

SAFETY FACTORS FOR XYLEM FAILURE BY IMPLOSION AND AIR-SEEDING WITHIN ROOTS, TRUNKS AND BRANCHES OF YOUNG AND OLD CONIFER TREES

Jean-Christophe Domec^{1,*}, Jeffrey M. Warren², Frederick C. Meinzer³ and Barbara Lachenbruch⁴

SUMMARY

The cohesion-tension theory of water transport states that hydrogen bonds hold water molecules together and that they are pulled through the xylem under tension. This tension could cause transport failure in at least two ways: collapse of the conduit walls (implosion), or rupture of the water column through air-seeding. The objective of this research was to elucidate the functional significance of variations in tracheid anatomical features, earlywood to latewood ratios and wood densities with position in young and old Douglas-fir and ponderosa pine trees in terms of their consequences for the safety factors for tracheid implosion and air-seeding. For both species, wood density increased linearly with percent latewood for root, trunk and branch samples. However, the relationships between anatomy and hydraulic function in trunks differed from those in roots and branches. In roots and branches increased hydraulic efficiency was achieved at the cost of increased vulnerability to air-seeding. Mature wood of trunks had earlywood with wide tracheids that optimized water transport and had a high percentage of latewood that optimized structural support. Juvenile wood had higher resistance to air-seeding and cell wall implosion. The two safety factors followed similar axial trends from roots to terminal branches and were similar for both species studied and between juvenile and mature wood.

Key words: Cell wall, embolism, juvenile wood, mature wood, tracheid, water transport.

INTRODUCTION

Two failure modes can cause stem xylem water columns to become discontinuous. The first occurs when xylem pressure (P) falls below the air-seeding threshold allowing air

1) Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27795, USA.

2) Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA.

3) USDA Forest Service, Forestry Sciences Laboratory, 3200 SW Jefferson Way, Corvallis, OR 97331, USA.

4) Department of Wood Science and Engineering, Oregon State University, Corvallis, OR 97331, USA.

*) Corresponding author [E-mail: jdomec@ncsu.edu].

bubbles to be pulled into adjacent conduits through pit membrane pores (Sperry & Hacke 2004). In the case of coniferous torus-margo pit membranes, after a pit is aspirated and the torus is blocking the aperture, the torus can be pulled further through the aperture, exposing some of the margo to the adjacent tracheid lumen. Air-seeding then occurs through this margo portion (Hacke *et al.* 2004; Domec *et al.* 2006a). The air bubble rapidly expands to fill the conduit resulting in an air-seeded embolism (Zimmermann 1983), causing conduit conductivity to be lost unless the embolized cell is refilled with water. The second mode of failure occurs when a water-filled conduit physically collapses from the difference in P between its interior and an adjacent air-filled conduit at atmospheric pressure (Hacke *et al.* 2001). Although xylem collapse has not been documented in wood, it has been observed in needles (Cochard *et al.* 2004; Brodribb *et al.* 2005). The consequence of these two modes of failure is reduced hydraulic conductivity, which can in turn lead to a cascade of physiological responses such as stomatal restriction of transpiration and photosynthesis (Sperry *et al.* 1994; Santiago *et al.* 2004) or leaf abscission (Vilagrosa *et al.* 2003).

