

Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA

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Summary

1. Xylem hydraulic properties and vulnerability to cavitation (determined using the air-injection method) were studied in six Pinaceae of the northern Rocky Mountains: *Pinus ponderosa*, *Pseudotsuga menziesii*, *Larix occidentalis*, *Pinus contorta*, *Pinus albicaulis* and *Abies lasiocarpa*. We tested whether species extending into drier habitats exhibited increased resistance to water stress-induced cavitation, and whether there is a trade-off between xylem transport capacity and resistance to cavitation.

2. At lower elevations the more drought-tolerant *P. ponderosa* was much less resistant to cavitation than the codominant *P. menziesii*. Greater vulnerability to cavitation in *P. ponderosa* was compensated for, at least in part, by increased stomatal control of water loss (inferred from carbon isotope discrimination) and by increased sapwood to leaf area ratios. Similar differences, but less pronounced, were found in codominant species at higher elevations.

3. Leaf specific hydraulic conductivity was negatively correlated with mean cavitation pressure. When species were separated into pines and non-pines, sapwood specific conductivity and mean cavitation pressure were also negatively correlated within each of the two groups.

4. Our results indicate that within the evergreen conifers examined, greater resistance to water stress-induced cavitation is not required for survival in more xeric habitats, and that there is a trade-off between xylem conductance and resistance to cavitation.

Key-words: Drought tolerance, hydraulic conductance, montane conifers, sapwood to leaf area ratio, xylem cavitation

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Introduction

Since the first comprehensive review by Tyree & Sperry (1989), extensive research has stressed the importance of xylem cavitation and its negative consequences for plant water transport. It has been suggested that xylem resistance to cavitation may be the most important character determining drought tolerance in plants (Tyree & Ewers 1991). Cavitation refers to the abrupt change of phase of water within the xylem, from a metastable liquid state under tension to a vapour state. Water stress-induced cavitation is nucleated by air bubbles aspirated through interconduit pit membranes when xylem tension exceeds a critical value, resulting in the breakage of the water column (Crombie, Hipkins & Milburn 1985; Jarbeau, Ewers & Davis 1995; Sperry & Tyree 1990). Because embolized conduits no longer conduct water, hydraulic conductivity decreases when cavitation increases and, under water stress, xylem tension within the remaining functional conduits increases.

Ultimately, catastrophic xylem dysfunction may occur through the entire xylem, resulting in the death of the plant (Tyree & Sperry 1988). In general, woody plants from dry habitats that develop low xylem pressures exhibit greater resistance to water stress-induced cavitation than plants from moist habitats (Kolb & Sperry 1999; Linton, Sperry & Williams 1998; Tyree & Ewers 1991). However, species with distinct alternative mechanisms to avoid low xylem pressures under drought (e.g. deep roots, drought-deciduousness or crassulacean acid metabolism) might be able to persist in drier habitats relative to species more resistant to xylem cavitation (Kolb & Davis 1994).

Drought-induced cavitation may be avoided by reducing water loss (via stomatal closure and/or reductions in leaf area), or by increasing the xylem transport capacity (hydraulic conductivity) of the hydraulic pathway (Tyree & Ewers 1991). Zimmermann (1983), however, suggested that there is a trade-off between transport capacity of the xylem and cavitation resistance. This trade-off theory was based on observed increases in xylem conductance with increases in conduit diameter,

and on the assumption that wider conduits were more vulnerable to water stress-induced cavitation. This theory remains controversial, as several studies have shown that vulnerability to water stress-induced cavitation is not related to conduit diameter (Alder, Sperry & Pockman 1996; Sperry & Ikeda 1997), but rather to the structural properties of the interconduit membranes (Sperry & Tyree 1990; Sperry *et al.* 1996). Thus both the existence of (Linton *et al.* 1998; Tyree, Davis & Cochard 1994) and lack of a trade-off between (Alder *et al.* 1996; Sperry & Saliendra 1994; Sperry *et al.* 1994) xylem conductance and resistance to cavitation have been documented.

