

Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings

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Summary The objectives of this study were to assess the range of genotypic variation in the vulnerability of the shoot and root xylem of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings to water-stress-induced cavitation, and to assess the trade-off between vulnerability to cavitation and conductivity per unit of stem cross-sectional area (k_s), both within a species and within an individual tree. Douglas-fir occupies a broad range of environments and exhibits considerable genetic variation for growth, morphology, and drought hardiness. We chose two populations from each of two varieties (the coastal var. *menziesii* and the interior var. *glauca*) to represent environmental extremes of the species. Vulnerability curves were constructed for shoots and roots by plotting the percentage loss in conductivity versus water potential. Vulnerability in shoot and root xylem varied genetically with source climate. Stem xylem differed in vulnerability to cavitation between populations; the most mesic population, coastal wet (CW), was the most susceptible of the four populations. In the roots, the most vulnerable population was again CW; the interior wet (IW) population was moderately susceptible compared with the two dry populations, coastal dry (CD) and interior dry (ID). Root xylem was more susceptible to cavitation than stem xylem and had significantly greater k_s . The trade-off between vulnerability to cavitation and k_s , however, was not evident across populations. The most vulnerable population (CW) had a shoot k_s of $0.534 \pm 0.067 \mu\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$, compared with $0.734 \pm 0.067 \mu\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ for the less vulnerable CD stems. In the roots, IW was more vulnerable than ID, but had the same k_s .

Keywords: conductivity, cross-sectional area, mesic versus xeric environments, stomata.

Introduction

Water transport in woody plants is limited by the hydraulic sufficiency of the xylem. When xylem water potential (Ψ_x) becomes sufficiently negative, cavitation occurs with air introduced into the tracheids or vessels, forming an embolism

(Crombie et al. 1985, Sperry and Tyree 1990). The introduction of air into the sapwood of a woody plant increases resistance to water flow, resulting in stomatal closure (Sperry and Pockman 1993, Sperry et al. 1993), foliage loss (Kavanagh and Zaerr 1997), and eventually mortality (Tyree and Sperry 1988).

Measuring the loss of xylem hydraulic conductivity (k) with decreasing Ψ_x allows construction of a profile of vulnerability to cavitation. Variability in vulnerability profiles is found between species (Tyree and Dixon 1986, Sperry and Tyree 1990, Cochard 1992), within species (Neufeld et al. 1992, Sperry and Saliendra 1994, Alder et al. 1996), and even within an individual tree (Sperry and Saliendra 1994, LoGullo et al. 1995, Alder et al. 1996). The mechanistic basis for this variability is not fully understood. Initially, variability was believed to be a function of conduit diameter, with an evolutionary trade-off between maximizing conductivity per unit of stem cross-sectional area (k_s) and the resultant increased vulnerability to cavitation. Within several species, larger-diameter xylem conduits cavitate at higher water potentials (Jarbeau et al. 1995) because of increased permeability at the air–water interface (Tyree and Sperry 1988, LoGullo et al. 1995). This relationship is less consistent among species; in several cases, species with larger-diameter conduits are less vulnerable to cavitation than species with small tracheids or vessels (Tyree and Dixon 1986, Tyree and Sperry 1988, Sperry and Sullivan 1992, Sperry et al. 1994). Subsequent research has indicated that it is pit membrane permeability—which among species, but not within species, is independent of conduit size—that is responsible for “air-seeding” the sapwood during periods of water stress (Sperry 1995).

One of the benefits of high k_s is the maintenance of a favorable water flux to the leaf without low (and possibly cavitation-inducing) Ψ_x . In several tree species, the Ψ_x values at which stomata close are just above those that initiate xylem cavitation (Tyree and Sperry 1988, Jones and Sutherland 1991, Sperry and Pockman 1993, Sperry et al. 1993), indicating an environmental adaptation that keeps Ψ_x above the cavitation threshold. Inherent in this theory is an expectation that populations within a species may adapt to more xeric environments

by becoming more resistant to cavitation, allowing for increased stomatal function during periods of water stress. However, this hypothesis has never been tested experimentally for populations of a single species adapted to different conditions along an extreme environmental gradient.

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has a distribution that ranges from very wet to extremely dry. There are two major geographic races, the coastal var. *menziesii* and the interior var. *glauca*. Genetic variation in maximum growth rates and drought hardiness has been documented both between the two races (Ferrell and Woodward 1966, Pharis and Ferrell 1966) and among sources within var. *menziesii* (Zavitkovski and Ferrell 1968, 1970, White 1987, Joly et al. 1989).

