Xylem Permeability and Embolism Susceptibility in Seedlings of *Eucalyptus camaldulensis* Dehnh. from Two Different Climatic Zones

P. J. Franks[AB], A. Gibson[A] and E. P. Bachelard[A]

[A] *Department of Forestry, Australian National University, Canberra, ACT 0200, Australia.*
[B] *Present address: Environmental Biology Group, Research School of Biological Sciences, Australian National University, GPO Box 475, Canberra, ACT 2601, Australia; corresponding author, facsimile: +61 6 249 4919.*

Abstract. We examined the hydraulic architecture of *Eucalyptus camaldulensis* seedlings from two climatically different provenances: Petford in north Queensland, which is humid; and Tennant Creek in the Northern Territory, which is semi-arid. Xylem liquid specific permeability (K) was calculated from measurements of xylem air permeability (K_g) and hydraulic resistances (R) were also calculated. Embolism susceptibility curves were constructed by measuring K_g in the stems of young seedlings. Canopy leaf areas were mapped and sap flows through the Tennant Creek and Petford seedlings were simulated. Results showed that the permeability of stem wood in the Tennant Creek seedling was about 40% higher than in Petford, and the permeability of its branch wood was about 25% higher. The threshold water potential for initiation of embolisms (ψ_t) was slightly lower in Tennant Creek seedlings (-3.3 MPa compared with -3.0 MPa) and the number of embolisms with decreasing ψ_t was lower for Tennant Creek seedlings. Sap flow simulations showed differences in the distribution of water throughout the seedling canopies. The results are discussed in terms of the ecology of the two eucalypt provenances.

Introduction

It has been known for some time that the xylem network within a tree has variable hydraulic properties which could contribute to non-uniform water potentials in its canopy (see review by Tyree and Ewers 1991). These properties, known collectively as the 'hydraulic architecture', have been shown to vary characteristically between species, and are thought to exert a strong influence on canopy water relations and gas exchange, thereby influencing plant productivity and survival in different environments.

Adding to the complexity of the hydraulic architecture are its changing properties under different environmental conditions, in particular the increase in xylem hydraulic resistance associated with the occurrence of embolisms at low plant water potentials. Embolism susceptibility is thought to be a major factor limiting the productivity and threatening the survival of plants which experience low water potentials (Schulze and Matthews 1988; Tyree and Sperry 1988, 1989; Jones and Sutherland 1991).

In this paper we examine the hydraulic architecture of *Eucalyptus camaldulensis* seedlings from two climatically different provenances: Petford in north Queensland, which is humid, and Tennant Creek in the Northern Territory, which is semi-arid. Seedlings originating from these provenances exhibit distinctly different morphologies (Gibson *et al.* 1991) and it was

hypothesised that they might also exhibit different hydraulic architectures.

Because *E. camaldulensis* exhibits the xylem anatomy of a 'diffuse porous hardwood' it was possible to use air permeability measurements to calculate xylem hydraulic resistances, according to Comstock (1967). In this unorthodox approach air permeability (K_g) of a stem segment is first measured, and then with the application of the Klinkenberg correction (Klinkenberg 1941) the liquid specific permeability (K) is obtained, allowing the hydraulic resistance of the xylem (R_x) to be calculated. The attraction of this method is that the potential errors associated with blockage by microbial growth or persistent xylary air bubbles (Zimmermann 1978; Sperry *et al.* 1988*a*, 1988*b*; Cochard and Tyree 1990) are absent. However, the suitability of this method is restricted to hardwoods (Bolton and Petty 1978).

The air permeability technique was used here to measure the extent of embolism in seedlings at low water potentials, and these data were used to construct embolism susceptibility curves. Then, with the xylem resistance of successive stem segments combined to give an overall estimation of stem resistance, and together with the measurement of individual leaf areas, steady-state xylem sap fluxes and pressures were simulated. The results are discussed in terms of their relevance to the ecology of these two eucalypts.