We studied the hydraulic properties of shoots of several Pinaceae species common in the Northern Rocky Mountains to address two questions. (1) Are evergreen conifer species known to extend into drier habitats more resistant to water stress-induced cavitation than functionally related species restricted to moister sites? (2) Among closely related species, is there a trade-off between xylem conductance and resistance to cavitation? We also examined whether differences in stomatal control between coexisting species relate to their resistance to cavitation. We addressed our first question by comparing two pairs of codominant species: *Pinus ponderosa* (Ponderosa Pine) versus *Pseudotsuga menziesii* (Douglas Fir) at lower elevations, and *Pinus albicaulis* (Whitebark Pine) versus *Abies lasiocarpa* (Subalpine Fir) at higher elevations. At lower elevations, Ponderosa Pine extends into drier sites where Douglas Fir is absent or rare (Daubenmire & Daubenmire 1968; McMinn 1952; Pfister *et al.* 1977). In the subalpine zone, Whitebark Pine also extends into drier habitats than Subalpine Fir (Weaver & Dale 1974). To answer the second question, we added two species typical of intermediate elevations: *Larix occidentalis* (Western Larch) and *Pinus contorta* (Lodgepole Pine). We hypothesized that: (1) evergreen conifer species found in drier habitats would be more resistant (less vulnerable) to water stress-induced cavitation than codominant species restricted to moister sites; and (2) there is a trade-off between xylem conductance

and resistance to cavitation in this group of closely related conifer species.

Methods

STUDY SITE AND PLANT MATERIAL

The study site was located in the Northern Rocky Mountains, near Missoula, Montana, USA (46°55' N, 114°05' W). The region has warm summers and very cold winters, with average January and July temperatures of -5.5 °C and 19.4 °C, respectively, and an annual precipitation of 340 mm.

Sampling was conducted in early September 1997 on south- and west-facing slopes along an elevation gradient at the Butler Creek valley (Lolo National Forest, Missoula, Montana). Relevant characteristics of the studied species and sampling sites are shown in Table 1. The number of freeze-thaw events at both ends of the elevation gradient was not significantly different: at the highest point there were more events from April to September, but fewer from October to March (data not shown). Therefore the effect of the number of freeze-thaw events on the hydraulic properties of the species studied (Sperry *et al.* 1994) can be ignored. At each location we sampled one fully sun-exposed branch with a non-ramified length of at least 15 cm, and with a diameter of 7–15 mm from each of 10 different trees. The diameter at breast height of the sampled trees ranged between 10 and 20 cm. Each branch was enclosed in a plastic bag and transported to the laboratory, where a proximal segment at least 15 cm long was cut, marked, and kept refrigerated at 4 °C until measurement (within 1 week of sampling). All distal needles of each branch were detached and the projected area of a subsample (consisting of at least 100 needles) was measured with an image analysis system (Moccha Jandel Scientific, San Rafael, CA, USA). All leaves from each branch were oven-dried at 105 °C for 24 h and weighed. The specific leaf mass of the leaf subsample was used to estimate the total projected leaf area of the corresponding branch.

Table 1. Species studied, sampling altitude, stand characteristics, minimum annual precipitation where the species is dominant, drought tolerance rankings from Minore (1979) and minimum xylem water potential measured in the field. Superscript letters indicate the source reference. ^aPfister *et al.* (1977), ^bBurns & Honkala (1990), ^cRunning (1976), ^dA. Sala, unpublished results, ^eKeane, Morgan & Running (1996), ^fRunning (1980), ^gFetcher (1976). na, Data not available

Species	Sampling altitude (m)	Stand characteristics	Min. annual precipitation (mm)	Relative drought tolerance ranking*	Min. xylem water potential (MPa)
<i>Pinus ponderosa</i> Laws.	1500	Mixed <i>P. ponderosa</i> and <i>P. menziesii</i>	277 ^a	1	-1.8 ^c - 2.0 ^d
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	1500	Mixed <i>P. ponderosa</i> and <i>P. menziesii</i>	452 ^a	3	-2.0 ^{c,d}
<i>Larix occidentalis</i> Nutt.	1750	Mixed <i>L. occidentalis</i> and <i>P. menziesii</i>	460 ^b	4	-1.5 ^e
<i>Pinus contorta</i> Dougl.	2000	Dominant species in the stand	250 ^b	2	-1.4 ^f - 1.7 ^g
<i>Pinus albicaulis</i> Engelm.	2400	Mixed <i>P. albicaulis</i> and <i>A. lasiocarpa</i>	718 ^a	na	-1.5 ^d
<i>Abies lasiocarpa</i> (Hook) Nutt.	2400	Mixed <i>P. albicaulis</i> and <i>A. lasiocarpa</i>	1016 ^a	5	-1.5 ^d

*Drought tolerance is broadly defined as the ability of a species to survive in dry environments.