Xylem failure through air-seeding is affected by the morphology of bordered pits (Hacke *et al.* 2004; Domec *et al.* 2006a; Choat *et al.* 2008), whereas xylem failure by implosion would be determined by the tracheid cell wall thickness in relation to the lumen diameter (Hacke *et al.* 2001; Pittermann *et al.* 2006). Simple calculations have suggested that the pressure differentials between adjacent water- and air-filled conduits are not sufficient to cause rupture of lignified cell walls (Rundel & Stecker 1977; Baas 1986; Jacobsen *et al.* 2005). However, these calculations did not take into account the complexity of xylem geometry. Using more sophisticated models, Hacke *et al.* (2001) calculated that water-filled conduits experience large tensile hoop stresses (stresses around the circumference of the conduit) that could lead to cell collapse under drought conditions if neighboring cells did not provide sufficient mechanical support. In addition, they showed that xylem implosion pressures calculated from cell anatomical dimensions are correlated with wood density. The basis for this relationship is that the double-cell wall shared by adjacent cells behaves in a manner similar to a long plate of width b (cell diameter) and thickness t (double-cell wall thickness), and this plate will buckle under a force proportional to $(t/b)^2$ (Hacke *et al.* 2001). As a consequence, dense wood, which is characterized on average by a high t for a given b (because of a higher proportion of cell wall volume compared to lumen volume), is more resistant to cell wall collapse than is less dense wood. However, the density of a coniferous wood sample is mainly dependent on the latewood proportion (Zobel & Sprague 1998; Rosner *et al.* 2007), whereas hydraulic conductivity and resistance to embolism are largely determined by the properties of earlywood (Domec & Gartner 2002a). Therefore an adjustment of lumen diameter/wall-thickness ratios in the earlywood could enhance conductivity and reduce resistance to cell wall collapse without compromising overall wood density and mechanical strength if the latewood percentage remains constant.

We used the concept of safety factor to help evaluate the adequacy of xylem design for hydraulic functionality, by comparing the P that would cause failure by either mode, to the most negative values of P (P_{\min}) likely to be encountered annually. Both P and P_{\min} (which generally occurs at mid-day during summer) vary markedly by position

in the tree. For example, P_{\min} decreases from roots to trunk to branches. We defined the safety factors as the ratio of threshold P causing hydraulic dysfunction by either air-seeding or implosion to P_{\min} (Domec & Gartner 2002b) and looked at the spatial pattern of different safety factors to estimate which part of the root-to-terminal-branch hydraulic pathway is likely to fail first under field conditions.

Studies of xylem conductivity and vulnerability to embolism in larger and older trees are almost always based on measurements of branch or root segments (Cochard 1992; Martínez-Vilalta *et al.* 2002; Burgess *et al.* 2006) and rarely on segments from the main stem (Dunham *et al.* 2007, 2008; Rosner *et al.* 2008). Much of the published research that relates xylem anatomy to water transport properties is also based on branch samples because branches are convenient for methodological reasons (Jacobsen *et al.* 2005; Pittermann *et al.* 2006). Because branches have a different xylem anatomy than other plant parts (Fegel 1941; Dunham *et al.* 2007), the relationships derived from branches are not necessarily applicable trunks or roots (Dunham *et al.* 2008). Within trees, the relationship between structure and function is not expected to be straightforward because plant parts (*i.e.*, roots, branches, and trunk) have several functions (Gartner 1995). For example, roots also serve in nutrient uptake, storage, and anchorage (Weiner & Thomas 2001) and have been identified as a weak link in the hydraulic continuum under drought conditions (Jackson *et al.* 2000). Moreover, in conifers the tracheids are responsible for both support and conduction functions, leading to a potential trade-off between these functions. Several hypotheses predict how xylem structure should change along the root-to-terminal branch water transport pathway to optimize whole tree hydraulic efficiency and safety for embolism (Comstock & Sperry 2000; McCulloh & Sperry 2005) but there are only a few studies that have sampled more than two points along the entire pathway (Domec & Gartner 2002b, 2003; Domec *et al.* 2005; Choat *et al.* 2005; Dunham *et al.* 2007, 2008). Trees are structurally complex and by studying different locations within them we may better understand the intricacies of the design criteria that govern xylem structure and function (Domec & Gartner 2001; McElrone *et al.* 2004; Burgess *et al.* 2006).

In addition to varying with height above the ground, it is well known that wood structure varies along the radial axis, as it transitions from juvenile to mature wood (*i.e.*, Dinwoodie 2000). However, the selection pressures that have shaped these radial variations remain unknown, in spite of several studies that have addressed one purported purpose or another of juvenile and mature wood for tree function (Gartner 1995; Mayr 2002; Domec & Gartner 2003; Rosner 2006; Gartner 2006). The proportionality between cell wall reinforcement and embolism resistance in reference to the function of juvenile and mature wood has never been studied directly within the trunks of tall trees.