The objectives of this study were to assess the range of genotypic variation in the vulnerability of the xylem of Douglas-fir to water-stress-induced cavitation, and to assess the trade-off between this vulnerability and k_s , both within a species and within an individual. Intra-tree variation was examined by comparing vulnerability in shoot and root xylem.

Materials and methods

Plant material

Douglas-fir seedlings from four populations—coastal wet (CW) and coastal dry (CD) var. *menziesii* and interior wet (IW) and interior dry (ID) var. *glauca* (Table 1, Figure 1), each represented by five open-pollinated families—were grown from seed. The seed was spring sown in a greenhouse, fall transplanted after one growing season to outdoor raised beds at the Forest Research Laboratory in Corvallis, OR, where they and the resultant seedlings were grown under irrigation for an additional 2 years.

Measurements of vulnerability to cavitation

After three growing seasons (2.5 years from seed), 17 randomly chosen seedlings from each family were carefully dug from the soil with roots intact, wrapped in plastic, and immediately transported to an adjacent lab for measurement. In the lab, the terminal stem was removed from 10 seedlings per family, and an upper lateral root taken from the other seven seedlings; vulnerability profiles were determined by an adaptation of the air-injection method described by Sperry and

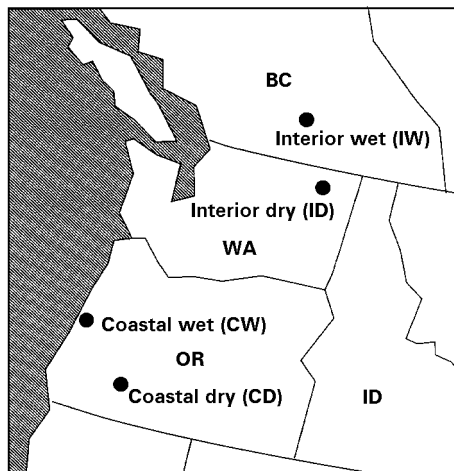


Figure 1. The locations of Douglas-fir populations used in this study.

Saliendra (1994). A 2- to 3-cm section was removed from each sample before measurement and stained with safranin dye to check for prior cavitation. If cavitation was evident, the sample was discarded.

Samples with no sign of prior cavitation were prepared by removing all branches, needles, and bark and recutting the proximal end under water. Tubing containing a solution of 10 μM oxalic acid was then connected to the proximal end. The solution was prepared with deionized distilled water, filtered to 0.22 μM , degassed, and pressurized to 10 kPa by gravity. The sample was then placed in a stainless steel pressure sleeve (PMS Instruments, Corvallis, OR) with proximal and distal ends of the stem or root protruding, and the sleeve sealed around the stems on each end. Initial flux (F) was measured at 60-s intervals for a total of 4 min with a balance to weigh the outflow of solution. Flux was then remeasured following pressurization to 3.0, 4.5, 5.0, 5.5 and 6.8 MPa for stem segments and 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, 5.0, 5.5 and 6.8 MPa for root segments (as needed). Following each 10 s pressurization, the pressure was released before F was remeasured. Entry of air into the tracheids was facilitated by the removal of branches and needles or rootlets directly attached to the segment. Initial tests indicated 10 s of pressurization was sufficient to achieve full cavitation.

Table 1. Geographic and climatic data for the four locations from which Douglas-fir populations were sampled. Climatic data are 15-year means.

	Coastal population		Interior population	
	Wet (CW)	Dry (CD)	Wet (IW)	Dry (ID)
Latitude	44°09'	42°27'	50°50'	48°30'
Longitude	124°00'	122°08'	119°00'	118°30'
Mean elevation (m)	250	1540	400	950
Mean annual precipitation (mm)	1822	721	627	438
Mean June–August precipitation (mm)	117	48.6	156	84.3
Mean annual maximum temperature (°C)	14.2	11.2	12.4	14.5
Mean June–August maximum temperature (°C)	17.6	21.7	25.2	27.5

Overall length and the diameter of the small end were measured for each sample, and k_s was calculated:

$$k_s = F \frac{(l/p)}{a}, \quad (1)$$

where F = flux, l = segment length, p = pressure gradient, and a = segment cross-sectional area.

To determine the vulnerability profile, the percent loss in k_s relative to the initial measurement was plotted against pressure.