Materials and Methods

Plant Material

Seeds of Petford and Tennant Creek provenances of *E. camaldulensis* were obtained from the Australian Tree Seed Centre, CSIRO Division of Forestry and germinated in a humid spraying cabinet on punnets of vermiculite and perlite (1:1 v/v). After 2–3 weeks seedlings were transplanted individually into small pots and grown in a naturally illuminated glasshouse for a further 3 weeks. A number of seedlings were then selected for uniformity in size and development and transferred to large pots (15 mm diameter PVC stormwater pipe cut into 1 m lengths, capped on the bottom with two layers of shade cloth to prevent soil loss). The soil used was a 2:3 river sand:loam mixture to which Osmocote (1 g pot^{-1}), a general slow release fertiliser, lime (10 mg pot^{-1}) and trace elements (Librel BMX; 15 mg pot^{-1}) were added. All plants were grown in a glasshouse where day/night temperatures were controlled at 35/25°C. Relative humidity was 50–60% for most of the day, but rose to about 85% at night. Plants were well watered until they reached sufficient size for the embolism susceptibility experiment (see below). Seedlings were approximately 20 weeks old at the time of harvesting.

Air Permeability: Apparatus and Measurements

Air permeability of stem segments was measured with the apparatus shown in Fig. 1, which is similar to that described by Petty (1970), the only difference being the specimen holder (Fig. 2). The system is evacuated down to a known pressure (P_s) with the vacuum pump, and dry air from the atmosphere is bled in through the freeze-dried stem specimen via the needle valve at a measured volume flow rate (Q) at the high pressure side. The flow of air through the specimen creates a pressure differential along it (ΔP) which is measured with manometer M1, and the average pressure in the stem specimen ($\bar{P}$) is equal to ($P_s + \Delta P/2$). The large reservoir forming part of the evacuated system ensures that P_s is held relatively constant throughout a single flow measurement. Air permeability of the stem segment (K_g) can then be calculated using Darcy's Law for viscous flow of gases (Siau 1984),

$$K_g = \eta QLP/(A_x\Delta P\bar{P}), \tag{1}$$

where η is the viscosity of the air, L is the length of the stem segment, A_x is the cross sectional area of the stem segment and P is the pressure at the high pressure end of the specimen.

The length of the stem segment is of particular importance to permeability measurements. Most investigators attempt to cut their
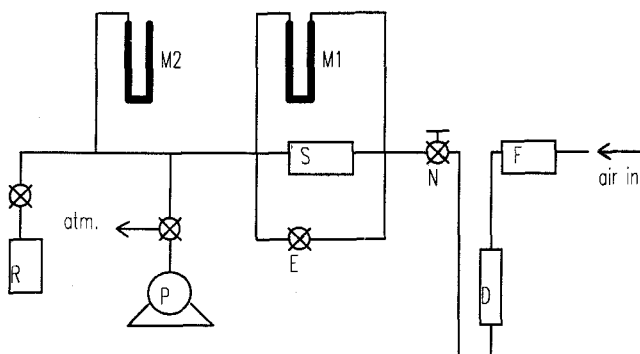

Fig. 1. Diagram of air permeability apparatus (adapted from Petty 1970): F, air flow rate meter; D, vial filled with desiccant; N, needle valve; M1, oil manometer; M2, mercury manometer; R, vacuum reservoir (15 L vacuum desiccator); P, vacuum pump; E, equalising valve; S, specimen holder.
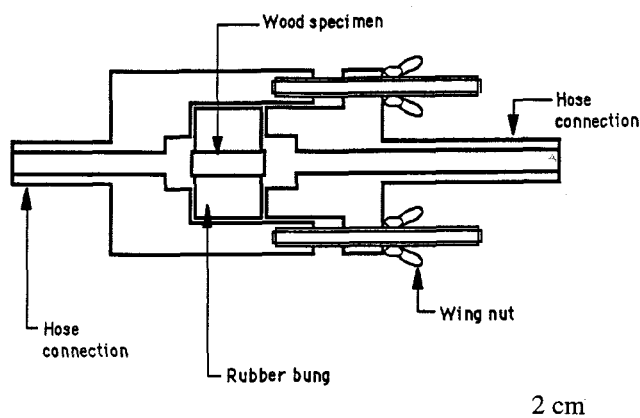

Fig. 2. Longitudinal section through specimen holder of air permeability apparatus.

segment longer than the longest tracheary element so that there is no chance of an element being open at both ends to allow a misleadingly high volume of air to pass through it relative to other elements, thereby giving a falsely high permeability value. Such measurements are possible with softwoods where the tracheids are only a few millimetres long. However, in hardwoods some vessels are usually quite long, possibly running the whole length of the tree (Zimmermann and Jeje 1981).