The main objective of this research was to assess the functional significance of axial and radial variation in wood structure from roots to upper branches in coniferous trees and its consequences for the safety factors for failure by implosion and air-seeding. We also made comparisons of juvenile and mature wood to learn how the competing demands placed on tracheids to avoid air-seeding-induced embolism and to be sufficiently strong to resist implosion are reconciled at different points along the stem.

MATERIALS AND METHODS

Plant materials

We compared wood function in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) using physiological and anatomical measurements on new and previously-collected samples. For roots, trunks and branches we used the physiological data already published from old (110-year-old) and young (9-year-old) Douglas-fir trees (Domec & Gartner 2001, 2002b; Domec *et al.* 2004), and from old (245-year-old), mature (72-year-old) and young (32-year-old) ponderosa pine trees (Domec & Gartner 2003; Domec *et al.* 2004) as follows. In general, we used 5–6 trees of each age group. Shallow roots sampled at 20 cm depth ranged between 3 and 4 mm in diameter and were between 4- and 7-year-old. Four positions had been sampled along the trunk of the old trees at nodes 5, 15, 35 and 110 (the base) in the Douglas-fir trees and at nodes 15, 35, 65 and 245 (the base) in the ponderosa pine trees (Table 1). Node number refers to the whorl number counting down from the tree top. At all the heights except the uppermost ones, two radial positions (inner and outer sapwood) had been measured. In addition, three branch samples taken near the base of the branches attached at nodes 5, 15 and 35 were sampled in three other 110-year-old Douglas-fir trees from the same site. In the young trees, we had sampled one trunk position and one branch, both from node 5 in Douglas-fir and both from node 15 in ponderosa pine. Within the mature ponderosa pine trees, we had sampled node 15 and inner and outer sapwood at node 50. For both tree species, all branches sampled were 5- to 6-year-old. We defined juvenile wood as samples located <20 rings from the pith, and mature wood as samples located >40 rings from the pith because of published radial wood density profiles (*i.e.*, Abdel-Gadir *et al.* 1993; Bouffier *et al.* 2003). Because of their ages, all branches and roots were considered as made of juvenile wood.

Hydraulic parameters and wood density

Vulnerability curves (VCs) of xylem to water-stress-induced embolism were taken from our published values (see above), and had been determined using the air injection method (Cochard *et al.* 1992). The pressure required to cause a 50% loss of hydraulic conductivity by embolism (P_{50}) was derived from the VCs. For the current study, we also made additional measurements of P_{50} on six 5- to 6-year-old deep roots (located 40–60 cm below the surface) as well as on six 5-year-old branches from the top (node 15) of the mature and old-growth ponderosa pine trees. Our dataset, therefore, included a wide range of P_{50} values from a maximum of -0.7 MPa in roots to a minimum of -6.6 MPa in branches (Table 1).

Trunk and branch minimum summer xylem pressures (P_{\min}) were taken from published data measured on the same Douglas-fir (Domec & Gartner 2002b) and ponderosa pine trees (Domec *et al.* 2005) and at the same branch and trunk locations as the ones for which we determined P_{50} (Table 1). Briefly, trunk P_{\min} at the base of the trees was estimated using temperature-corrected stem psychrometers (Dixon & Tyree 1984; PWS Instruments, Guelph, Ontario). Trunk P_{\min} in the upper crown was estimated using a pressure chamber (PMS, Albany, Oregon) and the bagged-shoot technique (Begg & Turner 1970). For shallow roots, P_{\min} was estimated using vulnerability curves and field values of percent loss of conductivity obtained by comparing native conductivities

of roots collected in the field with those obtained after flushing out emboli (Domec *et al.* 2004). This calculation assumed that no refilling in roots occurred during the summer. For deep roots, P_{\min} was estimated using minimum summer soil water potential measured at 40–60 cm on the same site (Warren *et al.* 2005).

Wood density (g/cm^3) was calculated on each sample tested hydraulically as the ratio of dried weight over fresh volume. Wood samples were oven-dried at 65°C for 48h, and fresh volume was determined by Archimedes' principle.

