

Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation

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Summary Variations in resistance to drought-induced xylem cavitation, xylem air-entry points, stomatal behavior, and hydraulic conductivity were measured in four populations of *Populus trichocarpa* Torr. & A. Gray collected along an east-west humidity and temperature gradient in Washington State, USA. Xylem air-entry points were less negative in trees from moist environments (−0.71 and −1.32 MPa in the Hoh and Nisqually populations, respectively) than in trees from dry environments (−1.55 and −1.67 MPa in the Palouse and Yakima populations, respectively). Xylem cavitation in response to experimental drought was consistent with air-injection measures of xylem air-entry points for a given population. Populations vulnerable to cavitation also exhibited higher stem specific hydraulic conductivities and limited stomatal control compared with resistant populations. Populations exhibiting vulnerability to cavitation and limited stomatal control desiccated more rapidly during drought compared with resistant populations. This study provides evidence of interpopulation variation in resistance to drought-induced xylem cavitation, stomatal behavior, and hydraulic conductivity within *Populus trichocarpa*.

Keywords: black cottonwood, drought stress, interpopulation variation, stomatal regulation, xylem embolism.

Introduction

Xylem cavitation in response to stress in plants has been recognized as an important limitation to water transport (Tyree and Dixon 1986, Sperry and Tyree 1990, Cochard et al. 1992b). High xylem tension, freezing and thawing of the xylem water, and some pathogens (e.g., tracheomycoses) are stresses that can cause xylem conduits to become air-filled (i.e., cavitated) and nonfunctional (Edwards and Jarvis 1982, Newbanks et al. 1983, Zimmermann 1983, Salleo and Lo Gullo 1989). Our study focuses on the xylem cavitation response to decreasing water potentials experienced by plants during drought.

Cavitation during drought apparently depends on the pressure differential across the pit membranes that connect xylem elements to other air-filled components of the plant. The air-water meniscus at the pit membrane is pulled into the func-

tional element until a micro-bubble of air enters the element thereby producing an embolism and decreasing the xylem hydraulic conductivity (Crombie et al. 1985). Vulnerability to drought-induced cavitation has been measured for many plant species and variation in vulnerability among species has been well established (Cochard and Tyree 1990, Cochard 1992, Sperry et al. 1994, Jarbeau et al. 1995). Tyree and Sperry (1988) suggested plants achieve maximum gas exchange by maintaining a small margin of safety from cavitation. Therefore stomatal responses to drought stress should be related to the cavitation threshold. Stomatal conductance is thought to be maintained below values that lead to xylem cavitations (Sperry and Pockman 1993, Sperry et al. 1993).

Populus trichocarpa Torr. & A. Gray (black cottonwood) is morphologically and physiologically variable across its range in Washington State (Bassman and Zwier 1991, Dunlap 1991, Carlin 1996). An individual *P. trichocarpa* from the eastern part of the range was shown to exhibit higher water-use efficiency and greater stomatal control compared with a second individual from the western part of the range (Bassman and Zwier 1991). In a greenhouse study, Carlin (1996) found that several trees representing populations originating from dry environments showed higher resistance to drought than populations originating from wet environments. Because *P. trichocarpa* is a riparian species and is found in environments where soil water is readily available, Dunlap (1991) and Carlin (1996) speculated that variation within this species was in response to differences in potential evapotranspiration across its range. Rood and Mahoney (1990) and Tyree et al. (1994) have suggested that declines in poplar forests associated with regulated stream flows may be caused by drought-induced xylem cavitation.

We examined four populations of the riparian species *P. trichocarpa* growing across a gradient in potential evapotranspiration within Washington State to determine if drought-induced xylem cavitation, stomatal behavior and xylem hydraulic conductivity varied within this species. We hypothesized that trees from populations growing in environments of lower relative humidities and higher summer temperatures (i.e., populations on the eastern side of the Cascade Mountains) would show greater stomatal control, higher resistance to drought-induced cavitation, and tighter coupling of

stomatal behavior to cavitation thresholds than trees from populations growing in more humid environments with lower summer temperatures (i.e., populations on the western side of the Cascade Mountains).