Seedlings of *E. camaldulensis* were tested for maximum vessel length by passing low pressure air (about 5 kPa) through freshly cut stems and watching for bubbles emerging from one end which was held just under water. The low pressure was sufficient to allow flow through open vessels but inadequate to dislodge a meniscus at a pit pore. Bubbles emerging from the outer edge of the xylem confirmed that some vessels ran the full length of the shoot (about 1 m). Therefore, it was not certain that a stem segment could be cut longer than the longest vessel. However, unlike tracheids, pit pores in hardwoods contribute little to total xylem resistance (Jarvis 1975), and therefore, xylem resistance could be measured on stem segments cut shorter than the shortest vessel. Tests on internodal stem segments between 10 and 20 mm in length revealed constant permeability while maintaining Q proportional to ΔP (laminar flow), indicating that most vessels in this length range were open at both ends. Vessels shorter than 10 mm would have made up only a very small percentage of the total (Skene and Balodis 1968). Therefore, stem segments used in air permeability measurements were all internodal sections about 20 mm in length. Prior to permeability measurement each freeze-dried stem segment was examined under a light microscope for cracks and the central pith area plugged with putty.

Embolism Susceptibility

After seedlings had grown to a height of about 1 m, with an average stem diameter of 6 mm, all water was withheld to allow the plants to dehydrate slowly over a period of 2–3 weeks. Leaf water potential (ψ_l) was monitored by measuring ψ_l of randomly sampled leaf discs using a Wescor C-52 psychrometer chamber. At successive stages of decreasing ψ_l the lower stem of one plant from each provenance was snap frozen by pouring liquid nitrogen into a polystyrene cup secured around the stem. The frozen stem segments were then detached and dropped immediately into a flask of liquid nitrogen for storage.

With the air permeability apparatus set up inside a frost room controlled at − 5°C, stem segments were removed from storage in

liquid nitrogen. An internodal section was cut to a length of 20 mm (with a miniature hacksaw and then trimmed with a razor) and air permeability due to embolised vessels (K_{ge}) measured at $P_s = 50$ kPa. Vessels not embolised remained blocked by ice at this stage. If at this point any of the embolised vessels had their ends in the stem segment they would not be air-permeable and a slight underestimation of K_{ge} would result. However, the steps taken to ensure that most vessels were longer than the stem segment considerably reduced this possible error. Stem segments were then freeze-dried to clear all vessels and maximum air permeability (K_{gm}) was measured at room temperature at $P_s = 50$ kPa. The percentage embolism in each seedling stem at the time of snap freezing was then calculated as,

$$\% \text{ embolism} = 100 K_{ge}/K_{gm}. \qquad (2)$$

Embolism susceptibility curves were then constructed by plotting the percentage embolism against ψ_l. Five plants were used from each provenance.

Minimum Leaf Resistance

Minimum leaf resistance ($r_{l(min)}$) causes maximum flow rates through the xylem for given atmospheric conditions, and is therefore, representative of the worst case in terms of demand placed on the hydraulic system. For the purpose of simulation, a value of $r_{l(min)}$ for *E. camaldulensis* grown under greenhouse conditions was estimated from data of Pereira and Kozlowski (1976), this value being $4 \text{ m}^2 \text{ s mol}^{-1}$. Although it is possible that the two eucalypt provenances exhibit different values for $r_{l(min)}$, assigning the same value to both provenances was considered a conservative approach which would highlight any significant differences between their hydraulic systems.

Simulating Water Flow Through the Shoot

One healthy seedling was chosen from each provenance and K_g for each stem internode, as well as the first internode of each branch, was measured as described above. The specific permeability, K, was then calculated from K_g using the Klinkenberg correction (Klinkenberg 1941; Scheidegger 1963; Comstock 1967). The xylem resistance for each internode, R_x, was calculated from:

$$R_x = \eta L_i/(K A_x), \qquad (3)$$

where η is the viscosity of water in the stem xylem and L_i is the total length of the internode. The leaf area of each leaf was measured with a leaf area meter (John Morris Scientific Pty Ltd, Sydney, Aust.) and

its location on the shoot was recorded. With the above measurements and for set climatic conditions (net radiation balance of each leaf $= 370 \text{ W m}^{-2}$, air temperature $= 40°C$, relative humidity $= 40\%$, leaf boundary layer resistance $= 1.6 \text{ m}^2 \text{ s mol}^{-1}$, chosen to represent the most extreme demands placed on the hydraulic system), methods described thoroughly elsewhere (Slatyer 1967; Monteith 1981) were used to calculate steady-state transpiration rates. This allowed simulation of flow rates, Q, through each internode on the intact shoot, and the hydrodynamic pressure drop per unit length, dP_E/dx, which is the result of Q, was obtained from,

$$dP_E/dx = R_x Q/L_i. \qquad (4)$$

Hydraulic maps of each shoot were then constructed by assigning a value of zero water potential to the base of the shoot and plotting x against P_E (x being the distance from the base of the shoot along the xylary flow path). Using the embolism susceptibility results, the effect on dP_E/dx of increased xylem resistance due to embolisms was also assessed. This simplified approach, which ignores stomatal feedback control over transpiration, does not necessarily depict the behaviour of these plants in the field, but serves only to highlight differences in hydraulic architecture.