Table 1. Mean xylem pressure causing 50% loss of conductivity (P_{50}) and mean minimum *in situ* xylem pressure (P_{\min}) for root (5–7 years old), trunk and branch (5–6 years old) samples collected along the length of young and old Douglas-fir and ponderosa pine trees (mean values; $n = 5-6$).

Species Position	Nodes from top	Mean height (m)	P_{50} (MPa)	P_{\min} (MPa)
Douglas-fir				
Roots				
old trees		-0.2	-1.0	-0.7
young trees		-0.2	-1.4	-1.5
Trunk				
old trees	5	42	-4.7	-2.3
old trees	15	39	-3.6	-2.1
old trees	35	35	-3.3	-1.9
old trees	110 (base)	0.33	-3.3	-1.5
young trees	5	5.6	-3.2	-1.6
Branch				
old trees	5	42	-6.6	-2.5
old trees	15	39	-5.9	-2.3
old trees	35	35	-5.8	-2.0
young trees	5	5.6	-5.9	-2.1
Ponderosa pine				
Roots				
old trees shallow		-0.2	-1.2	-1.1
old trees deep		-0.5	-1.9	-1.0
mature trees		-0.2	-1.4	-1.0
young trees		-0.2	-0.7	-1.4
Trunk				
old trees	15	31	-3.7	-1.6
old trees	50	25	-3.2	-1.5
old trees	65	21	-3.1	-1.4
old trees	240 (base)	0.4	-3.3	-1.2
mature trees	15	8.6	-2.5	-1.8
mature trees	49 (base)	0.8	-2.9	-1.5
young trees	15	3.3	-4.1	-1.8
Branch				
old trees	15	31	-4.8	-2.0
mature trees	15	8.6	-4.6	-1.7
young trees	15	3.3	-4.5	-1.8

Light microscopy observations of tracheid dimensions

We made transverse and radial sections from each of the wood samples that had been used to produce vulnerability curves. Sections were made with a sliding microtome to 20 μm thick, and then stained with safranin-O and mounted in glycerin for image analysis using NIH Image software 1.62 (<http://rsbweb.nih.gov/nih-image>). On transverse sections, the first step was to estimate tracheid diameter distributions for calculation of mean hydraulic diameter ($D = \Sigma d^5 / \Sigma d^4$, where d = individual conduit diameter, Kolb & Sperry 1999). Inside tracheid diameters were calculated by measuring the lengths of lines drawn across the lumen. For each sample separately, six radial files of tracheids were randomly selected and all the tracheids in each file were measured in the radial direction for diameter. The use of tracheids of mean hydraulic diameter is useful because it is this segment of the tracheid population that embolizes right at P_{50} . After determining the mean hydraulic diameter for a section, we then made measurements to estimate $(t/b)^2$ for each sample as follows. The cell diameter, b , was measured on tracheids with diameters within 10% of D , and cell wall thickness, t , was measured as the distance across the double cell wall between two adjoining tracheid lumen (Hacke *et al.* 2001). About 65–80 tracheids were used to measure t and b . Transverse sections were then used to estimate latewood proportion, taken as the mean of the average latewood proportion of all the growth rings present in a sample. Radial sections were used to measure the bordered pit diameter (D_p) and the pit aperture diameter (D_a) on about 100–125 bordered pits per sample.

Resistance of cells to implosion

The critical pressure difference between adjacent cells that will cause the cells to implode (the implosion pressure) was estimated from anatomical data on all samples as described in Sperry and Hacke (2004) as:

$$P_{\text{impl}} = (W/\beta) \left(\frac{t}{b}\right)^2 Le \left(\frac{I_h}{I_s}\right) \quad (1)$$