Materials and methods

Collection sites and plant culture

Four populations of the riparian species *Populus trichocarpa* were selected along a gradient of potential evapotranspiration across Washington State, USA. Two populations were collected from a coastal climate west of the Cascade Mountains and two populations were collected from drier climates east of the Cascade Mountains. Coastal collection sites were located in the Hoh and Nisqually River Basins. The Hoh and Nisqually River Basins exhibit a mean growing season (April–September) potential evapotranspiration (PET) of 45.0 and 50.0 cm, respectively. Collection sites along the eastern drier portion of the transect were located in the Palouse and Yakima River Basins. Mean growing season PET values in the Palouse and Yakima River Basins are 54.3 and 60.4 cm, respectively (Phillips 1964, Phillips 1968, Phillips and Donaldson 1972, Donaldson 1979). These four riparian sites provided a generally constant soil water environment and a gradient of potential evapotranspiration.

Individuals were collected as cuttings from the Hoh and Nisqually River basins in the winter of 1985–1986 and were planted in a clone bank at the Washington State University Puyallup Research and Extension Center in the spring of 1986 (Dunlap 1991). Genetically distinct cuttings from the Hoh and Nisqually populations were collected for this study from this same clone bank on January 27, 1995. Individuals were collected as cuttings from the Yakima and Palouse River basins on February 4 and 25, 1995, respectively (Carlin 1996).

Between May 27 and 29, 1995, cuttings from the four populations were planted in 10 × 40 cm pots filled with a commercial soil consisting of a 2:1:1 mix of peat, moss, and vermiculite. Plants were grown outdoors with supplemental watering and NPK fertilizer through the summer of 1995 on the Washington State University campus. In February 1996, plants were transplanted to 10-l pots filled with the same commercial soil mixture, moved to a greenhouse, and grown for three months at a constant temperature of 25 °C with supplemental lighting. Experiments were initiated on June 4, 1996.

Laboratory methods: vulnerability to xylem cavitation

We investigated the resistance of xylem to cavitation at various tensions by generating vulnerability curves following the procedures described by Cochard et al. (1992a) and Sperry and Saliendra (1994). Air pressure injection was used to simulate increasing xylem tensions and arrays of conductance values were collected at a low-pressure head of water. Five vulnerability curves, one for each individual, were generated for each population. Before measurement, stem segments greater than 1 m in length and 11–13 mm in diameter were harvested from well-watered trees and recut to between 0.2 and 0.25 m under

water to avoid introduction of additional emboli. As recommended by Sperry and Saliendra (1994), small-notched cuts were made in each segment to increase air access to the vascular system. The segments were enclosed in a double-ended pressure chamber and the proximal end attached with clear Tygon tubing to a low-pressure head. Filtered (0.2 µm) water, adjusted to pH 2 to avoid microbial growth, was passed through the stem at low pressure (approximately 0.01 MPa). Hydraulic conductance (k) was defined as the mass flow rate of water through the stem divided by the low-pressure head.

We generated a vulnerability curve by first pressurizing the chamber to 0.05 MPa to avoid water extrusion from side branches or the transverse cuts, and equilibrated for 10 min. Once equilibrated, flow was increased by raising the pressure head, and conductance through the stem was measured over one-minute intervals by collecting effluent from the distal end of the stem in pre-weighed vials filled with absorbent cotton until the measurements were repeatable. This conductance measure was defined as the initial conductance (k_i). After the initial measurement, the pressure head of water was lowered and the chamber air pressure raised by preset increments (approximately 0.25 MPa) and allowed to equilibrate for 10 minutes. Flow was reduced between conductance measurements to minimize clogging caused by any suspended microparticles in the solution. After equilibrating at a chamber air pressurization, the chamber pressure was reduced to 0.05 MPa, the pressure head raised to increase flow, and the conductance measured (k_m) for the given pressurization treatment. This process was repeated until conductance of the segment was negligible.