HYDRAULIC CONDUCTIVITY AND VULNERABILITY CURVES

Hydraulic conductivity was measured according to the method of Sperry, Donnelly & Tyree (1988). Vulnerability curves were obtained following the double-end, air-injection method of Cochard, Cruziat & Tyree (1992) and Sperry & Saliendra (1994). The air-injection method has been verified against the standard dehydration method for several species, including conifers (Cochard 1992; Sperry & Ikeda 1997; Sperry & Tyree 1990).

The two-ended pressure chamber used to construct the vulnerability curves was designed to measure six stems simultaneously. Stem segment diameters (excluding bark) ranged between 5 and 12 mm, with a mean of 8 mm. Prior to mounting through the chamber, stems were soaked in distilled water for 1 h to allow removal of the bark and cambium, and three shallow cuts were made in the central part of each section to facilitate the entry of air into the tracheids. Both ends of each stem were then cut with a sharp blade at least 1 cm from the ends before connecting the proximal end to the tubing system.

Degassed, filtered (0.22 µm) water, acidified to approximately pH 2 with HCl, was initially flushed through the stems for 1 h at 100 kPa to eliminate possible pre-existing embolism. The acidified solution was then applied through the stem segments at a pressure of ≈ 6 kPa obtained with a pressure head of solution. Water flowing through the distal end of each segment was collected in preweighed vials filled with cotton wool. Maximum hydraulic conductivity (k_h , in $m^4 MPa^{-1} s^{-1}$) was calculated from the volumetric flow rate through the segment ($F = \Delta V / \Delta t$), the segment length (Δl), and the pressure difference applied (ΔP), according to:

$$F = \Delta V / \Delta t = k_h (\Delta P / \Delta l) \quad \text{eqn 1}$$

Vulnerability curves were obtained as follows. After measuring the maximum hydraulic conductivity, air was injected into the chamber up to a pressure of 1 MPa for 10 min to induce embolism in the stems. During air injection an air vent was created in the proximal end of each stem to avoid filling the tubing system with air. The pressure was released 10 min later, and the air trapped in the tubing system was eliminated to re-establish water flow through the stems. Fifteen minutes after re-establishing the flow, hydraulic conductivity was again measured, and the percentage loss of conductivity (PLC) relative to the maximum was calculated. This procedure was repeated at 2, 3, 4, 5, 6 and 7 MPa. A residual pressure of ≈ 10 kPa was maintained inside the chamber to avoid any possible refilling of embolized tracheids. Once the vulnerability curves had been obtained, stem length, diameter and sapwood to heartwood ratio (by observation of the wood colour) were measured.

In order to compare the hydraulic transport capacity of different stems, k_h was normalized against the cross-sectional area of the stem, sapwood or leaf area supported by the corresponding segment to calculate,

respectively, wood (k_w), sapwood (k_s) and leaf specific hydraulic conductivity (k_l), in $m^2 MPa^{-1} s^{-1}$.

Mean cavitation pressure ($\Psi_{50\%}$), the pressure causing a 50% loss of hydraulic conductivity, was estimated by fitting vulnerability curves to the function (Pammenter & Vander Willigen 1998):

$$PLC = 100 / \{1 + \exp[a(P - b)]\} \quad \text{eqn 2}$$

where P is the injection pressure; b is the pressure causing a 50% loss of hydraulic conductivity ($\Psi_{50\%}$); and a is proportional to the slope of the curve.

FOLIAR $^{13}C/^{12}C$ RATIO AND TOTAL N CONTENT

As shown for other conifers (Sun *et al.* 1996), foliar $^{13}C/^{12}C$ ratios were used as indicators of time-integrated ratios of leaf internal to ambient CO_2 concentrations (C_i/C_a) (Farquhar O'Leary & Berry 1982; Farquhar & Richards 1984). We emphasized comparisons between coexisting species in a given site, thus eliminating potential effects of varying evaporative demand on water use (Marshall & Zhang 1994). All needles from each sampled branch were oven-dried and coarsely ground to homogenize the leaf tissue. A subsample from each branch was finely ground (60 mesh) for $^{13}C/^{12}C$ and total nitrogen (percentage dry mass) analyses. Samples were analysed at the Stable Isotope Facility of the University of California, Davis, CA. $^{13}C/^{12}C$ was measured relative to PDB (PeeDee Belemnite) and expressed as discrimination (Δ) following Farquhar & Richards (1984): $\Delta (\delta^{13}C_{air} - \delta^{13}C_{plant})$, where $\delta^{13}C_{air}$ was assumed to be -8‰, and $\delta^{13}C = \{[(^{13}C/^{12}C)_{sample} / (^{13}C/^{12}C)_{standard}] - 1\} 1000$.