where W is the strength of the wall material taken as 80 MPa (Hacke *et al.* 2001), β is a coefficient that depends on the ratio of b to the tracheid length and was taken at 0.25 (Young 1989), and $(t/b)^2$ is the square of the cell wall thickness to cell tangential diameter (the thickness-to-span ratio). The moment ratio, I_h/I_s , represents the ratio of the second moment of area of a wall with pit chambers (I_h) to that of a solid wall with no pit chamber present (I_s). Hacke *et al.* (2004) showed that I_h/I_s does not change with air-seeding pressure, and averages about 0.95 in conifers. The L_e is the “ligament efficiency”, which quantifies the spacing of the pit apertures in the wall, and is equal to $1 - D_a/(D_p + s)$, where s is the distance between pits or between pits and the edge of the tracheid. The value of s is very small, so L_e is mostly a function of the diameters of the pit aperture and the pit diameter ($L_e \approx 1 - D_a/D_p$). Equation 1 can be simplified and calculated as follows (Hacke *et al.* 2004):

$$P_{\text{impl}} \approx 304 \left(1 - \frac{D_a}{D_p}\right) \left(\frac{t}{b}\right)^2 \quad (2)$$

Safety factors and data analysis

For safety factors, we compared the ratio of the value that would cause xylem failure (P_{impl} or P_{50}) to the minimum summer xylem pressure (P_{min}) for that plant part and species. The safety factor for xylem failure by implosion was estimated as $P_{\text{impl}}/P_{\text{min}}$. The safety factor for xylem failure by embolism (air-seeding) was estimated as P_{50}/P_{min} , which represents the factor by which P_{50} is greater than the most negative P_{min} actually experienced. We used P_{50} as an index for the maximum pressure difference because it represents the pressure at which tracheids with diameter representing the mean hydraulic diameter embolized.

Means of anatomical and physiological data were compared within and between trees with *t*-tests at a significance level of $p = 0.05$. Statistical analyses were performed using SAS (Version 9.1, Cary, NC, USA) and curve fits (also tested at $p = 0.05$) were performed using SigmaPlot (version 9.0, SPSS Inc. San Rafael, CA, USA). Means \pm SE are cited in the text.

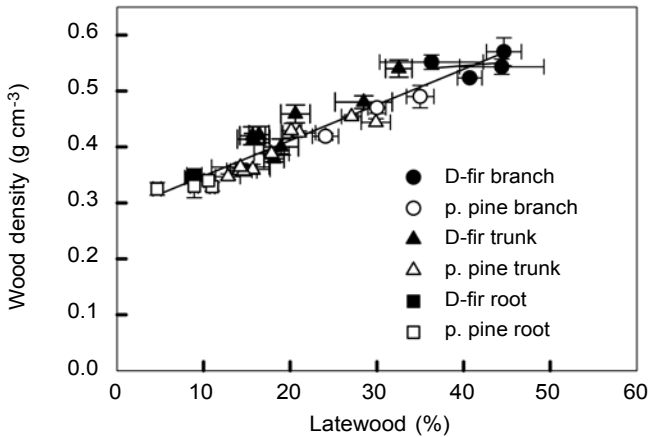


Figure 1. Wood density versus latewood percentage in root, trunk and branch samples from Douglas-fir (D-fir) and ponderosa pine (p. pine) trees. All measurements are mean \pm SE.

RESULTS

There was a strong positive correlation between latewood percentage and wood density (Fig. 1). Data for both species fell on the same line. Wood density and percent latewood were highest in branches (0.48–0.54 g/cm³ and 35–45%, respectively), and declined basipetally within the trunk and in roots (0.32–0.35 g/cm³ and 7–14%, respectively) (Table 2).

Within trees, P_{50} was more negative at the top of the trunk than at the trunk's base, which was more negative than the roots for both species (Table 1). At a given height, branches had more negative values of P_{50} than did trunks (Table 1). Across all samples, P_{50} was negatively correlated with latewood percentage ($p < 0.01$, Fig. 2a). Exclusion of the mature trunk wood samples increased the significance of the regression (thick

Table 2. Hydraulic diameter (D in μm), earlywood tracheid thickness-to-span ratio $(t/b)^2$, wood density ($Density$ in g/cm^3) and air-seeding pressure (P_{50} in MPa) in root, trunk and branch samples of Douglas-fir and ponderosa pine trees. For roots and branches, values represent the mean of the different sampling depths or heights, respectively ($n = 5-6$). The standard errors of the means are not given in the table, but they never exceeded 9%, 11% and 6% of the mean values in root, trunk and branches, respectively.