Experimental drought-induced xylem cavitation

Drought treatments were applied to 12, 9, 19, and 23 individual trees from the Hoh, Nisqually, Palouse, and Yakima populations, respectively. Plants were watered normally until the experimental drought began at which time all watering ceased. Leaf water potentials were monitored with a pressure chamber (PMS, Corvallis, OR) every four hours during daylight hours throughout the experiment. Individuals were randomly harvested over a seven-day period for measurement of hydraulic conductivity and loss of hydraulic conductivity. Leaf water potential measurements ranged from –0.6 to –2.9 MPa.

Hydraulic conductivity and loss of hydraulic conductivity were measured on individual stems following the procedures of Sperry et al. (1988). Maximum vessel lengths for these populations of *P. trichocarpa* were determined to be approximately 4 cm by forcing air through stem segments of various lengths. Therefore, stems greater than 1 m in length and 9–11 mm in diameter were harvested and recut to 10-cm segments under water before mounting on the positive flow hydraulic conductivity apparatus. Hydraulic conductivity of each segment was measured before and after removal of embolism by high pressure (150 kPa) flushing of water through the xylem. Hydraulic conductivity was expressed as a ratio (k_i/k_{max}) of initial (k_i) and maximum measurements (k_{max}) of conductivity for any particular segment.

Stomatal response to decreasing leaf water potential

A drought treatment was applied to five trees from each population separate from those used in other experiments, by withholding irrigation. Stomatal conductances and leaf water potentials were monitored at two-hour intervals during daylight hours with a steady-state porometer (LI-1600, Li-Cor, Inc., Lincoln, NE) and a pressure chamber (PMS), respectively. The pressure chamber was used to measure the pressure potential of leaves, which approximates leaf water potential if solute potentials are near zero. Measurements of leaf water potential continued until leaves wilted and balance pressures were no longer attainable because of cell death and a corresponding change in leaf solute potential. Once measurement was no longer possible, the individual was harvested and losses in xylem hydraulic conductivity were measured with the positive flow hydraulic conductivity apparatus.

Statistical analysis

Analysis of variance (ANOVA) was performed by the general linear model (GLM) procedure (SAS Institute, Cary, NC) to test for significant differences between populations. Duncan's least significant difference test was used to test differences between means (Littel et al. 1991). Differences between air-entry points generated by the air-injection technique compared to the experimental drought technique were analyzed by Student's *t*-tests.

Vulnerability curves were analyzed by procedures analogous to determining the air-entry point (Ψ_e) in soils under increasing tensions (Brooks and Corey 1966, Campbell 1974). In plants, vulnerability curves often exhibit a point, here defined as the air-entry point, beyond which hydraulic conductivity decreases rapidly because of increased cavitation of the xylem (Edwards and Jarvis 1982, Zimmermann 1983). Plots of relative conductivity (k/k_{max}) against the absolute value of the stem water potential on a logarithmic scale result in two distinct intersecting lines before and after an abrupt change in slope near the air-entry point (Figure 1). A power function fit of the line after the intersection point gives a linear relationship of the form:

$$k/k_{max} = a|\Psi|^b, \quad (1)$$

where k/k_{max} is the relative conductivity, Ψ is the tension applied to the system, and a and b are fitting parameters. By rearranging and solving this equation for maximum conductance (i.e., $k/k_{max} = 1$) we can calculate the air-entry point (Ψ_e):

$$\Psi_e = -(1/a)^{1/b}. \quad (2)$$

The air-entry point in plants is an estimate of the xylem tension at which pit membranes are overcome within the conducting tissue and cavitation begins. We used the air-entry point as a parameter for comparisons between vulnerability curves.