To allow quantitative comparison of the curves, hydraulic conductivity loss functions were determined from loss of hydraulic conductivity at each pressure by a Weibull function (Rawlings and Cure 1985, Neufeld et al. 1992):

$$H = \alpha \exp\left(-\left(\frac{\Psi_1}{\phi}\right)^\sigma\right), \quad (2)$$

where H = the percentage of maximum conductivity at value Ψ_1 , α = an estimate of maximum percent conductivity, Ψ_1 = absolute water potential, ϕ = the absolute value of Ψ at which α is reduced to 37% of maximum, and σ = a dimensionless parameter controlling the shape of the curve. Curves were fitted and parameters tested for significance with the nonlinear procedure of the SAS statistical software package (SAS Institute, Cary, NC).

Results

Climatic data

Climatic data were obtained from a weather station in the vicinity of each source. Table 1 shows mean annual rainfall and maximum temperatures compiled over a period of at least 15 years. Rainfall varied widely among the sites; the CW location received a yearly total of 1822 mm, compared with 438 mm at ID. Although rainfall was much higher overall for populations CW, CD and IW, all populations had significantly less rainfall during the growing season than during other months except IW, which is the only source with an even distribution of precipitation; it received 25% of its total in the summer months, compared with 7% at CD and 19% at ID.

The most mesic source included in this study is the CW location, where high yearly rainfall combined with low maximum summer temperatures limit both soil water stress and transpirational water stress. In comparison, IW, with relatively high summer rainfall, has low soil water stress but potentially high transpirational stress because of high maximum summer temperatures.

Vulnerability

Douglas-fir seedlings grown under well-watered conditions had statistically significant differences in shoot and root vulnerability related to source environment (Figure 2). The population from the most mesic environment (CW) was the most

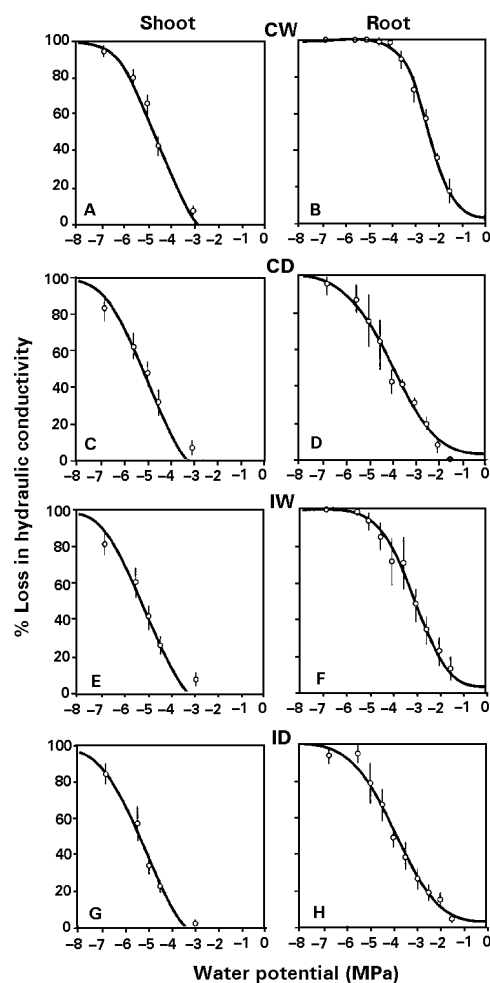


Figure 2. Vulnerability curves showing percent loss in hydraulic conductivity versus xylem tension (MPa) in shoot and root xylem of 3-year-old Douglas-fir from four populations (Figure 1). Points represent means over different xylem tensions ($n = 10$ for shoots and $n = 7$ for roots). Curves are derived from the Weibull function (Equation 2). Error bars represent SE.

vulnerable to cavitation in both shoot and root xylem. In stems, CW seedlings initiated cavitation at -3.0 MPa compared with -3.5 MPa for all other populations (Figure 2). The highly susceptible roots initiated cavitation at -1.0 MPa, with samples from the relatively mesic populations, CW and IW, being more vulnerable than those from CD and ID, as indicated by the steep slopes of their curves.

All populations exhibited a threshold response, reflected in the σ parameter in the Weibull function, which indicated that a complete loss in hydraulic conductivity occurred (Tables 2 and 3). In stems, the threshold was reached at 1 MPa higher for the CW source than for the other sources (Figure 2). The threshold in roots was reached at -4.0 , -8.0 , -5.5 and -8.0 MPa for CW, CD, IW and ID, respectively. The only Weibull parameter showing significant variation among the populations was ϕ , which reflects the Ψ at which a 37% loss in hydraulic conductivity occurs.