Results

At low elevations the more drought-tolerant *P. ponderosa* (Table 1) was more vulnerable than *P. menziesii* to water stress-induced cavitation (Fig. 1, Fig. 2a, Table 2). Similarly, at higher elevations *P. albicaulis*,

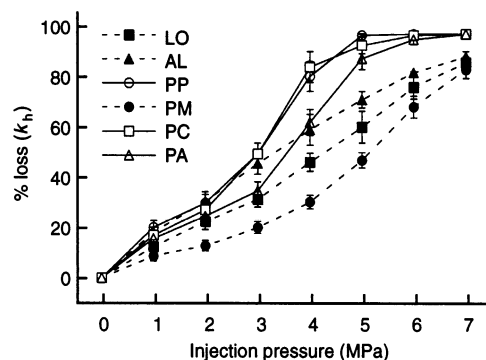


Fig. 1. Vulnerability curves, i.e. percentage of loss in hydraulic transport capacity in stems (k_h) in relation to air-injection pressure. Each value is the arithmetic mean of nine to 11 branches. Vertical bars indicate the standard error. PP, *P. ponderosa*; PM, *P. menziesii*; PA, *P. albicaulis*; AL, *A. lasiocarpa*; PC, *P. contorta*; LO, *L. occidentalis*.

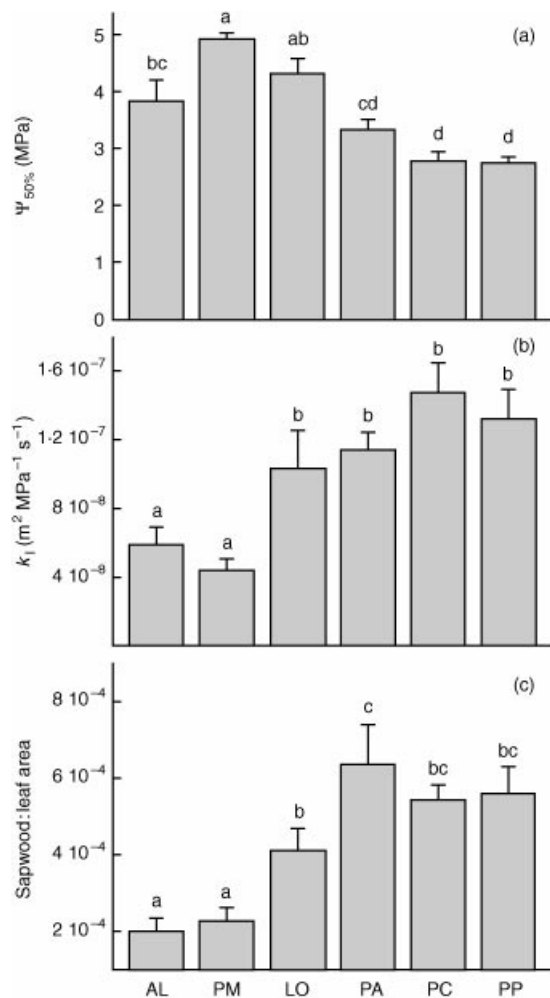


Fig. 2. Mean cavitation pressure (a), leaf specific hydraulic conductivity (b), and sapwood area per unit of leaf area (c). Each value is the arithmetic mean of nine to 11 branches. Vertical bars indicate the standard error. Statistically different means ($P < 0.05$) have different letters (least significant difference *a posteriori* test, Sokal & Rohlf 1995).