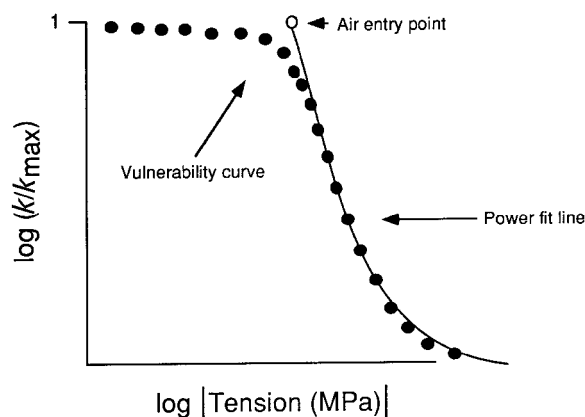


Figure 1. Method of determining xylem air-entry points (Ψ_e) based on vulnerability curve data. The relative conductance (k/k_{max}) versus the absolute value of pressure applied or tension induced in the system (dependent on technique) plotted on a logarithmic scale results in two linear phases. The second steep-sloped phase can be fit with a power relationship and solved for maximum conductance (i.e., $k/k_{max} = 1$) giving the calculated air-entry point into the xylem.

Results

The four populations of *Populus trichocarpa* showed differences (ANOVA, $F = 38.68$, $P < 0.0001$) in loss of conductance following pressurization by the air-injection technique (Figure 2, Table 1). The Hoh and Nisqually populations exhibited less negative air entry points (-0.71 ± 0.11 MPa and -1.32 ± 0.07 MPa, respectively, Table 1) compared to the Palouse and Yakima populations (-1.55 ± 0.03 MPa and -1.67 ± 0.01 MPa, respectively, Table 1). Air-entry points differed among populations except between the Palouse and Yakima populations (Duncan's LSD, $P = 0.05$ for all comparisons). The Hoh and

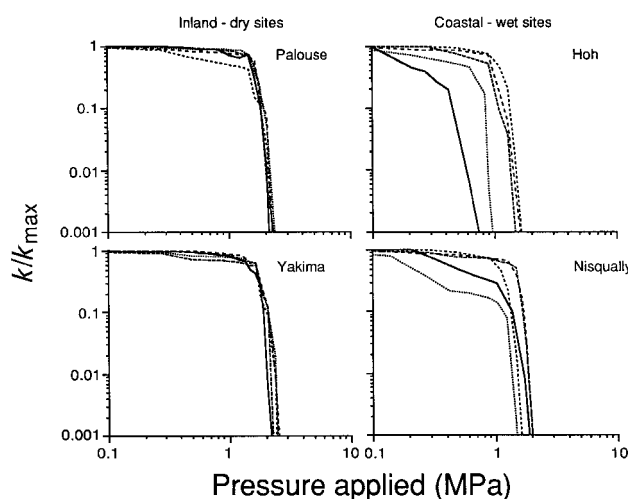


Figure 2. Plots of relative conductance over applied pressure, based on the air-injection technique, for four populations of *Populus trichocarpa* originating from different environments. Values are plotted on a logarithmic scale to show the break in the relationship defining the air-entry point. Each line represents an array of conductance measures of one tree within a given population.

Table 1. Power fit parameters of vulnerability curves. Model fits were of the form: $k/k_{\max} = a|\Psi|^b$ where k/k_{\max} is the relative conductivity, Ψ is the tension applied to the system, and a and b are fitting parameters. The slope of the relationship (b) represents the rate of decrease in conductance after air entry into the xylem. All r^2 values for power fits were > 0.802 and ranges of means are ± 1 SE. Also listed are air pressures and water potentials at the calculated air-entry points (Ψ_e) both in MPa. Letter designations among populations in the fitting parameter b and air-entry points indicate significant differences (Duncan's LSD, $P = 0.05$).