Results and Discussion

Embolism Susceptibility

Embolism susceptibility curves are shown in Fig. 3. Both curves are in the form of a second order polynomial fitted through the scatter of data points ($r^2 = 0.946$ for Petford and $r^2 = 0.871$ for Tennant Creek). The fact that both curves start near 0% embolism implies that there was no native embolism, which is not surprising given that the plants were only 20 weeks old at harvest and had been well watered until the beginning of the drying phase. In comparing the two curves it seems that the onset of embolism in Tennant Creek seedlings occurs at a slightly lower leaf water potential than in Petford seedlings and that the increase in the extent of vessel embolisms with decreasing water potential is greater in Petford seedlings than in Tennant Creek seedlings.
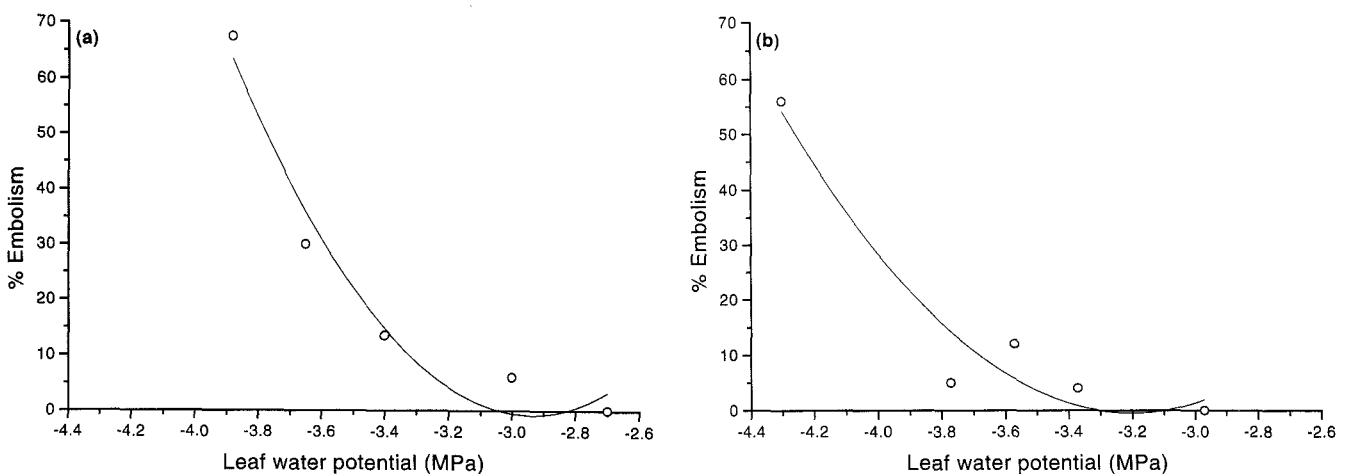

Fig. 3. Embolism susceptibility curves for *E. camaldulensis* seedlings of (*a*) Petford and (*b*) Tennant Creek provenances.

The embolism susceptibility curves shown here are very similar in form to those published for other hardwoods by Sperry *et al.* (1988*b*) and Tyree and Sperry (1989) who used very different methods. There is a general trend of no embolisms down to a threshold water potential, followed by an increase in the extent of embolisms with a further decrease in water potential. The threshold water potential (ψ_t) for Petford seedlings was about -3.0 MPa, and for Tennant Creek about -3.3 MPa.

Typical values of ψ_t reported for other species range from -1.0 MPa for the tropical tree *Schefflera morotoni* (Tyree *et al.* 1991) to -3.5 MPa for *Juniperus virginiana* (Sperry and Tyree 1990). A more extreme value of $\psi_t = -10.0$ MPa has been reported for the chaparral species *Ceanothus megacarpus* (Kolb and Davis 1991). *Eucalyptus camaldulensis* may therefore, be regarded as having a relatively low ψ_t and capable of maintaining full use of its hydraulic system in moderately dry soils.

