New Phytol. (1999), **143**, 365–372

The importance of xylem constraints in the distribution of conifer species

T. BRODRIBB* AND R. S. HILL

Department of Plant Science, University of Tasmania, PO Box 252–55, Hobart 7001, Australia

Received 25 February 1999; accepted 23 April 1999

SUMMARY

Vulnerability of stem xylem to cavitation was measured in 10 species of conifers using high pressure air to induce xylem embolism. Mean values of air pressure required to induce a 50 % loss in hydraulic conductivity (φ_{50}) varied enormously between species, ranging from a maximum of 14.2 ± 0.6 MPa (corresponding to a xylem water potential of -14.2 MPa) in the semi-arid species *Actinostrobus acuminatus* to a minimum of 2.3 ± 0.2 MPa in the rainforest species *Dacrycarpus dacrydioides*. Mean φ_{50} was significantly correlated with the mean rainfall of the driest quarter within the distribution of each species. The value of φ_{50} was also compared with leaf drought tolerance data for these species in order to determine whether xylem dysfunction during drought dictated drought response at the leaf level. Previous data describing the maximum depletion of internal CO_2 concentration (c_i) in the leaves of these species during artificial drought was strongly correlated with φ_{50} suggesting a primary role of xylem in effecting leaf drought response. The possibility of a trade-off between xylem conductivity and xylem vulnerability was tested in a sub-sample of four species, but no evidence of an inverse relationship between φ_{50} and either stem-area specific (K_a) or leaf-area specific conductivity (K_l) was found.

Key words : xylem cavitation, air-seeding, drought stress, conifer distribution, xylem conductance.

INTRODUCTION

Xylem tissue is the principal medium for water flow in terrestrial tracheophytes and as such it is a primary determinant of a plant's ability to survive in its environment. The last decade has seen considerable research interest in the mechanisms and characteristics of water flow from the soil to the leaves in the xylem of vascular plants, and the importance of the hydraulic conductance of the xylem pathway in regulating plant growth and even limiting plant size (Mencuccini & Grace, 1996; Ryan & Yoder, 1997) is only now being realised. Changes in xylem conductance in the short term have been shown to affect stomatal conductance of individual leaves (Sperry, 1986; Sperry & Pockman, 1993), and in more recent studies it has been suggested that transpiration at the branch and crown levels are closely associated with the conductance of the sapwood xylem (Cochard *et al.*, 1997; Andrade *et al.*, 1998).

The conductivity of xylem in stems, roots and leaves has been shown to be a function of the tissue water potential, decreasing as the water tension in the plant increases (Tyree, 1997). As the xylem water potential (ψ_x) decreases, air is believed to enter xylem elements by breaking the surface tension of water at the inter-conduit pits (a process known as 'air-seeding'), rendering them non-functional (Sperry & Tyree, 1988). Xylem vulnerability to cavitation is highly variable among taxa, with significant differences recorded even in closely related species growing under identical conditions (Kolb & Davis, 1994; Jarbeau *et al.*, 1995; Tognetti *et al.*, 1998). However, intraspecific variation in vulnerability of stem xylem is quite small, even amongst individuals from contrasting environments (Franks *et al.*, 1995; Alder *et al.*, 1996).

One of the explanations for this large range in xylem vulnerability to cavitation is that a trade-off exists between xylem conductivity and xylem vulnerability. Evidence of such a trade-off has been reported both within the xylem tissue of individual plants (Sperry & Saliendra, 1994; Lo Gullo *et al.*, 1995; Hacke & Sauter, 1996) and between plants (Hargrave *et al.*, 1994; Lovisolo & Schubert, 1998) and has been attributed to an increased vulnerability to cavitation (particularly freezing-induced) as vessel size increases (Tyree *et al.*, 1994). Because angiosperms possess vessel elements which can vary

*Author for correspondence (tel +61 362 262596; fax +61 362 262698; e-mail brodribb@utas.edu.au).

CAMBRIDGE UNIVERSITY PRESS

enormously in length and diameter (Zimmermann & Jeje, 1981) a large potential exists for variation in xylem conductance and susceptibility to cavitation. Such variability appears to allow even ecologically closely associated angiosperms to adopt a variety of different water use strategies resulting in a lack of any good correlation between environmental water availability and xylem vulnerability to cavitation (Kolb & Davis, 1994; Jarbeau *et al.*, 1995).

In contrast to angiosperms, conifers do not possess xylem vessels, relying rather on the much smaller tracheid cells for xylem conduction. For this reason conifers are quite restricted in terms of maximum conduit size and xylem conductivity and hence the potential for large trade-offs between xylem vulnerability and conductivity is reduced. Conifers are thus particularly suitable for investigating the possibility that the distributional limits on a group of plants might be defined by wood characteristics. However, few studies have attempted to quantify the response of conifer wood to water potential, perhaps because the standard technique for measuring the amount of non-functional cavitated xylem depends on a comparison with uncavitated wood, requiring the flushing of embolisms from a wood sample (Sperry *et al.*, 1988). Unfortunately the usual practice of flushing embolisms by introducing high pressure water into the stem has proved to be an unreliable technique for most conifers (Sperry & Tyree, 1990) probably due to difficulties in forcing water through bordered pits.