Population	Air-injection method		Induced-drought experiment	
	b	Ψ_e (air pressurization)	b	Ψ_e (water potential)
Hoh	-10.38 ± 1.86^a	-0.71 ± 0.11^a	-9.613	-1.02
Nisqually	-17.92 ± 1.41^b	-1.32 ± 0.07^b	-13.01	-1.43
Palouse	-17.69 ± 1.05^b	-1.55 ± 0.03^c	-11.23	-1.50
Yakima	-19.68 ± 1.77^b	-1.67 ± 0.01^c	-14.91	-1.68

Nisqually populations exhibited higher standard errors in the measurement of conductance loss within populations than the Palouse and Yakima populations (Table 1). The Hoh and Nisqually populations contained individuals that rapidly lost conductance at very low pressurizations (e.g., $> 30\%$ loss in conductance at 0.5 MPa) and all individuals of these populations reached zero conductance at 2.3 and 2.4 MPa, respectively. Individuals from the Palouse and Yakima populations showed little loss of conductance during initial pressurizations and did not exhibit losses in conductance greater than 30% until pressurizations of > 1.1 MPa. All individuals from the Palouse and Yakima populations reached zero conductance by 2.7 MPa.

During an experimental drought, patterns of loss of hydraulic conductivity were similar to those found with the air injection technique (Figure 3). Loss in hydraulic conductivity over a range of leaf water potentials generated air-entry points of -1.02 , -1.43 , -1.50 , and -1.68 MPa for the Hoh, Nisqually,

Palouse, and Yakima populations, respectively (Figure 3, Table 1). The use of multiple trees measured at a variety of leaf water potentials permitted us to calculate only one air-entry point per population and no inferential statistics were performed; however, air-entry points generated for each population during experimental drought did not differ from those generated by the air-injection technique (Student t -test).

Stomatal behavior at decreasing leaf water potentials differed among populations (Figure 4). Stomatal conductances across all populations ranged from 200 to $900 \text{ mmol m}^{-2} \text{ s}^{-1}$ during the drought treatment and all populations exhibited a decrease in stomatal conductances at leaf water potentials less than -1.5 MPa. Plants from the Palouse and Yakima populations exhibited stomatal conductances of $< 1 \text{ mmol m}^{-2} \text{ s}^{-1}$ at leaf water potentials less than -1.5 MPa. In contrast, the Hoh and Nisqually populations maintained conductances of approximately $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ at leaf water potentials less than -1.5 MPa and continued to transpire until leaf material wilted and leaf water potentials were no longer measurable.

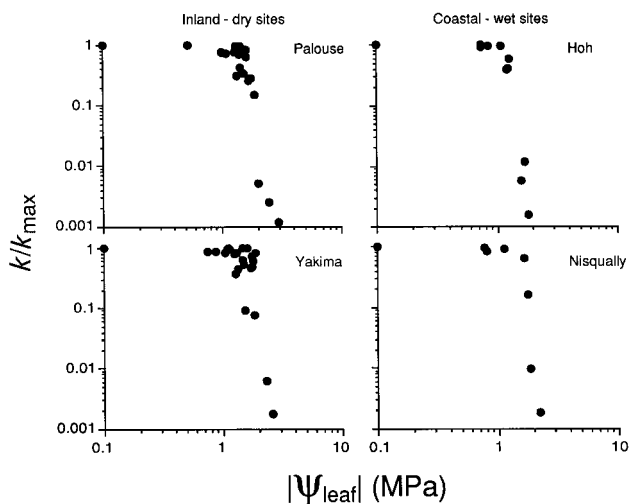


Figure 3. Plots of relative conductance over the leaf-water potential measured at the time of harvest during an experimental drought treatment. Values for each axis are plotted on a logarithmic scale to show the break point defining the air-entry point. Each point represents a single tree from a given population. Air-entry points were similar to those generated using the air-injection technique (Student's t -test). See Table 1 for air-entry values.