Although with the use of a fitted curve a value for ψ_t may be estimated, care should be taken with the interpretation of this figure. It represents a region of water tension in which embolisms could begin to occur in the xylem. For a metastable system such as this, it is difficult to predict exactly at what tension a return to stability via embolism might occur. For example, work by Couzens and Trevena (1969) on a single water column subjected to pulses of increasing tension concluded that there was a region of tension spanning about 0.9 MPa in which cavitation occurred only sporadically. This suggests that the difference in ψ_t between Petford and Tennant Creek seedlings in our work may not be significant. What is significant, however, is the different amounts by which embolisms appear to increase with decreasing ψ_l. For a given decrease in ψ_l beyond ψ_t, seedlings of Petford provenance appear to experience a greater number of embolisms.

The differences in embolism susceptibility presented here might be attributed largely to a difference in the physical properties of the xylem. While Tyree and Sperry (1989) report that vulnerability to embolism is not correlated with the nature of the xylem element (i.e. whether the conduit is a hardwood vessel or a softwood tracheid), and also that there is no correlation between vulnerability and conduit diameter, it is known that anatomical properties at a microscopic level, such as pit pore diameter (Sperry and Tyree 1988) have a strong influence on embolism susceptibility. The 'air-seeding' hypothesis (Salisbury and Ross 1985; Sperry and Tyree 1988), which is the most widely accepted model for embolism in the xylem, states that emboli are initiated when small air

bubbles are introduced into the xylem sap from outside via pores in the pit membrane or cell wall. To test this hypothesis it would be appropriate to further investigate the nature of intercellular and cell wall air spaces and, especially with regard to hardwoods and embolisms within leaf tissue, the arrangement of cell types associated with the xylem tissue.

Many papers have discussed the ecological implications of a low cavitation threshold water potential and low embolisim susceptibility (Tyree and Ewers 1991). However, these physiological properties describe only one component of the overall hydraulic system. Knowledge of the conditions which lead to the development of ψ_t in the plant is now providing a more complete understanding of how some plants maintain turgor where others cannot.

Xylem Permeability and Resistance

Specific permeability values provide much information about the hydraulic architecture of shoots, while resistance values, although informative in themselves, are more meaningful when considered in the context of the flow demands placed upon them by the canopy. The specific permeabilities of stem wood in the Tennant Creek seedling were consistently higher than in the Petford seedling (Tables 1 and 2). Tennant Creek stem wood was about 40% more permeable than Petford, and the permeability of branch wood in Tennant Creek was about 25% higher than that of Petford. The ratio of stem permeability to adjacent branch permeability was between 1.7 and 2.2 in Tennant Creek and between 2.3 and 2.6 in Petford. Resistances to water flow at 25°C (R_{25}), which are partly a function of permeability, reflect similar trends

Table 1. Specific permeabilities (K) and resistances at 25°C (R_{25}) for one whole *E. camaldulensis* seedling from Petford provenance
Branch values (a, b) are for the first internode of the branch. Internode sections are numbered from the base of the shoot

Internode	$10^{-11} \times K$ (m²)		$10^5 \times R_{25}$ (MPa s m⁻³)	
	Stem	Branch	Stem	Branch
1	1.41	—	1.52	—
2	1.70	—	1.36	—
3, 3a	1.45	0.26	2.1	175
3b	—	0.35	—	119
4	1.50	0.44	2.49	86.6
5, 5a	1.75	0.75	2.99	62.1
5b	—	0.48	—	106
6, 6a	1.55	0.60	4.11	68.7
6b	—	0.60	—	64.7
7, 7a	1.46	0.50	7.32	87.0
7b	—	0.48	—	82.0
8, 8a	1.17	0.43	11.23	117
9	1.20	—	16.18	—
10	0.40	—	68.90	—

Table 2. Specific permeabilities (K) and resistances at 25°C (R_{25}) for one whole E. camaldulensis seedling from Tennant Creek provenance

Branch values (a, b) are for the first internode of the branch. Internode sections are numbered from the base of the shoot

| Internode	$10^{-11} \times K\,(m^2)$		$10^5 \times R_{25}\,(MPa\ s\ m^{-3})$	
	Stem	Branch	Stem	Branch
1, 1a	1.87	0.80	1.09	21.3
2	1.68	—	1.46	—
3	1.70	—	1.10	—
4	2.18	—	1.72	—
5	2.07	—	2.31	—
6, 6a	2.07	0.89	2.58	30.3
6b	—	0.90	—	26.8
7, 7a	1.64	0.98	4.87	23.6
7b	—	0.80	—	34.7
8, 8a	1.40	0.80	8.82	36.3
9, 9a	1.15	0.75	17.8	39.8
10	1.10	—	28.4	—

to those described above for K. Hence, both stem and branch resistances were lowest in Tennant Creek, and branch resistances were much lower in Tennant Creek than in Petford seedlings.