In this study we examined the vulnerability to cavitation in stem xylem of a group of southern Hemisphere conifers, and tested for a relationship with environmental water availability. Problems associated with flushing embolisms from wood were avoided by establishing maximum stem conductances using glasshouse plants grown under conditions of high water availability and low evaporative demand, in which xylem embolism should have been minimal. Vulnerability to cavitation was measured by the technique of Sperry & Saliendra (1994) which uses air pressure to seed embolisms while hydraulic conductivity is monitored. Plants believed to be free of embolisms were also used to test for the existence of a vulnerability-conductivity trade-off in conifer species.

This study also examines the relationship between drought tolerance at the leaf and wood level in these species, and investigates the possibility that xylem dysfunction is a causal factor in the expression of leaf drought tolerance. The conifers used here were the same species used in previous studies examining the leaf response to drought (Brodribb & Hill, 1998) and light (Brodribb & Hill, 1997). It has been shown that during controlled drought, decreasing stomatal conductance causes the concentration of CO_2 in the leaf (c_i) to drop as photosynthesis becomes limited by CO_2 supply. Decreasing c_i continues until a water potential is reached where incipient leaf damage causes c_i to rise, and in conifers the minimum attainable c_i provides a physiological index of drought tolerance (Brodribb, 1996). This index is expressed as the minimum value of c_i as a fraction of the ambient CO_2 concentration $(c_i/c_a)_{min}$. Here we compared the leaf character $(c_i/c_a)_{min}$ and the vulnerability to cavitation of the xylem to test for a correlation in 10 conifer species from a diverse range of habitats.

MATERIALS AND METHODS

Plant material

Cuttings, and where possible, seeds, were collected from plants in the field. A description of species habit and distribution is given in Table 1. Cuttings of *Acmopyle pancheri* (Brongn. & Gris.) Pilger, *Dacrycarpus compactus* (Wasser) de Laub., *Lagarostrobos franklinii* (Hook.f) Quinn and *Podocarpus lawrencei* Hook.f., and seeds from *Actinostrobus acuminatus* Parlatore, *Athrotaxis selaginoides* D.Don, *Callitris rhomboidea* R.Br., *Dacrycarpus dacrydioides* (Rich.) de Laub., *Podocarpus drouynianus* F. Muell., and *Widdringtonia cedarbergensis* Marsh, were propagated in sand in Hobart. Upon establishment, all plants were transferred to a pine bark potting mix in 3-l pots and grown under ambient light in a well irrigated, heated glasshouse near sea-level in Hobart. All species were represented by at least five plants (and in the case of the cuttings, from at least three parent trees), except for *Acmopyle pancheri*, which could only be propagated from two cuttings due to difficulty in collection (this species is restricted to New Caledonia) and extreme sensitivity to light and humidity conditions during striking. All plants were aged between 5 and 8 yr at the time of harvesting branches for conductance measurements.

Induction of embolism

The following method works on the assumption that embolism occurs by air-seeding, and that the external application of air pressure corresponds exactly with the effects of lowering internal water potential. These two assumptions are supported by a large number of recent studies (see Sperry *et al.*, 1996 and Tyree, 1997 for review).

Stem segments of around 350 mm in length, and 3–6 mm in diameter were cut from the branches of glasshouse plants. Bark and all side branches were removed and segments inserted into a double-ended pressure bomb similar to that described in Sperry & Saliendra (1994), with air vents at both ends. Stems were then trimmed under water to lengths of between 200 and 250 mm and connected to the apparatus for measuring hydraulic conductance. The design of this apparatus was also similar to that of

Table 1. *Habit, distribution and minimum quarterly rainfall for the 10 species investigated*

Species	Habit	Distribution	Dry quarter rainfall (mm)
Acmopyle pancheri PODOCARPACEAE	Rainforest understorey to canopy tree	New Caledonia	394
Dacrycarpus dacrydioides PODOCARPACEAE	Rainforest tree	New Zealand	378
Dacrycarpus compactus PODOCARPACEAE	Sub-alpine small tree to shrub	Papua New Guinea	373
Lagarostrobos franklinii PODOCARPACEAE	Rainforest tree	Southern Australia	330
Athrotaxis selaginoides CUPRESSACEAE	Rainforest tree to sub-alpine shrub	Southern Australia	249
Podocarpus lawrencei PODOCARPACEAE	Sub-alpine shrub	Southern Australia	208
Podocarpus drouynianus PODOCARPACEAE	Open forest shrub	Western Australia	70
Callitris rhomboidea CUPRESSACEAE	Dry forest tree	Southern Australia	62
Actinostrobus acuminatus CUPRESSACEAE	Semi-arid shrub to small tree	Western Australia	14
Widdringtonia cedarbergensis CUPRESSACEAE	Dry forest small tree	South Africa	18