Table 2. Percent loss of hydraulic conductivity in shoots from four Douglas-fir populations, calculated from the Weibull function.

Population	Xylem water potential (MPa)				Weibull parameter estimates ¹		
	-3.5	-4.5	-5.5	-6.5	α	ϕ	σ
CW	13.75 a ²	45.59 a	76.01 a	93.5 a	118.06	4.83	3.59
CD	5.04 b	31.02 b	60.92 b	84.27 b	118.06	5.34	3.59
IW	2.63 b	26.62 b	55.62 b	80.16 b	118.06	5.53	3.59
ID	1.31 b	24.14 b	52.47 b	77.52 b	118.06	5.65	3.59

¹ Parameter estimates were calculated from the absolute value of Ψ and the percent of maximum conductivity.

² Values within a column sharing the same letter are not significantly different at $P = 0.05$.

Table 3. Percent loss of hydraulic conductivity in roots from four Douglas-fir populations, calculated from the Weibull function.

Population	Xylem water potential (MPa)				Weibull parameter estimates ¹		
	-1.5	-2.5	-3.5	-4.5	α	ϕ	σ
CW	17.66 a ²	55.32 a	88.36 a	98.91 a	97.76	2.71	2.97
CD	5.76 b	17.31 b	37.96 b	62.55 b	97.76	4.56	2.97
IW	9.64 b	31.74 c	63.16 c	87.53 c	97.76	3.52	2.97
ID	6.03 b	18.36 b	40.08 b	65.20 b	97.76	4.45	2.97

¹ Parameter estimates were calculated from the absolute value of Ψ and the percent of maximum conductivity.

² Values within a column sharing the same letter are not significantly different at $P = 0.05$.

Shoot conductivity

Population CD had the highest k_s for shoots, whereas the other dry population, ID, had the lowest k_s (Table 4). The wet representatives from the two genetic varieties, CW and IW, had similar k_s values. There was no correlation between xylem diameter and k_s (Figure 3). Overall, shoot k_s was not well correlated with xylem vulnerability; CW, with the highest vulnerability to cavitation (Figure 4) had a k_s well below that of CD (Table 4).

Root conductivity

Roots had much higher k_s values than shoots (Table 4). Roots from the relatively wet coastal soil (CW) had a k_s of $3.34 \mu\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$, which is 75% greater than any other population tested. This high k_s was associated with high vulnerability to cavitation (Figures 2 and 4) compared with that of shoots. However, k_s values for roots were not well correlated with vulnerability in the other populations (see Figure 4, Table 4).

For example, IW and ID roots had similar k_s values but varied widely in their relative vulnerability to cavitation.

Discussion

In Douglas-fir seedlings, vulnerability to cavitation in shoot and root xylem varies significantly with population, with this genetic variability related to source climate. Of the sources tested, Douglas-fir seedlings from climates with high maximum temperatures (CD, ID and IW) exhibited the most resistance to stem cavitation; this resistance enables them to maintain more open stomata with declining Ψ_x than seedlings from the mesic CW source. In addition, seedlings from sites with low summer rainfall (CD and ID) had root xylem with low vulnerability and can therefore generate Ψ_x low enough to extract water from drying soils while avoiding lethal cavitation. The IW seedlings, adapted to a climate with high maximum temperatures but an even distribution of rainfall, had shoot xylem that was relatively resistant to cavitation but roots

Table 4. Xylem diameter and specific hydraulic conductivity of shoots and roots used in the vulnerability profiles.

Population	Shoots		Roots	
	Xylem diameter (mm)	k_s ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)	Xylem diameter (mm)	k_s ($\mu\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
CW	4.22 ± 0.45 a ¹	0.534 ± 0.067 a	0.76 ± 0.11 a	3.34 ± 0.85 a
CD	3.44 ± 0.38 b	0.734 ± 0.067 b	1.87 ± 0.46 b	1.52 ± 0.23 b
IW	2.75 ± 0.37 c	0.501 ± 0.033 a	0.96 ± 0.12 c	1.69 ± 0.33 bc
ID	1.72 ± 0.07 d	0.251 ± 0.017 c	0.93 ± 0.06 c	1.89 ± 0.40 c

¹ Values are means \pm SE. Means within a column with the same letter are not significantly different at $P < 0.05$.