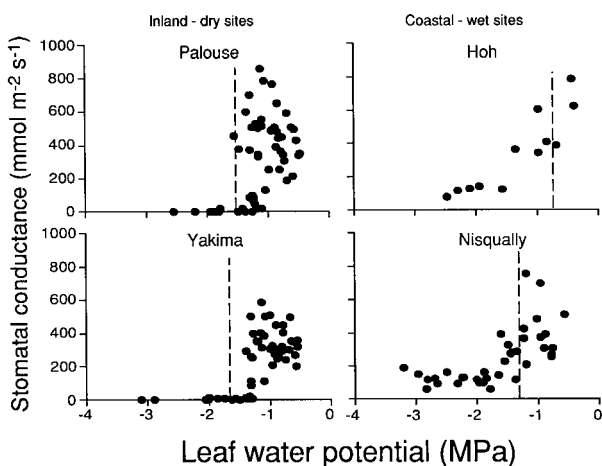


Figure 4. Patterns of stomatal conductances at decreasing leaf water potential in four populations of *Populus trichocarpa*. Five trees were used for each population and each data point represents a single measurement. The calculated air-entry point for each population as determined by the air-injection technique are indicated by dashed lines (-0.71 ± 0.11 , -1.32 ± 0.07 , -1.55 ± 0.03 and -1.67 ± 0.01 in the Hoh, Nisqually, Palouse, and Yakima populations, respectively).

Stomatal behaviors and the resultant leaf water potentials of similar sized plants differed among populations during a seven-day drought treatment (Figure 5). Plants from the Hoh and Nisqually populations showed a decrease in leaf water potentials from -0.2 to -2.9 MPa during the first two days of treatment. Stomatal conductances were greater than $100 \text{ mmol m}^{-2} \text{ s}^{-1}$ initially, but the plants were dead and leaf material was dry by the end of the second day. Stems harvested at the end of the second day of treatment showed a 100% loss in xylem hydraulic conductivity. In contrast, plants from the Palouse and Yakima populations showed greater stomatal closure (conductances $< 10 \text{ mmol m}^{-2} \text{ s}^{-1}$) after the second day of treatment and leaf water potentials were maintained above -1.5 MPa until the sixth and seventh day, respectively. After six days, leaf water potentials decreased rapidly, the plants wilted, and were harvested. Stems harvested after the sixth day of treatment showed between 85 and 100% loss in xylem hydraulic conductivity.

Maximum specific hydraulic conductivities for a given cross-sectional stem area differed between populations (Figure 6; ANOVA, $F = 6.76$, $P < 0.001$) and were higher in the Nisqually population than in the other populations. Maximum conductivities in the Hoh population were higher than those in the Palouse and Yakima populations. Maximum conductivities did not differ significantly between the Palouse and Yakima populations (Duncan's LSD, $P > 0.05$ for all comparisons).

Discussion

Populations of the riparian tree species *Populus trichocarpa* were similar with respect to their resistance to xylem cavitation when measured by the air injection technique (Figure 2, Ta-

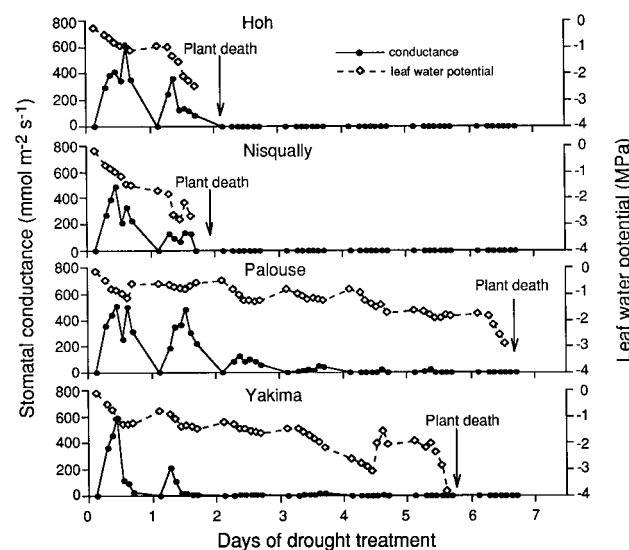


Figure 5. Stomatal conductances (●) and leaf water potentials (◇) of similar size trees from four populations of *Populus trichocarpa* over a seven-day drought treatment. Figure shows only one tree per population, but responses were similar across replicates ($n = 5$ per population). Plant death was defined as the point where the balance pressure was no longer attainable because of cell death.