	Douglas-fir				Ponderosa pine			
	D	$(t/b)^2$	$Density$	P_{50}	D	$(t/b)^2$	$Density$	P_{50}
Roots								
young trees: juvenile wood	39	0.022	0.35	-1.4	40	0.013	0.33	-0.7
old trees: juvenile wood	38	0.017	0.34	-1.0	39	0.016	0.32	-1.5
Trunk								
young trees: juvenile wood	29	0.053	0.39	-3.2	28	0.066	0.38	-4.1
old trees: juvenile wood	26	0.059	0.42	-4.1	27	0.043	0.36	-3.5
old trees: mature wood	37	0.039	0.50	-3.3	36	0.029	0.44	-3.2
Branches								
young trees: juvenile wood	19	0.120	0.55	-6.1	25	0.087	0.47	-4.5
old trees: juvenile wood	18	0.119	0.54	-5.9	23	0.098	0.49	-4.7

regression line, Fig 2a). Within the wood samples of the trunk there was no significant relationship between P_{50} and percent latewood ($p = 0.67$).

Mean hydraulic diameter (D) decreased significantly from roots to branches ($p = 0.02$) with intermediate values for trunk (Table 2; Fig. 2b). There was also a decrease in D with increasing latewood percentage (Fig. 2b). Again, the regression became more significant when mature trunk wood samples were excluded from the regression (thick regression line, Fig. 2b). In contrast to roots and branches, D increased significantly with increasing latewood percentage ($p < 0.01$) in the trunk wood samples (dashed line, Fig 2b).

Tracheid thickness-to-span ratio, $(t/b)^2$, was positively correlated with latewood percentage (Fig. 2c). Excluding the mature trunk wood samples increased the significance of the regression (thick regression line, Fig. 2c). However, when only the trunk samples were considered, the data suggested that $(t/b)^2$ had no relationship to percent latewood ($p = 0.14$).

Across all samples, P_{50} decreased linearly with increasing wood density ($p < 0.001$; Fig. 3a) and increased linearly with D ($p = 0.02$; Fig. 3b). In both relationships, the regressions became more significant by excluding the mature-wood trunk samples (thick regression lines, Fig. 3a & b). P_{50} was independent of both wood density and D ($p > 0.85$) when data for trunk samples (Fig. 3, triangles) were considered separately.

In old trees of both species, the trunk tracheid $(t/b)^2$ increased logarithmically with height (Table 2; Fig. 4a) and decreased logarithmically with cambial age (Fig. 4b). Extrapolation to the y-axis implied a minimum $(t/b)^2$ value of about 0.032 for trunks at ground level (tree height of 0) (Fig. 4a), which would correspond to a minimum