Simulated Water Potential Gradients

The pressure gradient along a section of stem associated with transpiration induced flow (dP_E/dx) is referred to here as the hydrodynamic xylem pressure gradient, which is in addition to the prevailing hydrostatic tension or xylem water potential of the shoot (Pickard 1981). Using the model and climatic conditions described above, values of dP_E/dx were obtained for the Petford and Tennant Creek seedlings

for two values of leaf water potential: $\psi_l = -1.0$ MPa and $\psi_l = -3.8$ MPa. The results are illustrated in Fig. 4, where each line represents a length of stem or branch, the slope of which is dP_E/dx. The steeper the slope of the line (i.e. the lower the value of dP_E/dx) the easier it is for water to flow to leaves fed by that length of xylem.

At $\psi_l = -1.0$ MPa, assuming no loss of hydraulic conductivity due to embolisms, both seedlings appear similar in their lower stem, but the pronounced steepening of dP_E/dx in the tip of the Petford stem would suggest much easier supply of water to its shoot apex. Also, in Petford branches the dP_E/dx values (only the first internode was measured) were much lower than in the stem, suggesting greater difficulty in supplying water to leaves in a branch adjacent to a stem segment than leaves on the shoot above that segment. These architectural properties suggest a young tree with strong apical control which is predisposed to shedding of branches (Zimmermann 1983), making it highly competitive in the forest environment (Halle *et al.* 1978). In contrast, the dP_E/dx values in Tennant Creek branches were similar to those in the stem, suggesting almost equal ability to supply branches and shoot apex with water and implying a greater likelihood of branch retention than Petford. These seedling properties do appear to prevail in the adult tree. In a study by Otegbeye and Samarawira (1991) on 18-year-old *E. camaldulensis* trees from 10 provenances it was found that those from Petford grew consistently tall and straight, while those from Tennant Creek were much shorter and retained the highest number of branches.
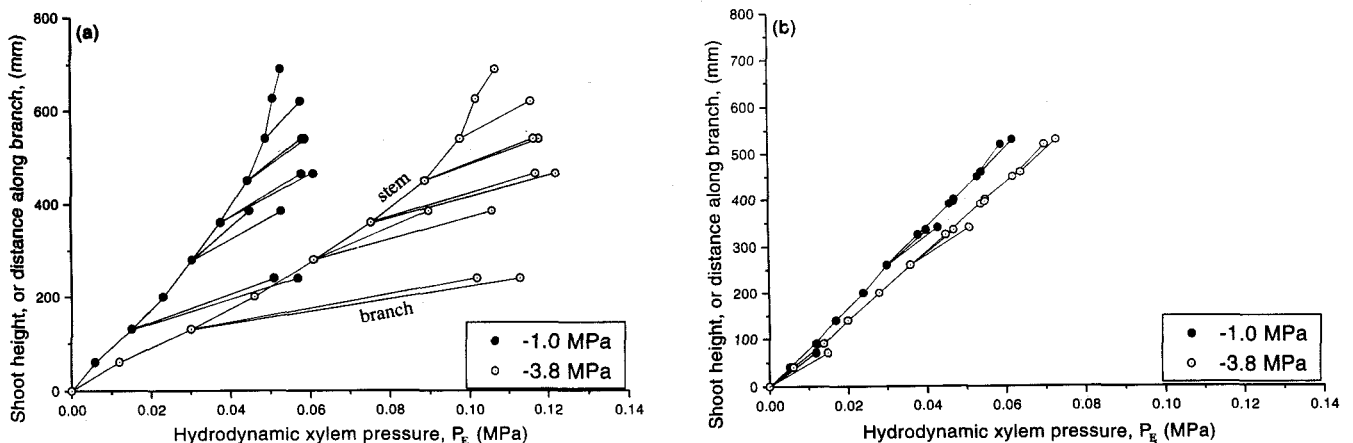
Fig. 4. Differences in the hydrodynamic pressure gradients in stems and branches of (*a*) Petford and (*b*) Tennant Creek seedlings at $\psi_l = -1.0$ and -3.8 MPa, as predicted from the hydraulic resistances and embolism susceptibility curves. At $\psi_l = -1.0$ MPa it was assumed there were no embolisms and subsequently no increase in the minimum hydraulic resistances occurring at a xylem temperature of 40°C. At $\psi_l = -3.8$ MPa hydraulic resistances in Petford are effectively double their value at $\psi_l = -1.0$ MPa, due to an estimated 50% loss of conducting vessels through embolisms. For ease of illustration P_E at the base of the shoot is given the reference value of 0.0 MPa. Note that in Tennant Creek the branches and stem follow a similar dP_E/dx gradient, which makes them difficult to distinguish in the diagram.