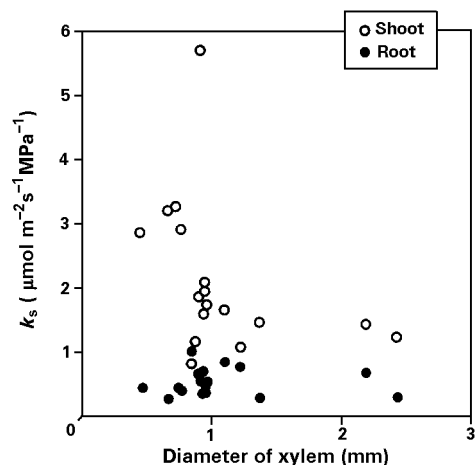


Figure 3. Specific conductivity (k_s) versus xylem diameter for shoots and roots. There are no significant correlations.

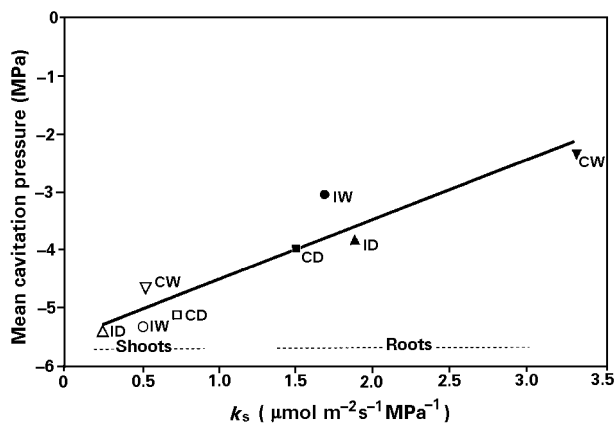


Figure 4. Mean cavitation pressure versus mean xylem specific conductivity (k_s) for shoots and roots of each population. The correlation is significant ($P < 0.01$) for collective shoot and root data only.

that were more vulnerable than those from CD and ID; the CW population, which was adapted to ample soil water and relatively cool summer temperatures, had shoot and root xylem that was highly vulnerable to cavitation.

Genetic adaptation of xylem to meet native environmental conditions is also evident in *Quercus* species, with the most mesic species, *Quercus robur* L., having higher vulnerability than *Q. petraea* L. ex Liebl., *Q. cerris* L. and *Q. pubescens* Willd. (Higgs and Wood 1995). In a test of stem vulnerability and response to climatic variation, a single population of Scots pine (*Pinus sylvestris* L.) was planted on mesic and xeric sites; no acclimation in cavitation vulnerability was detected after several decades of growth (Jackson et al. 1995). Alder et al. (1996), on the other hand, found changes in root vulnerability in individual *Acer grandidentatum* Nutt. seedlings growing in adjacent mesic and xeric microsites, with the roots of seedlings from the more mesic microsite having more vulnerable xylem;

however, there was no accompanying change in stem xylem vulnerability.

In adapting to drought, a tree must adjust to both dynamic water stress during periods of rapid transpirational flux and low soil water when water uptake is severely limited. Our results suggest that shoots adapt to minimize cavitation during periods of dynamic water stress, whereas roots minimize cavitation during periods of extreme soil drought.

Current models predict that during periods of dynamic water stress, cavitation is most likely to occur in xylem where resistance to water flow is the highest (Zimmermann 1983, Tyree and Sperry 1988). In the Douglas-fir seedlings studied, k_s was at least twice as high in the roots as in the shoots, with the CW population roots 7.5 times as efficient in water transport as the shoots. Based on these results, we predict that, during periods of dynamic water stress, gas exchange will be limited by the likelihood of xylem cavitation in the shoot. In a study of young Douglas-fir seedlings, Lassoie (1982) showed that even with a predawn water potential (Ψ_{pd}) of -0.5 MPa, well above the initiation of root cavitation, stomatal conductance declined when the transpirational flux, indicated by water vapor deficit, increased. However, as Ψ_{pd} declined, Douglas-fir stomata closed more readily as atmospheric water deficits increased, with complete closure occurring at approximately -1.6 MPa (Waring et al. 1981, Lassoie 1982), well before stem xylem cavitation is possible (Figure 2).