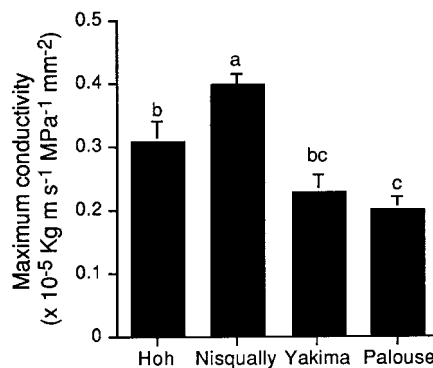


Figure 6. Mean maximum specific stem hydraulic conductivity for four populations of *Populus trichocarpa*. Letters represent significant differences between populations (Duncan's LSD, $P < 0.05$, $n = 20$ per population). Error bars are $+1$ SE.

ble 1) or their vulnerability to xylem cavitation in response to experimental drought (Figure 3, Table 1). Trees originating from west of the Cascade Mountains (Hoh and Nisqually populations) exhibited less negative air-entry points, a shallower decline in xylem conductivity after air entry, and larger standard errors within populations (Table 1) than populations originating from east of the Cascade Mountains (Palouse and Yakima populations). The Hoh and Nisqually populations showed a wider range of air-entry points compared to the Palouse and Yakima populations (Figure 2, Table 1) implying within-population variation was greater for these populations.

Variation in resistance to drought-induced xylem cavitation has previously been demonstrated among species (Sperry and Tyree 1990, Sperry and Sullivan 1992, Kolb and Davis 1994, Sperry et al. 1994), among cultivars of the same species (Neufeld et al. 1992), and among tissues of the same individual plant (Sperry and Saliendra 1994). However, few studies have focused on the variability within a single species found over a broad range of environmental conditions. Franks et al. (1995) reported that seedlings of *Eucalyptus camadulensis* Dehnh. from drier environments in Australia exhibited higher resistances to drought-induced xylem cavitation compared with seedlings from wetter environments. More recently, Mencuccini and Comstock (1997) showed differences in vulnerability to cavitation related to differences in the environment of origin among populations of the desert shrub *Ambrosia dumosa* (Gray) Payne when grown in a common garden. Our data set suggests similar variation in resistance among populations of *Populus trichocarpa* and these differences parallel differences in the environment of origin. We found that populations from high potential evaporation environments tend to exhibit high resistances to drought-induced xylem cavitation.

Variable stomatal behavior in response to drought has also been shown within and among plant species (Shulze and Hall 1982, Hartung and Slovik 1991, Sperry et al. 1993, Fuchs and Livingston 1996). Further, several species of *Populus* are known to exhibit interpopulation variation in stomatal behavior (Bassman and Zwier 1991, Dunlap et al. 1993, Carlin 1996). Ceulemans et al. (1987) reported that some individuals

of *Populus trichocarpa* display little stomatal closure with decreasing leaf water potential, which is similar to the Hoh and Nisqually populations found in this study. They also found other individuals respond to decreasing leaf water potential with rapid stomatal closure as we report for the Palouse and Yakima populations in this study. In general, our data set supports these earlier studies showing stomatal behavior varies among populations of *Populus trichocarpa* (Figures 4 and 5).

Schulte et al. (1987) found preconditioning plants with a period of nonfatal drought stress modified the stomatal responses of individual *Populus trichocarpa* to changing leaf water potential. Although the trees used in this study had not previously experienced drought stress, previous work with these same populations in common garden studies (Carlin 1996) showed repeated drought treatments had no effect on subsequent stomatal behavior. The reasons for the discrepancy between these data sets is not known, and preconditioning may have altered stomatal responses in some individuals.

