suggesting that the curves were representative of what occurred in the field. This verification step could not be performed for *C. camphora* because of refilling of excised branches during hydraulic measurements. Comparisons between *C. camphora* and the other

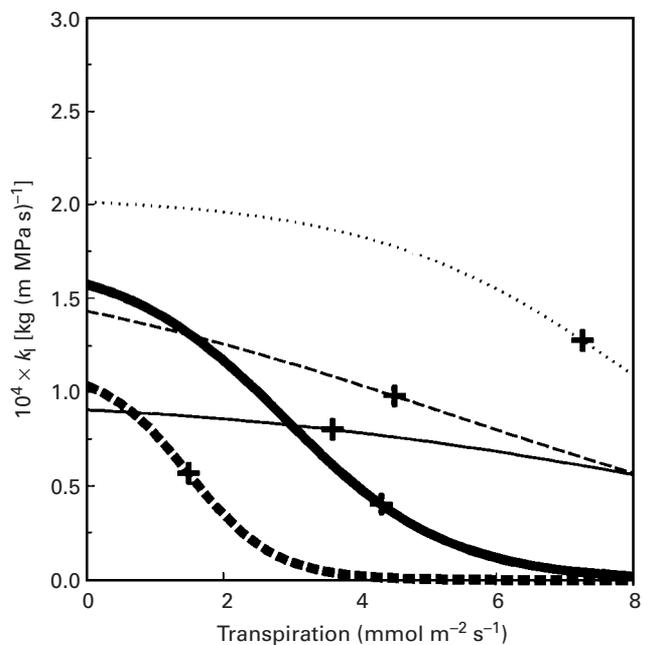


Fig. 6. Modelled relationship between transpiration rate and leaf-specific conductivity, calculated from equations for relationships illustrated in Figs 4 and 5 and the data in Fig. 3c. Crosses mark the measured maximum midday transpiration rates. *Podocarpus latifolius* (bold dashed line); *Tecomaria capensis* (fine dashed line); *Cinnamomum camphora* (bold unbroken line); *Trichilia dregeana* (fine unbroken line); *Barringtonia racemosa* (dotted line).

species are complicated by the fact that vulnerability in this species was estimated from acoustic emission data. However, Lo Gullo & Salleo (1991) and Cochard (1992) *inter alia* have demonstrated good correspondence between vulnerability curves estimated by hydraulic and acoustic emission methods. The differences among the vulnerability curves of the species in this study (Fig. 4) suggest that, unlike leaf-specific conductivity, xylem vulnerability to cavitation is not environmentally driven. Similar conclusions have been drawn by Vander Willigen & Pammenter (1998) for *Eucalyptus* clones, and by Tyree *et al.* (1998) for a wide range of tropical trees growing on contrasting soil types.

The vulnerability of the species described in this study would classify them all, along with other tropical species, as relatively drought sensitive (Patiño *et al.*, 1995). However, it is the absolute conductivity remaining, rather than the proportion lost, that is pertinent to the delivery of water to the leaves. From the maximum conductivity and the vulnerability curves, leaf-specific conductivity can be calculated for decreasing water potentials, and the actual conductivity under midday transpiration conditions estimated (Fig. 6). The model suggests that actual midday conductivities do vary among the species, but the differences are similar in magnitude to those found for maximum values. *Cinnamomum camphora* in particular appears to suffer considerable loss of conductivity during the day, without ad-

versely affecting transpiration rates (and presumably stomatal conductance). Conductivities of branches excised early in the morning were generally close to maximum (5–14 PLC), indicating overnight refilling.

The slope of the decline in water potential with increasing transpiration rate is a measure of soil–leaf hydraulic resistance. Three clear groups could be identified (Fig. 5), despite the similarities in maximum leaf-specific conductance. The differences in slope could not be explained by the actual midday leaf-specific conductances. These discrepancies are probably a result of differences among the species in path length (above-ground path lengths varied from 2 m in *T. capensis* to 10 m in *C. camphora*), and differences in the way leaf-specific conductances varied with branch dimensions throughout the conducting pathway (Tyree & Ewers, 1991).

We conclude that, for the species examined in the present study, xylem conduit dimensions (and thus maximum xylem-specific conductivity) and pit pore sizes (and hence vulnerability to cavitation) are genetically determined. Leaf area supplied by the hydraulic pathway is phenotypically plastic and leads to convergence in leaf-specific conductivities under the same environmental conditions.

In their review of the effects of elevated CO₂ on plant–water relations, Tyree & Alexander (1993) commented on possible effects on hydraulic characteristics, including vulnerability to xylem cavitation. The data presented in the present paper suggest that, in long-lived trees, Huber values may respond to changes in global climate, but that xylem vulnerability is not phenotypically plastic and that the vulnerability of new xylem tissue may not respond in an adaptive manner as Huber values may. However, the plasticity of hydraulic conductivity and the importance of xylem refilling (Holbrook & Zwieniecki, 1999; Tyree *et al.*, 1999), in conjunction with reported changes in transpiration and stomatal conductance with elevated CO₂ and climate change (Jarvis *et al.*, 1999), suggest that the genotypic rigidity of xylem vulnerability to cavitation may not in fact have the predicted implications for plant distribution with climate change.

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