As soil dries, Douglas-fir seedlings reach a point at which, in order to extract water from the soil, root Ψ_x must decline to values causing cavitation. For example, in roots of all four populations of Douglas-fir seedlings, initial cavitation occurred at Ψ_x of -1.0 MPa, with -2.5 MPa resulting in a percent loss of 55 for population CW, 17 for CD, 32 for IW, and 18 for ID (Table 3). Soil water potentials below the value resulting in significant root cavitation are absent in the mesic Oregon Coast Range, where Ψ_{pd} for seedling Douglas-fir rarely exceeds -0.75 MPa (Cole and Newton 1986). On the remaining more xeric sites, Ψ_{pd} values below the initiation of cavitation are more common; in southwestern Oregon, Ψ_{pd} can reach -2.0 MPa (Wang et al. 1995) or -3.0 MPa (Waring et al. 1981).

Although minimum Ψ_x in the shoot is rarely low enough to cause cavitation, roots on xeric sites are commonly at or near a Ψ_{pd} causing significant cavitation. It has been suggested that root cavitation is beneficial to plant survival because water is released to the leaf and the rate of extraction from the soil is reduced, prolonging water availability during a drought and preventing cavitation at the root-soil interface (Sperry and Saliendra 1994, Alder et al. 1996, Sperry and Ikeda 1997). If this is the case, populations on more drought-prone sites should not only be more resistant to cavitation, but should have a vulnerability curve with a less steep slope, so that cavitation occurs gradually over a larger Ψ_{pd} range. Both the CD and ID sites have vulnerability curves that are less steep than the curves for other sources (Figure 2), resulting not only in less vulnerability but in a greater "safety margin" when cavitation is inevitable.

Within individual Douglas-fir seedlings, the correlation between hydraulic conductivity and vulnerability was evident. Roots are more vulnerable than shoots to cavitation (Figure 4).

Between populations, the correlation between hydraulic conductivity and vulnerability was less clear. For example, the vulnerability curves suggest that k_s would be highest in CW, but it was exceeded by the k_s for the more cavitation resistant CD. However, phenological patterns of xylem growth and the percentage of late wood may provide an explanation. Reduced k_s can occur for two reasons: (1) the individual tracheids in a stem cross section may have an overall smaller tracheid lumen; or (2) the early wood lumens may be similar in size, but there may be a greater proportion of small-diameter late wood tracheids, making the overall permeability lower. Douglas-fir from coastal Oregon has a much longer growing season than more drought-adapted populations, resulting in an increased percentage of late wood (Emmingham 1977). Late wood tracheids are significantly less efficient in terms of water transport; Zimmermann (1983) predicted, based on relative lumen diameter, that late wood would account for only 4% of water transport. Therefore it is not surprising that k_s for CW sources was not as high as predicted based on vulnerability. In addition, within an annual ring, early wood cavitates well before late wood (Dixon et al. 1984, Tyree et al. 1984, Sperry and Tyree 1990), resulting in an increased vulnerability to cavitation, but without the associated high k_s . Thus, the individual early wood tracheids may be larger for the CW source, resulting in a greater vulnerability to cavitation, but the increased proportion of late wood reduces the k_s of the overall sapwood cross-sectional area. In CW roots, which contain a small percentage of late wood, k_s is much higher than for shoots and correlates with relative vulnerability (Figure 2, Table 4).

Besides varying because of genetic adaptation, vulnerability to cavitation appears to vary with tree age. Vulnerability curves for branches from mature Douglas-fir trees were developed by Cochard (1992) and Sperry and Ikeda (1997). Although the geographical race (i.e., var. *menziesii* or var. *glauca*) was not specified, the xylem of branches was more vulnerable to cavitation than that in any of the seedling populations we tested; cavitation in mature Douglas-fir was initiated at -2.5 MPa, compared with -3.0 MPa in the most vulnerable seedling source tested. At -4.0 MPa, the CW seedlings experienced a 40% loss in k_s , but Cochard's mature Douglas-fir experienced an 80% loss. Sperry and Ikeda (1997) found that roots from mature trees were more vulnerable than those from younger trees. Roots less than 5 mm in diameter were more vulnerable than those from the seedling populations we tested. At -1.5 MPa, roots from mature trees experienced a loss in k_s of approximately 50%, compared with 17% for the most vulnerable seedling population we tested. This is not unexpected, because seedling roots are located in the more drought-prone upper soil profile. Differences in vulnerability between juvenile and adult *Betula occidentalis* Hook. (Sperry and Saliendra 1994) followed a similar pattern, with the juvenile populations more resistant to cavitation than the adults.

This study documents substantial variation in shoot and root vulnerability to cavitation, both between varieties and within populations; the next question is to examine the extent of adjustment to vulnerability within localized environmental gradients and tree age. Although there is no indication that

shoots adjust (Jackson et al. 1995), there are indications that roots are more plastic (Alder et al. 1996).

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