All populations in our study showed decreased stomatal conductances associated with lower leaf water potentials. However, trees from the Hoh and Nisqually populations maintained higher conductances (approximately $100 \text{ mmol m}^{-2} \text{ s}^{-1}$) at leaf water potentials $< -1.5 \text{ MPa}$ than trees from the Palouse and Yakima populations ($< 1 \text{ mmol m}^{-2} \text{ s}^{-1}$). Apparently stomata responsive to decreasing leaf water potential are present in trees from the Palouse and Yakima populations, whereas such responsiveness is reduced in trees from the Hoh and Nisqually populations. Further, when this stomatal behavior is compared with air-entry points of the xylem, it appears some individuals do not restrict stomatal conductances sufficiently to avoid the induction of xylem cavitation. These individuals with nonresponsive stomata and vulnerable xylem only persist in low potential evapotranspiration environments such as the Hoh and Nisqually River basins.

The ability of Palouse and Yakima trees to maintain high leaf water potentials by means of stomatal regulation and their decreased vulnerability to cavitation results in increased tolerance to drought (Figure 5). Similar size trees from the Hoh and Nisqually populations wilted and leaf water potentials were $< -1.5 \text{ MPa}$ by the second day of our drought experiment (Figure 5). In contrast, trees from the Palouse and Yakima populations were able to close stomata completely ($< 1 \text{ mmol m}^{-2} \text{ s}^{-1}$) after two to three days of drought and maintained leaf water potentials $> -1.5 \text{ MPa}$ until the sixth or seventh day of the experiment (Figure 5). All trees from all populations showed 85–100% loss in xylem conductivity during drought implying that cavitation occurred at leaf water potentials $< -1.5 \text{ MPa}$. Greater stomatal control and a higher resistance to cavitation apparently allowed Palouse and Yakima trees to tolerate drought longer than Hoh and Nisqually trees.

Poor stomatal control together with low resistance to xylem cavitation found in the Hoh and Nisqually populations are counterintuitive and the commingling effect of these characteristics would increase the probability of catastrophic failure of the conducting tissue. We hypothesize two alternative explanations. First, low xylem tensions are not experienced by trees in the Hoh and Nisqually environments and therefore air-entry points are never reached and cavitation does not occur. This

seems unlikely given that midday leaf water potentials reported in the literature for trees from similar western populations are lower ($> 0.2 \text{ MPa}$) than the air-entry points observed in this study (Schulte et al. 1987, Carlin 1996). Second, there may be a trade-off between resistance to cavitation and maximizing plant conductances such that highly resistant individuals would exhibit lower hydraulic efficiency of the xylem.

Our data set supports this second hypothesis. Less resistant trees from the Hoh and Nisqually populations tended to have higher specific hydraulic conductivities compared with more resistant trees from the Palouse and Yakima populations (Figure 6). Jones and Sutherland (1991) used plant conductance models to predict that, if the reduction in xylem conductivity was not rapid after the induction of cavitation (i.e., the slope of the relationship between conductivity and tension was shallow after air-entry), then loss of a proportion of the conducting tissue can be beneficial in terms of maximizing total plant water flux and short-term productivity. In this study, trees from the Hoh population exhibited a reduced slope after air-entry compared with trees from the other populations (Table 1), suggesting that, in a wet environment like the Hoh River basin, populations of *P. trichocarpa* may benefit from the induction of small amounts of cavitation, if this cavitation is associated with high daily water fluxes and increased growth. However, the model does not explain why some plants continue to transpire until they desiccate (Figure 5). Apparently, selection pressure for tight stomatal control is low in wet environments and individuals with an inability to control water loss persist in these environments. Tree mortality in this study was related to xylem transport failure. That is, the loss of xylem conductivity measured at the point of wilting and plant death (Figure 5) was always near 100% for all populations.

Populations of *Populus trichocarpa* originating from along a potential evapotranspiration gradient exhibited different resistances to drought-induced xylem cavitation, stomatal behavior, and xylem conductivity. This variation appears to be related to the evaporative demand present in the source environment and may be an example of adjustment in physiological characteristics to maximize plant conductances without inducing catastrophic xylem cavitation.

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