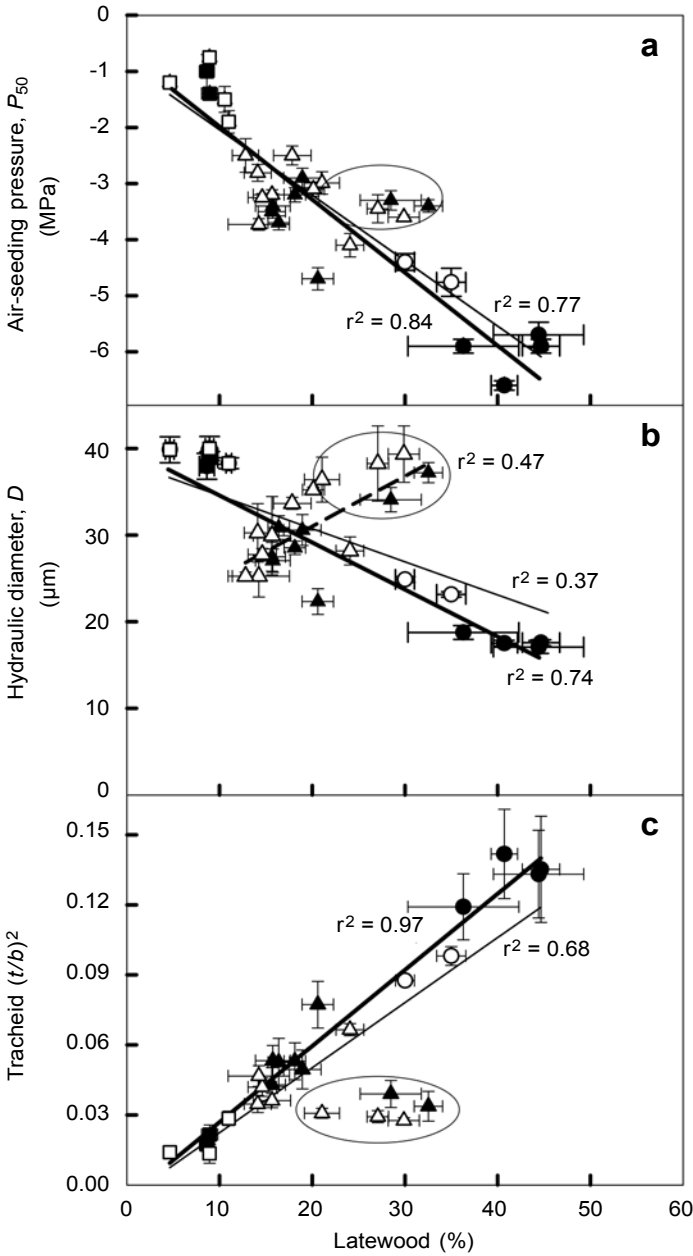


Figure 2. **a**: Air seeding pressure (pressure required to cause 50% loss of conductivity, P_{50}), **b**: mean hydraulic diameter, and **c**: the tracheid thickness-to-span ratio $(t/b)^2$ versus latewood percentage in root, trunk and branch samples from Douglas-fir and ponderosa pine trees. Symbols are as in Fig. 1. The circles encompass samples from the base of the trunks (mature wood). The thin and thick regression lines are plotted through all samples and through all samples minus mature wood, respectively. The dashed regression in **b** is plotted through trunk samples only (triangles). All measurements are mean \pm SE.

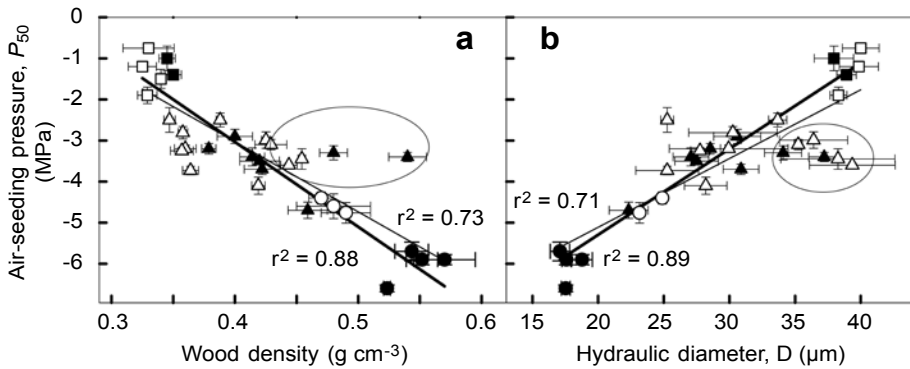


Figure 3. **a**: Pressure required to cause 50% loss of conductivity (P_{50}) versus wood density and **b**: tracheid mean hydraulic diameter (D) versus wood density in root, trunk and branch samples from Douglas-fir and ponderosa pine trees. Symbols are as in Fig. 1. Circles encompass trunk samples from mature wood. The thin and thick regression lines are plotted through all samples and through all samples