Sperry & Saliendra (1994), using an electronic balance to measure the mass flow of a filtered solution of HCl (of pH 2) through the stem segment under a head pressure of between 4 and 5 kPa. Conductance was calculated as the mass flow of water (kg s^{-1}) divided by the pressure gradient (MPa m^{-1}). Considering that high-pressure flushing was an ineffective means of ascertaining maximum conductance (K_m) (Sperry & Tyree, 1990; T. Brodribb, unpublished) the stem segments were assumed to be initially non-embolised. To ensure this was the case, stems were taken from glasshouse plants during the winter months during which time the glasshouse temperature did not exceed 20°C and relative humidity remained above 65%. Initial conductance measured was therefore recorded as K_m Following determination of K_m, pressure in the bomb was increased to 1 MPa and maintained for a period of 20 min which ensured saturation of the embolism response (a pressurization time of 15 min produced 93–100% saturation of the cavitation response in all species tested; unpublished data). The pressure was then gradually released and stem conductance (K_a) measured at 5 min intervals until readings stabilised. This procedure was repeated using increments of 1 MPa pressure until K_a was reduced to $<5\%$ of K_m. Loss of conductance was expressed as a percentage of K_m for each stem segment.

Vulnerability curves were then constructed for the stems of five individuals of each species (only two for *A. pancheri*). The shape of these curves was approximately that of a normal cumulative plot as would be expected if the size distribution of tracheids and pit apertures (and therefore the vulnerability distribution of tracheids per sample) was normal. Therefore the data were converted to linear plots using a probit transformation and the water potential at 50% loss of conductance (φ_{50}) determined from regression equations for each stem sample. From these data a mean and standard error for φ_{50} was calculated for each species.

Leaf and environmental parameters

Xylem cavitation data were compared with leaf physiological parameter $(c_i/c_a)_{min}$ for each species. The leaf physiology data for these species are taken from Brodribb (1996). Comparison of xylem vulnerability data with environmental water availability for each species was also undertaken. The most meaningful parameter in terms of maximum drought tolerance of a species was the minimum quarterly (three consecutive months) rainfall at the driest occurrence of each species. These data were compiled by combining distribution records for each species (many of which are quite restricted) and meteorological data from the nearest weather station (see Brodribb & Hill, 1998 for data references).

Specific conductivity on a stem and leaf area basis

The relationship between stem cross-sectional area, leaf area and K_m was examined in four of the 10 species. A sub-sample of four species was used because these measurements required the destruction of a number of larger stems, and few species possessed sufficient stem material for comparison. The species selected covered a large range of φ_{50} values. A total of 14 to 25 stems ranging in diameter from 2 mm to *c.* 10 mm (without bark) were harvested from three individuals of each species.

Segments of between 200 and 300 mm were cut from these stems, and side branches were removed. Segments were then re-cut underwater and connected to the hydraulic conductance apparatus described above. Flow rates were measured at 5 min intervals until steady. After conductance measurement the stem diameter (without bark) was measured and the leaf area distal to the stem segment was measured using a digital camera (EDC-1000, Electrim Corp., Princeton, USA) to count the silhouette area of leaves flattened between two sheets of glass. Stem area excluded cortex, but included pith area which was always very small (consistently *c.* 1% of the total stem area; T. Brodribb, unpublished).

Stem K_m was calculated by dividing the mass flow rate of water through the stem by the pressure gradient across the stem segment. The temperature of the stem segment was monitored by two thermocouples attached at each end, and the flow rate corrected for changes in the viscosity of water. Stem conductivity was expressed in terms of stem cross-sectional area ($K_a = K_m/A_s$; where K_a is the stem area specific conductivity and A_s is the stem cross-sectional area) and leaf area supplied ($K_l = K_m/A_l$; where K_l is the leaf area specific conductivity and A_l is the leaf area supplied). Means of K_a and K_l for each species were compared *post hoc* using a Scheffé test (Day & Quinn, 1989).