Table 2. Results of one-way ANOVAs with six levels, corresponding to the six species studied, for all the dependent variables analysed. Differences between pairs of species were tested with a least significant difference *a posteriori* test (Sokal & Rohlf 1995). Transformation of data was not necessary

Dependent variable	Source	DF	Mean square	F value	P > F
$\Psi_{50\%}$ (MPa)	Model	5	730.5	14.18	0.0001
	Error	53	51.5		
k_s ($m^2 MPa^{-1} s^{-1}$)	Model	5	$2.35 \cdot 10^{-8}$	0.80	0.55
	Error	58	$2.93 \cdot 10^{-8}$		
k_w ($m^2 MPa^{-1} s^{-1}$)	Model	5	$1.79 \cdot 10^{-8}$	1.19	0.33
	Error	60	$1.50 \cdot 10^{-8}$		
k_l ($m^2 MPa^{-1} s^{-1}$)	Model	5	$1.74 \cdot 10^{-14}$	6.66	0.0001
	Error	60	$2.62 \cdot 10^{-15}$		
$A_s:A_l$ ($m^2 m^{-2}$)	Model	5	$3.37 \cdot 10^{-7}$	12.2	0.0001
	Error	58	$2.77 \cdot 10^{-8}$		
Δ (‰)	Model	5	5.00	8.95	0.0001
	Error	53	0.56		
N (% dry weight)	Model	5	0.307	9.47	0.0001
	Error	53	0.0324		

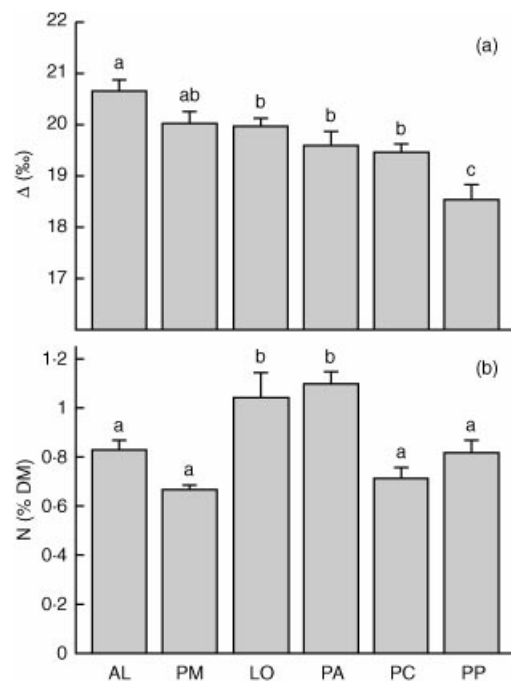


Fig. 3. $^{13}C/^{12}C$ (Δ) and total N concentration in leaves of the six species studied. Species codes are as in Fig. 1; statistical details as in Fig. 2.

which extends into drier microsites than *A. lasiocarpa* (Weaver & Dale 1974; Table 1), was also more vulnerable to cavitation than *A. lasiocarpa* (Fig. 1). However, differences were apparent only at high injection pressures, and $\Psi_{50\%}$ was not significantly different (Fig. 2a). $\Psi_{50\%}$ of *P. contorta* was similar to that of *P. ponderosa*, while $\Psi_{50\%}$ of *L. occidentalis* was similar to that of *P. menziesii* (Fig. 2a). When all six species were compared, the three *Pinus* species were more vulnerable than the three non-*Pinus* species, except for the non-significant difference between *P. albicaulis* and *A. lasiocarpa* (Fig. 2a).

Specific hydraulic conductivity (k_w , the permeability of the whole stem cross-section) and sapwood specific hydraulic conductivity (k_s , the permeability on a sapwood area basis) did not differ between species (Table 2; mean, SD: $k_w = 2.04 \times 10^{-4}$, $4.18 \times 10^{-5} m^2 MPa^{-1} s^{-1}$; $k_s = 2.54 \times 10^{-4}$, $4.61 \times 10^{-5} m^2 MPa^{-1} s^{-1}$). In contrast, leaf specific hydraulic conductivity (k_l) was greater in *P. ponderosa* than in *P. menziesii*, and greater in *P. albicaulis* than in *A. lasiocarpa* (Fig. 2a). As k_l is the product of k_s and $A_s:A_l$ (sapwood to leaf area ratio), and k_s was similar for all species, differences in k_l resulted from higher sapwood to leaf area ratios in pines (Fig. 2c). Decreased leaf area relative to sapwood area results in an increased water supply to leaves, thus increasing leaf specific conductivity.