At $\psi_l = -3.8$ MPa, using the embolism suscepti-bility curves (Fig. 3), the increase in xylem resistance due to embolisms in Petford seedlings resulted in a dramatic increase in dP_E/dx compared with Tennant Creek seedlings. This is because under these conditions Petford seedlings would have suffered about 50% loss of conductivity due to embolisms, while Tennant Creek seedlings would have lost only 15%. This reduction in the capacity of the hydraulic system could lead to water deficits in the canopy unless stomatal conductance was reduced accordingly. Reduced stomatal conductance following embolisms has been demonstrated in *Betula occidentalis* by Sperry and Pockman (1993), but they also found that after 1-2 weeks stomatal conductance and transpi-ration increased, leading to further embolisms and dieback. Perhaps the speed of recovery from embolisms is just as critical as reduced embolism susceptibility for the survival of plants experiencing periodically low water potentials.

In a study on *E. camaldulensis* by Gibson *et al.* (1991) the stomatal conductance of Petford seedlings was found to decrease under water stress, while that of Tennant Creek remained largely unaffected. It is not clear whether this was associated with the occurrence of embolisms in Petford, but it may to some extent result from differences in their hydraulic architec-tures. It is possible that the higher shoot xylem resist-ances found in Petford during our study contribute to leaf water deficits in the canopy, although there are other resistances such as those within the root system, and possibly at stem and leaf insertions, which need to be investigated for a more complete picture.

Of most significance in this study is that despite the close genetic relationship shared by these two proven-ances of *E. camaldulensis*, a striking difference was observed in their respective hydraulic architectures when grown together in the same environment. In a similar manner Neufeld *et al.* (1992) found large differences in conductivity, embolism susceptibility and gas exchange behaviour with four sugarcane clones. Further studies along these lines will not only enhance our understanding of gas exchange and overall productivity, as well as plant growth habit and biogeography, but may also indicate potential gains from modifying the plant hydraulic system through breeding programs.

References

Bolton, A. J., and Petty, J. A. (1978). The relationship between axial permeability of wood to dry air and a non-polar solvent. *Wood Science and Technology* **12**, 111-126.

Cochard, H., and Tyree, M. T. (1990). Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiology* **6**, 393-407.

Comstock, G. L. (1967). Longitudinal permeability of wood to gases and non swelling liquids. *Forest Products Journal* **17**, 41-45.

Couzens, D. C. F., and Trevena, D. H. (1969). Critical tension in a liquid under dynamic conditions of stressing. *Nature* **222**, 473-474.

Gibson, A., Hubick, K. T., and Bachelard, E. P. (1991). Effects of abscisic acid on morphological and physiological responses to water stress in *Eucalyptus camaldulensis* seedlings. *Australian Journal of Plant Physiology* **18**, 153-163.

Grace, P. G., Malcolm, D. C., and Bradbury, I. K. (1975). The effect of wind and humidity on leaf diffusive resistance in Sitka Spruce seedlings. *Journal of Applied Ecology* **12**, 931-940

Halle, F., Olderman, R. A. A., and Tomlinson, P. B. (1978). 'Tropical Trees and Forests: an Architectural Analysis.' (Springer Verlag: New York.)

Jarvis, P. G. (1975). Water transfer in plants. In 'Heat and Mass Transfer in the Biosphere'. Part 1. Transfer processes in the plant environment. (Eds D. A. de Vries and N. H. Afgan.) pp. 369-394. (John Wiley and Sons: New York.)

Jones, H. G., and Sutherland, R. A. (1991). Stomatal control of xylem embolism. *Plant, Cell and Environment* **14**, 607-612.