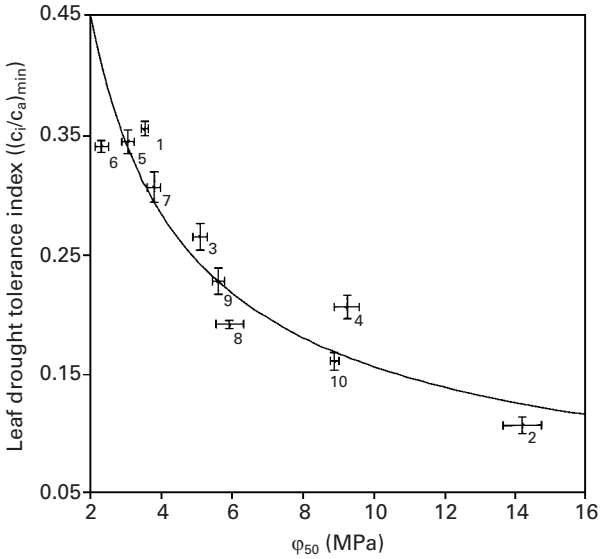


Fig. 1. The relationship between average ($n = 5$) air seeding pressure (equivalent to the negative water potential) which reduced stem conductance to 50% of the measured maximum (φ_{50}) and the average ($n = 3$) leaf drought tolerance index $(c_i/c_a)_{min}$ (Brodribb, 1996) in each of 10 conifer species. Species are labelled: 1, *Acmopyle pancheri*; 2, *Actinostrobus acuminatus*; 3, *Athrotaxis selaginoides*; 4, *Callitris rhomboidea*; 5, *Dacrycarpus dacrydioides*; 6, *Dacrycarpus compactus*; 7, *Lagarostrobos franklinii*; 8, *Podocarpus drouynianus*; 9, *Podocarpus lawrencei*; 10, *Widdringtonia cedarbergensis*. A highly significant exponential regression ($y = 0.71x - 0.66$, $r^2 = 0.89$, $P < 0.001$) is shown.

RESULTS

Xylem vulnerability to cavitation

An extremely large range in φ_{50} was found to occur among species (Table 2), with the most vulnerable species, *D. dacrydioides*, exhibiting a 50% loss in conductance at an average pressure of 2.3 ± 0.2 MPa (corresponding to ψ_x of -2.3 MPa), whereas at the other extreme, stems of *A. acuminatus* on average had lost 50% of K_m at a pressure of 14.2 ± 0.6 MPa (or ψ_x of -14.2 MPa). A good correlation was found to exist between xylem susceptibility to cavitation and the leaf drought tolerance index $(c_i/c_a)_{min}$. Values shown in Fig. 1 represent means and standard errors for each of the 10 species. A highly significant exponential regression ($P < 0.001$) described the relationship between φ_{50} and $(c_i/c_a)_{min}$ (Fig.1). This

Table 2. *Mean pressure (MPa ± SE) required to decrease xylem conductance to 50% of maximum (φ_{50}); positive pressures shown here are equivalent to negative water potentials in living stems*

Species	φ_{50}	K_a	$K_l \times 10^{-4}$
Acmopyle pancheri	3.7 ± 0.1	–	–
Actinostrobus acuminatus	14.1 ± 0.6	–	–
Athrotaxis selaginoides	5.1 ± 0.2	–	–
Callitris rhomboidea	9.2 ± 0.4	–	–
Dacrycarpus compactus	3.1 ± 0.2	–	–
Dacrycarpus dacrydioides	2.3 ± 0.2	0.28 ± 0.03	1.5 ± 0.2
Lagarostrobos franklinii	3.8 ± 0.2	0.27 ± 0.03	1.2 ± 0.2
Podocarpus drouynianus	5.9 ± 0.4	–	–
Podocarpus lawrencei	5.6 ± 0.2	0.25 ± 0.04	1.1 ± 0.2
Widdringtonia cedarbergensis	8.9 ± 0.1	0.68 ± 0.05	5.2 ± 0.5

Based on $n = 5$ except *Acmopyle pancheri* where $n = 2$. Mean conductance per unit stem area (K_a; kg $s^{-1}MPa^{-1}$ m^{-1}) and conductance per unit leaf area (K_l; kg $s^{-1}MPa^{-1}$ m^{-1}) are shown for a sub-sample of four species: *Dacrycarpus dacrydioides*, *Lagarostrobos franklinii*, *Podocarpus lawrencei* and *Widdringtonia cedarbergensis*, where $n = 15$, 25, 15, and 14 respectively.

CAMBRIDGE UNIVERSITY PRESS

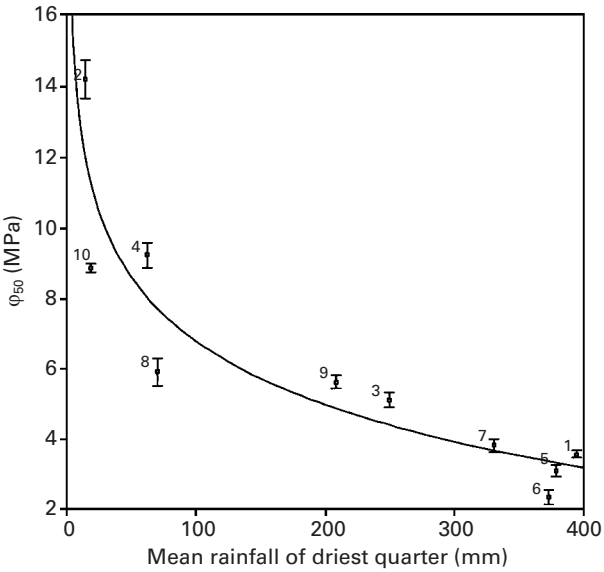


Fig. 2. Average φ_{50} versus mean rainfall of the driest 3 successive months within the distribution of each of the 10 conifer species (labelled as in Fig. 1). A log regression best described the relationship between these two variables ($y = -6.01 \log x + 18.8$; $r^2 = 0.85$, $P < 0.001$.