Leaf carbon isotope discrimination (Δ) was greatest in *A. lasiocarpa* and lowest in *P. ponderosa* (Fig. 3a). While there was no overall relationship between Δ and $\Psi_{50\%}$ for the six species studied, Δ in the low-elevation stand was smaller for *P. ponderosa* than for *P. menziesii*. Similarly, in the high-elevation

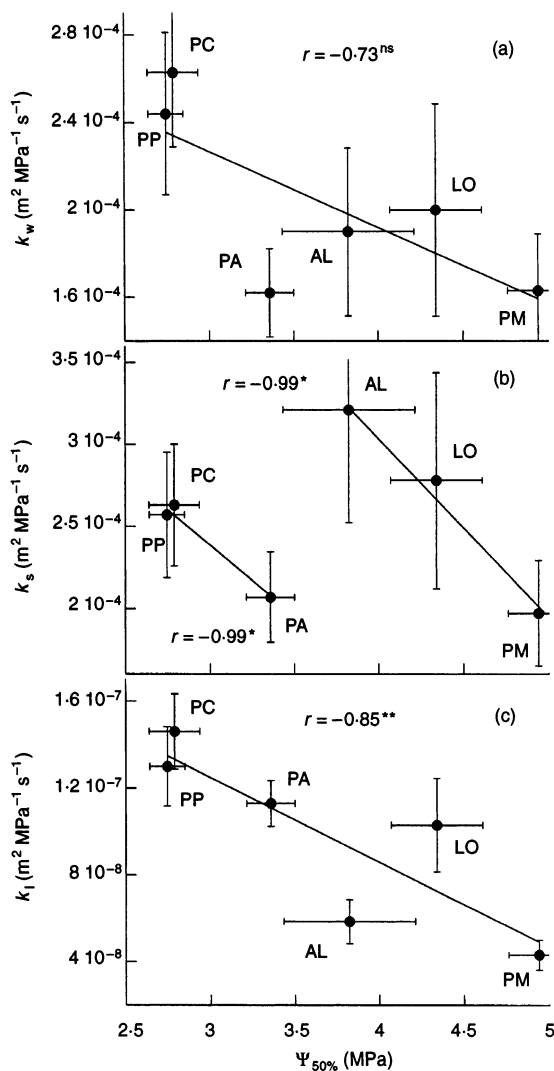


Fig. 4. Relationship between mean cavitation pressure ($\Psi_{50\%}$) and specific hydraulic conductivity (a), sapwood specific hydraulic conductivity (b), and leaf specific hydraulic conductivity (c). Each value is the arithmetic mean of nine to 11 branches. Vertical and horizontal bars indicate the standard error. The Pearson correlation coefficient between the two variables is indicated in each plot, except for k_s , where two different coefficients are given (one for *Pinus* sp., one for the other three species). Significance of the correlation coefficients: * $P < 0.1$; ** $P < 0.05$; ns $P > 0.1$.

stand Δ values were smaller for *P. albicaulis* than for *A. lasiocarpa*. Within each pair, the two species were subjected to the same air temperature and vapour pressure. Because for needle-leaved species leaf temperature often approaches air temperature (Campbell & Norman 1998), the leaf-to-air vapour pressure difference (the driving force for transpiration) was similar between the two species of each pair. Thus, assuming constant $\delta^{13}C_{air}$, differences in Δ indicate long-term differences of C_i/C_a between the species of each pair. Total N content (per unit leaf mass) was greatest in *L. occidentalis* and *P. albicaulis* and was relatively similar among the rest of the species (Fig. 3b).

The leaf specific conductivity, k_l , was negatively correlated with $\Psi_{50\%}$ (Fig. 4c, $P < 0.05$). There was no

relationship between sapwood (k_s) or whole-stem (k_w) specific conductivity and $\Psi_{50\%}$ when all species were considered (Fig. 4a,b). However, when the three *Pinus* and the other three species were considered separately, k_s and $\Psi_{50\%}$ within each group were related, although P values were < 0.1 due to the small sample size (Fig. 4b).