Klinkenberg, L. J. (1941). The permeability of porous media to liquids and gases. API Drilling Production Practice. Internal Technical Report No. 200, American Petroleum Industry.

Kolb, K. J., and Davis, S. D. (1991). Differential occurrence of xylem embolism between a coastal sage species and a chaparral shrub species growing at the same microsite. *Bulletin of the Ecological Society of America.* **72** (supplement), 165

Monteith, J. L. (1981). Coupling of plants to the atmosphere. In 'Plants and their Atmospheric Environment'. (Eds J. Grace, E. D. Ford and P. G. Jarvis.) pp. 1-29. (Blackwell Scientific Publications: Melbourne.)

Neufeld, H. S., Grantz, D. A., Meinzer, F. C., Goldstein, G., Crisosto, G. M., and Crisosto, C. (1992). Genotypic variability in vulner-ability of leaf xylem to cavitation in water stressed and well irrigated sugarcane. *Plant Physiology* **100**, 1020-1028.

Otegbeye, G. O., and Samarawira, I. (1991). Growth and form of *Eucalyptus camaldulensis* Dehnh. provenances in northern Nigeria. *Forest Ecology and Management*, **42**, 219-228.

Pereira, J. S., and Kozlowski, T. T. (1976). Leaf anatomy and water relations of *Eucalyptus camaldulensis* and *E. globulus* seedlings. *Canadian Journal of Botany* **54**, 2868-2880.

Petty, J. A. (1970). Permeability and structure of the wood of Sitka spruce. *Proceedings of the Royal Society of London Series B-Biological Sciences* **175**, 149-166.

Pickard, W. F. (1981). The ascent of sap in plants. *Progress in Biophysics and Molecular Biology* **37**, 181-229.

Salisbury, F. B., and Ross, C. W. (1985). 'Plant Physiology'. (Wadsworth Publishing Co.: Belmont.)

Scheidegger, A. E. (1963). 'The Physics of Flow Through Porous Media.' (University of Toronto Press: Toronto.)

Schulze, H. R., and Matthews, M. A. (1988). Resistance to water transport in shoots of *Vitis vinifera L.*: relation to growth at low water potential. *Plant Physiology* **88**, 718-724.

Siau, J. F. (1984). 'Transport Processes in Wood.' (Springer Verlag: New York.)

Skene, D. S., and Balodis, V. (1968). A study of vessel length in *Eucalyptus obliqua.* *Journal of Experimental Botany* **19**, 825–830.

Slatyer, R. O. (1967). 'Plant–Water Relationships.' (Academic Press: London.)

Sperry, J. S., Donnelly, J. R., and Tyree, M. T. (1988*a*). A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11**, 35–40.

Sperry, J. S., Tyree, M. T., and Donnelly, J. R. (1988*b*). Vulnerability of xylem to embolism in a mangrove vs an inland species of Rhizophoraceae. *Physiologia Plantarum* **74**, 276–283.

Sperry, J. S., and Tyree, M. T. (1988). Mechanism of water stress induced xylem embolism. *Plant Physiology* **88**, 581–587.

Sperry, J. S., and Pockman, W. T. (1993). Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis.* *Plant, Cell and Environment* **16**, 279–287.

Sperry, J. S., and Tyree, M. T. (1990). Water-stress-induced xylem embolism in three species of conifer. *Plant, Cell and Environment* **13**, 427–436

Tyree, M. T., Snyderman, D. A., Wilmot, T. R., and Machado, J.-L. (1991). Water relations and hydraulic architecture of a tropical tree (*Schefflera morotoni*). *Plant Physiology* **96**, 1105–1113.

Tyree, M. T., and Sperry, J. S. (1989). Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 19–38.

Tyree, M. T., and Ewers, F. W. (1991). Tansley Review No. 34. The hydraulic architecture of trees and other woody plants. *New Phytologist* **119**, 345–360.

Tyree, M. T., and Sperry, J. S. (1988). Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiology* **88**, 574–580.

Zimmermann, M. H. (1978). Hydraulic architecture of *Thuja occidentalis.* *Canadian Journal of Botany* **61**, 2105–2111.

Zimmermann, M. H., and Jeje, A. A. (1981). Vessel length distribution in stems of some American woody plants. *Canadian Journal of Botany* **59**, 1882–1892.

Zimmermann, M. H. (1983). 'Xylem Structure and the Ascent of Sap.' (Springer Verlag: New York.)