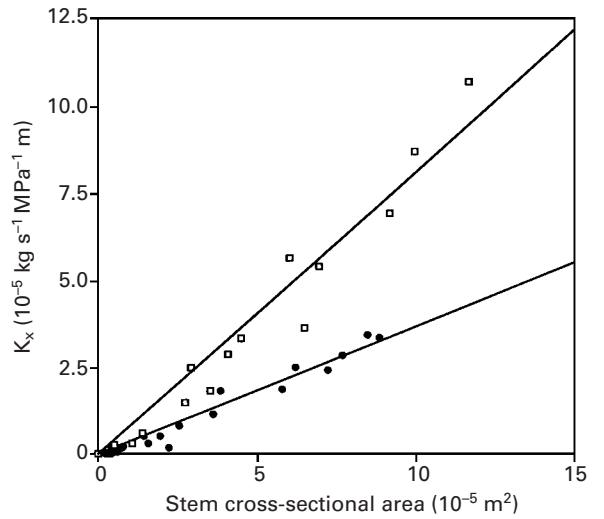


Fig. 3. The relationship between stem conductance (K_x) and stem cross-sectional area in *Widdringtonia cedarbergensis* (squares) and *Dacrycarpus dacrydioides* (circles). The high significance of these regressions ($r^2 = 0.99$ for both species) and similar ones for *Podocarpus lawrencei* and *Lagarostrobos franklinii* enabled a mean value of K_x to be calculated for each species.

exponential function provides the most logical description of the relationship, given that φ_{50} is limited to values above zero, and that chemistry of Rubisco restricts c_i/c_a in C_3 plants to a minimum of *c.* 0.1 (Azcon-Bieto *et al.*, 1981).

As expected, species from wet forest were found to be much more vulnerable to xylem cavitation than those from the arid zone (Fig. 2). The variation in average φ_{50} was small in species confined to rainforest (species 1, 5, 6 and 7 in Fig. 2), whereas those species from drier environments produced a large range of vulnerabilities. Xylem resistance to cavitation was significantly related ($P < 0.001$) to the log of minimum quarterly rainfall.

Specific conductivity on a stem and leaf area basis

Stem conductance was approximately proportional to stem area in the four species where it was measured on stems of larger diameters (Fig. 3 shows data from two of the four species), and thus a single mean value could be used to express stem area-specific hydraulic conductivity (K_a) for each of these species. There were small differences in the values of K_a for the species *L. franklinii*, *P. lawrencei* and *D. dacrydioides* whereas *W. cedarbergensis* exhibited a K_a of more than double the other three species (Table 2). A *post hoc* test of the mean K_a values for each species using Scheffé's test showed that *W. cedarbergensis* was the only species possessing a significantly higher mean K_a to the other species. Despite a range of more than 6 MPa in φ_{50}, no correlation between K_a and φ_{50} was observed in these four species, although unexpectedly, the highest K_a was recorded in the species with the most cavitation-resistant xylem (Table 2).

Stem conductance was also found to be proportional to leaf area in each species enabling a single value for K_l to describe each species. Mean K_l for *W. cedarbergensis* was significantly higher ($P < 0.001$; Scheffé test) than each of the other three species (Table 2), while in *L. franklinii*, mean K_l was significantly lower than the other species ($P < 0.05$; Scheffé test). Again no relationship between φ_{50} and K_l was evident despite the large range of values of K_l.

DISCUSSION

A strong relationship was observed between xylem vulnerability to cavitation and average rainfall during the driest 3 months (Fig. 2). Species from wet environments were highly vulnerable to cavitation while species from the semi-arid zone produced stem xylem which was extremely resistant to pressure-induced cavitation. Clearly this indicates an important, if not central role of xylem vulnerability in determining the distributional limits of these plants in terms of minimum water availability. Exactly how φ_{50} relates to the soil and whole plant conditions at the point of leaf and plant death requires further investigation.

Evidence of a strong linkage between leaf drought tolerance and stem cavitation characteristics is shown by a highly significant regression relating $(c_i/c_a)_{min}$ (or the inverse of maximum instantaneous water-use efficiency) with φ_{50} (Fig. 1) and by the fact that $(c_i/c_a)_{min}$ has previously been correlated with minimum rainfall requirement for each of the these species (Brodribb & Hill, 1998). The most obvious