Discussion

VULNERABILITY TO EMBOLISM AND DROUGHT RESISTANCE

Results from comparisons between *P. ponderosa* and *P. menziesii* and, to a lesser degree, between *P. albicaulis* and *A. lasiocarpa* (Fig. 1) do not support our initial hypothesis that evergreen conifers found in drier habitats are more resistant to xylem cavitation than functionally related, codominant species restricted to moister sites. Particularly relevant is the large difference between *P. ponderosa* and *P. menziesii*. We sampled the two species of each pair in a mixed stand at the same location. It could be that pines from dry habitats are more resistant to cavitation than those growing in moister sites, thus reducing or even reversing the differences we found. However, Stout & Sala (1999) found no differences in shoot vulnerability to cavitation between *P. ponderosa* from slope and riparian habitats. Available data in the literature for coniferous species also suggest that within-species variability in shoot resistance to cavitation is not enough to counteract the large differences we found between Ponderosa Pine and Douglas Fir (Kavanagh *et al.* 1999). The results of Alder *et al.* (1996) and Sperry & Ikeda (1997) indicate that vulnerability to cavitation in roots is related more to site water availability than to vulnerability in shoots, and that root cavitation may trigger stomatal closure before shoot cavitation occurs. Stout & Sala (1999), however, showed that roots of *P. ponderosa* in both riparian and slope habitats were more vulnerable than those of *P. menziesii*. Therefore, how *P. ponderosa* shoots avoid catastrophic xylem cavitation when subjected to water deficits remains unclear. If we substitute flow ($\Delta V/\Delta t$) by the product of transpiration rate (E) and leaf area (A), and E by the product of leaf conductance (g) and leaf-to-air vapour-pressure difference (Δw) in equation 1, then:

$$\Delta P/\Delta l = g \Delta w A/k_h \quad \text{eqn 3}$$

Since $k_l = k_h/A$, equation 3 can be rearranged:

$$\Delta P/\Delta l = g \Delta w/k_l \quad \text{eqn 4}$$

Our results show that *P. ponderosa* is less resistant to cavitation than *P. menziesii*. Thus, according to equation 4 and assuming that Δw is similar for both species, we should expect a relative decrease of stomatal conductance and/or an increase in the leaf specific conductivity (k_l) in *P. ponderosa* as a means of maintaining low xylem tensions ($\Delta P/\Delta l$) and avoiding catastrophic embolism. Our results are consistent

with these expectations: (1) *P. menziesii* had significantly lower k_i than *P. ponderosa* (Fig. 2a); and (2) Δ was smaller in *P. ponderosa* than in *P. menziesii* (Fig. 3a). Smaller Δ in pines indicates lower C_i/C_a , which may be due to increases in photosynthetic capacity and/or decreases of stomatal conductance. If we assume leaf N content to be a broad indicator of leaf photosynthetic capacity (Reich, Walters & Ellsworth 1997) then the similar leaf N concentration in *P. ponderosa* and *P. menziesii* (Fig. 3b) suggests that differences in Δ are mainly due to stomatal control of transpiration.

A caveat to this analysis is that it is assumed that differences in hydraulic conductivity of small stem segments between the two species are proportional to those for the entire flow path from soil to leaves. We have no direct data to validate this assumption. However, recent measurements indicate that differences in root hydraulic properties between *P. ponderosa* and *P. menziesii* parallel those found in stems (D. L. Stout and A. Sala, unpublished results), which suggest that k_h in small stems may be indicative of the k_h of the entire flow path.

Differences in shoot vulnerability to cavitation between *P. albicaulis* and *A. lasiocarpa* (Fig. 1) indicate inherent differences in wood structure. However, cavitation under injection pressures similar to the xylem tensions commonly measured in the field (Table 1) was similar between the two species (Fig. 2a). Increased $A_s:A_l$, leaf specific conductivity and stomatal control of transpiration (as suggested by the leaf Δ and nitrogen concentrations) in *P. albicaulis* compared to *A. lasiocarpa* may allow the former species to extend into drier, more exposed sites compared to the latter (Weaver & Dale 1974; Table 1).

Among the evergreen species studied, the ability of terminal branches to supply water to leaves (leaf specific conductivity, k_l) was greater in pines (Fig. 2a). This was due to higher $A_s:A_l$ (Fig. 2b) rather than to greater wood permeability (k_w or k_s). High $A_s:A_l$ in small branches of pines is maintained in whole trees and even at the stand level. Margolis *et al.* (1995) reported whole-tree $A_s:A_l$ ratios of $3.3\text{--}9.1 \times 10^{-4}$ in several pine species (including Lodgepole and Ponderosa Pines), $1.4\text{--}2.6 \times 10^{-4}$ for Douglas Fir, 2.0×10^{-4} for Western Larch, and 1.3×10^{-4} for Subalpine Fir. These are consistent with those we measured in terminal branches, with the exception of Western Larch, where $A_l:A_s$ did not differ from pines. Because significant amounts of water can be stored in sapwood (Waring & Running 1978; Waring, Whitehead & Jarvis 1979), relative increases in $A_s:A_l$ in species vulnerable to cavitation (such as pines) may provide a reliable supply of water to leaves during drought and reduce xylem tensions. While there are no striking functional differences between the evergreen species studied here, increased stomatal control of water loss and increased biomass allocation to sapwood appear to partly offset the relatively low xylem resistance to cavitation of pines, and contribute to their survival in dry habitats.