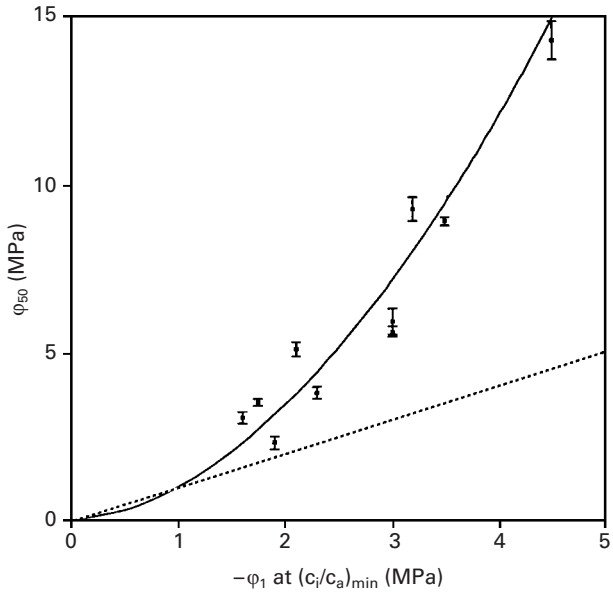


Fig. 4. The relationship between φ_{50} and xylem water potential (ψ_1) at $(c_i/c_a)_{min}$ for the 10 species used in this study (data from Brodribb, 1996). ψ_1 at $(c_i/c_a)_{min}$ represents ψ_1 at the threshold of miniumum stomatal conductance and a declining optimal quantum yield of PSII during drought. An exponential curve is fitted to the data illustrating an increasing discrepancy between φ_{50} and ψ_1 at $(c_i/c_a)_{min}$ with increasing values of φ_{50}. The vertical distance between the broken line and the regression line represents the safety margin between ψ_1 at stomatal closure and the water potential which causes a 50% loss in stem conductivity.

inference from this is that a loss of hydraulic conductance in the xylem during water shortage is the causal factor dictating a loss of leaf function during drought in these species. Such a hypothesis is supported by data suggesting that plants may operate close to the point of 'runaway cavitation', where a positive feed-back following xylem embolism has the potential to cause the vascular system to lose hydraulic conductivity rapidly unless transpiration is reduced (Sperry *et al*., 1993; Alder *et al*., 1996). However, several pieces of evidence point away from xylem dysfunction as the primary cause of leaf failure during drought, particularly for species from drier habitats. This evidence comes from previous work where it was found that complete stomatal closure and a loss of optimal quantum yield (indicating damage to PSII) in these species both occurred at leaf water potentials above the value corresponding to φ_{50} (Brodribb, 1996). The difference between φ_{50} and ψ_x at the point of stomatal closure increases exponentially with φ_{50} (Fig. 4) resulting in a large safety margin between stem water potential during active photosynthesis and that which would induce significant (or possibly runaway) cavitation. It seems unlikely, therefore, that the xylem water potential would approach φ_{50} unless plants were subject to severe water shortage. Considering that none of the species investigated are likely to suffer significant embolism by freeze–thaw cycles (Sperry *et al*., 1994), large-scale stem xylem cavitation probably only occurs when plants experience soil moisture conditions associated with φ_{50}.

The logarithmic relationship between minimum rainfall and φ_{50} (Fig. 2) illustrates a rapid increase of φ_{50} in species from increasingly arid environments. This can be explained by considering limitations imposed by the hydraulic conductivity of the soil in arid environments. During drought in the arid zone, soil water content is likely to drop to values where the hydraulic conductivity of the soil–plant continuum is entirely limited by the conductance of the rhizosphere (Sperry *et al*., 1998). This would be exacerbated by the coarse, often sandy soils which support the semi-arid species of *Actinostrobus* and *Widdringtonia* (Marsh, 1966; Hill, 1998). Under dry conditions where the conductance of the rhizosphere approaches zero, or where roots are disconnected from the soil by air-spaces in the soil (North & Nobel, 1998), water transpired by leaves is not replaced, and thus the plant water potential would decrease rapidly even with closed stomata, leaving plants particularly vulnerable to xylem cavitation. Thus one would expect these species to possess xylem tissue disproportionately resistant to low water potential in order to avoid severe cavitation during soil drying.

The species which produced the most extreme value of φ_{50} (*A. acuminatus*, 14.2 ± 0.6 MPa) grows in Western Australia under conditions of extremely low summer rainfall. Other species from similar habitats have also been found to exhibit low values of φ_{50}, with two angiosperm species from the Californian chaparral surviving embolism produced by xylem water potentials of -10 and -11 MPa (Kolb & Davis, 1994; Williams *et al*., 1997). The value for *A. acuminatus* is significantly lower than for these two shrubs, and substantially lower than the minimum leaf water potential measured in other Australian xerophytes (Van den Driessche *et al*., 1971), making it one of the most cavitation-resistant species yet measured. Conifer wood is well suited to resisting drought-induced cavitation in the same way that it appears to resist freeze–thaw cavitation (Sperry *et al*., 1994) probably due to the absence of xylem vessels. Narrow conduits are generally considered more cavitation-resistant than those of large diameter, although this generalization does not seem to be supported by inter-species comparisons (Sperry & Saliendra, 1994; Lovisolo & Schubert, 1998). Nevertheless, conifer xylem has been found to exhibit lower levels of embolism and a higher resistance to cavitation than associated angiosperms in studies where wood characteristics have been compared (Sperry *et al*., 1994; Tyree *et al*., 1998; Zwieniecki & Holbrook, 1998). However, the vessel-free wood of conifers is not necessarily linked to cavitation-resistance, and rainforest species from

New Zealand, Papua New Guinea, New Caledonia and Tasmania (*D. dacrydioides*, *D. compactus*, *A. pancheri* and *L. franklinii*, respectively) all exhibited average values of φ_{50} between 2.3 and 3.8 MPa (Fig. 2). These relatively high vulnerabilities are similar to those observed in other wet forest conifers from the tropics (Tyree *et al*., 1998) and North America (Sperry & Tyree, 1990), indicating that conifer wood is not simply predisposed to cavitation resistance, but rather that differences in vulnerability represent an adaptive response in these species.

In angiosperms, evidence of a trade-off between xylem vulnerability to cavitation and hydraulic conductivity has been found to occur within individual plants (Lo Gullo *et al*., 1995) and within samples of individual species (Salleo & Lo Gullo, 1989; Hargrave *et al*., 1994). From the enormous range of cavitation vulnerabilities observed here it was expected that there would be evidence of a conductivity–vulnerability trade-off in the sub-sample of species studied. However, this was not the case, with the most cavitation-resistant species from the sub-sample producing the highest values of K_a and K_l and no pattern evident amongst the other species (Table 2). Kavanagh *et al*. (1999) also found no evidence of a trade-off between stem−xylem conductivity and vulnerability in wet and dry populations of *Pseudotsuga menziesii*, suggesting that perhaps, in conifers at least, the trade-off for drought-induced cavitation resistance does not involve xylem conductivity. If xylem vulnerability is a function of tracheid pit-size then the effects of a reduction in pit-size on xylem conductivity might be offset by an increase in the number of pits per conduit, possibly allowing these two physical parameters to vary somewhat independently.

If it is accepted that vulnerability to cavitation is a detrimental feature of wood then it must be expected that resistance to cavitation comes at a price. Another possibility exists for a trade-off between a species' xylem cavitation-resistance and shade tolerance, contributing to the well documented interplay between shade and drought tolerance (Smith & Huston, 1989; Holmgren *et al*. 1997). There is good evidence that this is in fact the case for the species here, and data for the amount of PAR required to saturate photosynthesis (Brodribb & Hill, 1997) are closely correlated with φ_{50} values for the species here ($r^2 = 0.83$). The mechanics of such an interaction might involve high synthesis costs of cavitation-resistant wood, although this remains speculation.

Unfortunately limitations in plant size and numbers meant that we were restricted to using only stem material for species comparisons. However, given the good correlations with minimum rainfall and leaf drought tolerance from measurements on stem xylem, it is likely that the relativity was constant for other xylem tissues. The relationships observed here illustrate the importance of xylem characteristics in limiting the distribution of this group of conifer species, and highlight the potential for using xylem vulnerability characteristics to define limitations on the theoretical range of species, and perhaps to explain past movements in species boundaries.

ACKNOWLEDGEMENTS

This research was funded by a grant from the Australian Research Council. We would also like to thank Dr Greg Jordan for comments and statistical advice.

REFERENCES

Alder MN, Sperry JS, Pockman WT. 1996. Root and stem xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* **105**: 293–301.

Andrade JL, Meinzer FC, Goldstein G, Holbrook NM, Cavelier J, Jackson P, Silvera K. 1998. Regulation of water flux through trunks, branches, and leaves in trees of a tropical forest. *Oecologia* **115**: 463–471.

Azcon-Bieto J, Farquhar G, Caballero A. 1981. Effects of temperature, oxygen concentration, leaf age and seasonal variations on the CO_2 compensation point. *Planta* **152**: 497–504.

Brodribb T. 1996. Dynamics of changing intercellular CO_2 concentration (c_i) during drought and determination of minimum functional c_i. *Plant Physiology* **111**: 179–185.

Brodribb T, Hill RS. 1997. Light response characteristics of a morphologically diverse group of Southern Hemisphere conifers as measured by chlorophyll fluorescence. *Oecologia* **110**: 10–17.

Brodribb T, Hill RS. 1998. The photosynthetic drought physiology of a diverse group of southern hemisphere conifer species is correlated with minimum seasonal rainfall. *Functional Ecology* **12**: 465–471.

Cochard H, Peiffer M, Le Gall K, Granier A. 1997. Developmental control of xylem hydraulic resistances and vulnerability to embolism in *Fraxinus excelsior* L.: impacts on water relations. *Journal of Experimental Botany* **48**: 655–663.

Day RW, Quinn GP. 1989 Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**: 433–463.

Franks PJ, Gibson A, Bachelard EP. 1995. Xylem permeability and embolism susceptibility in seedlings of *Eucalyptus camaldulensis* Denh. from two different climatic zones. *Australian Journal of Plant Physiology* **22**: 15–21.

Hacke U, Sauter JJ. 1996. Drought-induced xylem dysfunction in petioles, branches and roots of *Poplus balsamifera* L. and *Alnus glutinosa* (L.) Gaertn. *Plant Physiology* **111**: 413–417.