Irvine *et al.* (1998) also reported that stomatal control in *Pinus sylvestris* was enough to prevent the development of any substantial xylem cavitation.

Increased resistance to water stress-induced cavitation enhances drought tolerance of woody plants (Kolb & Sperry 1999; Linton *et al.* 1998). However, large xylem resistance to cavitation would be unnecessary in plants able to maintain xylem pressure above that causing catastrophic cavitation, particularly if increased resistance to cavitation is related to a smaller xylem conductance (see below). Therefore xylem resistance to cavitation should be positively related to *in situ* minimum xylem pressure rather than to drought tolerance *per se* (Kolb & Sperry 1999). We did not find a significant relationship between minimum xylem water potential (Table 1) and resistance to cavitation (Fig. 2a). This might be because the minimum xylem water potentials we report refer only to the growing season rather than the entire year. Although we have no direct evidence, it is likely that these evergreen conifers experience their minimum xylem water potential during winter when cuticular water loss due to wind and ice abrasion coincides with limited water supply to leaves (winter desiccation; Havranek & Tranquillini 1995). The possibility exists that species most resistant to cavitation are those most susceptible to winter desiccation and therefore those that develop the lowest xylem pressures during winter.

TRADE-OFF BETWEEN HYDRAULIC CONDUCTANCE AND RESISTANCE TO CAVITATION OF THE CONDUCTING SYSTEM

In conifers, data on the potential trade-off between stem xylem conductance and resistance to cavitation (Zimmermann 1983) are contradictory. Results from Cochard (1992) and Kavanagh *et al.* (1999) indicate there is no such trade-off. In contrast, Sperry & Tyree (1990) found that among the conifer species they examined, branches with the highest hydraulic conductivity tended to be the most vulnerable. Linton *et al.* (1998) also found that in the pinyon-juniper community of the south-western USA, pines were less resistant to cavitation but had higher xylem conductance than junipers.

Our results suggest there is a trade-off between xylem conductance and resistance to xylem cavitation: *P. ponderosa* and *P. contorta* had the highest leaf specific hydraulic conductivity (k_l), but were more vulnerable to water stress-induced cavitation than Douglas Fir, Western Larch and Subalpine Fir (Fig. 4). When using sapwood specific conductivity (k_s) as a measure of xylem conducting efficiency, the trade-off was not apparent if the six species studied were pooled. However, when based on reported whole-tree $A_s:A_l$ ratios, the species fell into two groups: pines and non-pines. The trade-off then became evident within each group. The need to compare groups of species with similar whole-tree biomass allocation patterns

is reasonable because it is the sapwood that supplies water to the foliage. Adjustments of sapwood hydraulic properties in any given species are presumably related partly to $A_s:A_l$. Therefore trade-offs associated with these adjustments might be apparent only when species with similar $A_s:A_l$ are compared. The fact that, within each group, increases in sapwood conductance were associated with decreases in resistance to cavitation suggests there is a cost (increased vulnerability) associated with increased water-transport capacity.

Whether this trade-off is apparent may be explained by the differential effect of xylem anatomical properties on xylem conductance and vulnerability to cavitation. If cavitation occurs by air seeding between tracheids through pits (Zimmerman 1983), then the stronger the pit membrane, the more resistant the xylem is to cavitation. A stronger pit membrane probably would have a less porous margo and be less permeable to water transport, thus reducing xylem conductivity. Therefore a trade-off should be expected. However other factors, including tracheid length and diameter, number and area of pits per tracheid wall, etc., influence xylem hydraulic properties in complex ways. The expected trade-off could be masked by anatomical correlates of conducting efficiency that have little effect on vulnerability to cavitation.

Conclusions

Comparisons between *P. ponderosa* and *P. menziesii* and, to a lesser degree, between *P. albicaulis* and *A. lasiocarpa* showed that species extending into drier habitats were less resistant to water cavitation than codominant species restricted to moister sites. Greater vulnerability in species that persist in dry habitats (e.g. *P. ponderosa*) was partly compensated via physiological (stomatal control of water loss) and structural (increased relative biomass allocation to sapwood) adjustments. Our results also suggest a trade-off between xylem conductance and resistance to cavitation in the six species studied.

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