Hargrave KR, Kolb KJ, Ewers FW, Davis SD. 1994. Conduit diameter and drought-induced embolism in *Salvia mellifera* Greene (Labiatae). *New Phytologist* **126**: 695–705.

Hill KD. 1998. Pinophyta. *Flora of Australia* **48**: 545–596.

Holmgren M, Scheffer M, Huston MA. 1997. The interplay of facilitation and competition in plant communities. *Ecology* **78**: 1966–1975.

Jarbeau JA, Ewers FW, Davis SD. 1995. The mechanism of water-stress induced embolism in two species of chaparral shrubs. *Plant, Cell and Environment* **18**: 189–196.

Kavanagh KL, Bond BJ, Aitken SN, Gartner BL, Knowe S. 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. *Tree Physiology* **19**: 31–37.

Kolb K, Davis, SD. 1994. Drought tolerance and xylem embolism in co-occurring species of coastal sage and chaparral. *Ecology* **75**: 648–659.

Lo Gullo MA, Salleo S, Piaceri EC, Rosso R. 1995. Relations between vulnerability to xylem embolism and xylem conduit dimensions in young trees of *Quercus cerris*. *Plant, Cell and Environment* **18**: 661–669.

Lovisolo C, Schubert A. 1998. Effects of water stress on vessel size and xylem hydraulic conductivity in *Vitis vinifera* L. *Journal of Experimental Botany* **49**: 693–700.

Marsh JA. 1966. Cupressaceae. In: Codd JE, de Winter B, Rycroft HB, eds. *Flora of South Africa* (vol. 1). Pretoria, South Africa: Pretoria Government Printer, 43–48.

Mencuccini M. Grace J. 1996. Developmental patterns of above-ground hydraulic conductance in a Scots Pine (*Pinus sylvestris* L.) age sequence. *Plant Cell and Environment* **19**: 939–948.

North GB, Nobel PS. 1998. Root–soil contact for the desert succulent *Agave deserti* in wet and drying soil. *New Phytologist* **135**: 21–29.

Ryan MG, Yoder BJ. 1997. Hydraulic limits to tree height and tree growth. *BioScience* **47**: 235–242.

Salleo S, Lo Gullo MA. 1989. Xylem cavitation in nodes and internodes of whole *Chorisia insignis* H. B. plants subjected to water stress: relations between conduit size and cavitation. *Annals of Botany* **58**: 431–441.

Smith TM, Huston MA. 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* **83**: 49–69.

Sperry JS. 1986. Relationship of xylem embolism to xylem pressure potential, stomatal closure, and shoot morphology of the palm *Rhapis excelsa*. *Plant Physiology* **80**: 414–417.

Sperry JS, Alder FR, Campbell GS, Comstock JP. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment* **21**: 347–359.

Sperry JS, Alder NN, Eastlack SE. 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *Journal of Experimental Botany* **44**: 1075–1082.

Sperry LS, Donnelly JR, Tyree MT. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell and Environment* **11**: 35–40.

Sperry JS, Nichols KL, Sullivan JEM, Eastlack SE. 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* **75**: 1736–1752.

Sperry JS, Pockman WT. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* **16**: 279–287.

Sperry JS, Saliendra NZ. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* **17**: 1233–1241.

Sperry JS, Saliendra NZ, Pockman WT, Cochard H, Cruziat P, Davis SD, Ewers FW, Tyree MT. 1996. New evidence for large negative xylem pressures and their measurement by the pressure chamber method. *Plant, Cell and Environment* **19**: 427–436.

Sperry JS, Tyree MT. 1990. Water-stress-induced xylem embolism in three species of conifers. *Plant, Cell and Environment* **13**: 427–436.

Tognetti R, Longobucco A, Raschi A. 1998. Vulnerability of xylem to embolism in relation to plant hydraulic resistance in *Quercus pubescens* and *Quercus ilex* co-occurring in a Mediterranean coppice stand in central Italy. *New Phytologist* **139**: 437–447.

Tyree MT. 1997. The Cohesion–Tension theory of sap ascent: current controversies. *Journal of Experimental Botany* **48**: 1753–1765.

Tyree MT, Davis SD, Cochard H. 1994. Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *International Association of Wood Anatomists Journal* **15**: 335–360.

Tyree MT, Patino S, Becker P. 1998. Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. *Tree Physiology* **18**: 583–588.

Van den Driessche R, Connor DJ, Tunstall BR. 1971. Photosynthetic response of Brigalow to irradiance, temperature and water potential. *Photosynthetica* **5**: 210–217.

Williams JE, Davis SD, Portwood K. 1997. Xylem embolism in seedlings and resprouts of *Adenostoma fasciculatum* after fire. *Australian Journal of Botany* **45**: 291–300.

Zimmermann MH, Jeje AA. 1981. Vessel-length distribution in stems of some American woody plants. *Canadian Journal of Botany* **59**: 1882–1892.

Zwieniecki MA, Holbrook NM. 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). *Plant Cell and Environment* **21**: 1173–1180.

CAMBRIDGE UNIVERSITY PRESS