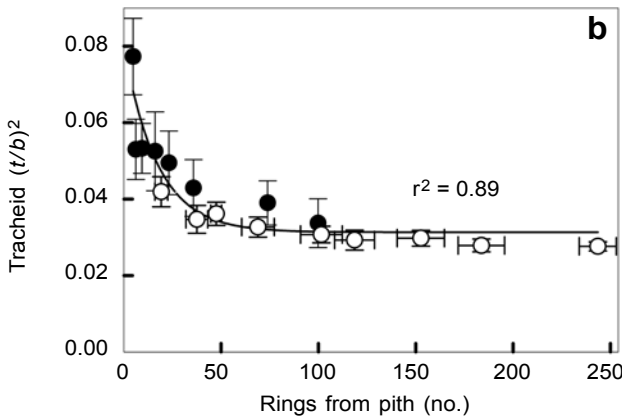
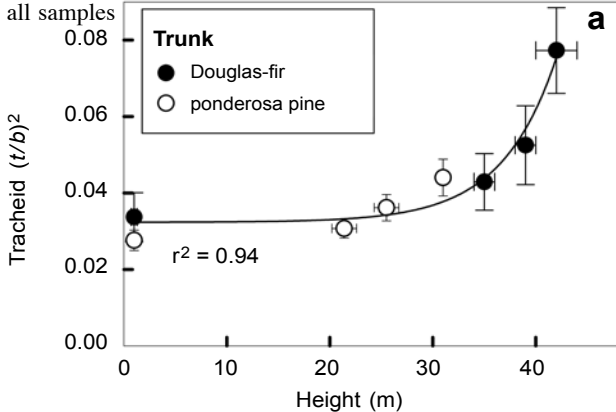


Figure 4. Tracheid thickness-to-span ratio $(t/b)^2$ in trunks in relation to **a** height, and **b** growth rings from pith in Douglas-fir and ponderosa pine trees. All measurements are mean \pm SE.

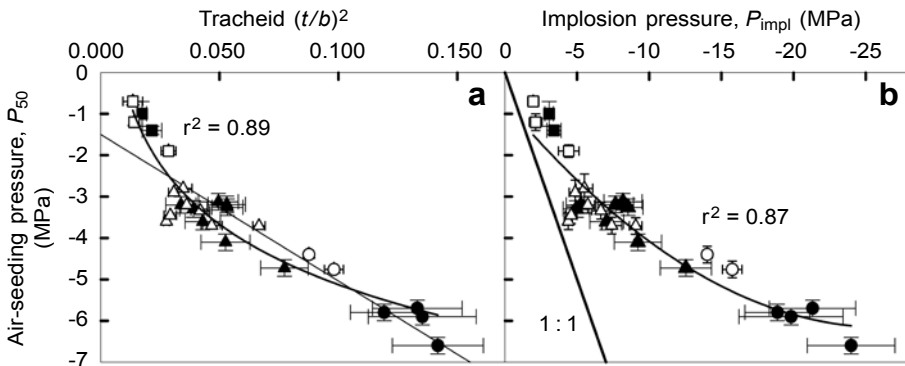


Figure 5. Pressure causing 50% loss of conductivity (P_{50}) versus **a** tracheid thickness-to-span ratio $(t/b)^2$ and **b** implosion pressure (P_{impl}) in root, trunk and branch samples from Douglas-fir and ponderosa pine trees. In **a** both logarithmic ($r^2 = 0.89$) and linear functions ($r^2 = 0.83$) are fitted to the data. Symbols are as in Fig. 1. All measurements are mean \pm SE.

trunk wood implosion pressure of 4.2 MPa (see comparison of Figures 5a and 5b). The age-dependent changes in $(t/b)^2$ were also common to both species with a logarithmic decrease to a threshold value of 0.031 (Fig. 4b).

Tracheid $(t/b)^2$ and P_{impl} were both strongly correlated with P_{50} among all types of wood samples (Fig. 5a, b). Logarithmic functions fitted to the relationships between $(t/b)^2$ and P_{50} and between P_{impl} and P_{50} yielded statistically better fits than linear relationships. Comparing the data plot in Figure 5b to the 1:1 line, one can see that the difference between P_{impl} and P_{50} increased significantly ($p < 0.02$) from roots (1–2 MPa) to trunks (2–5 MPa) to branches (10–20 MPa) (see also Table 1).

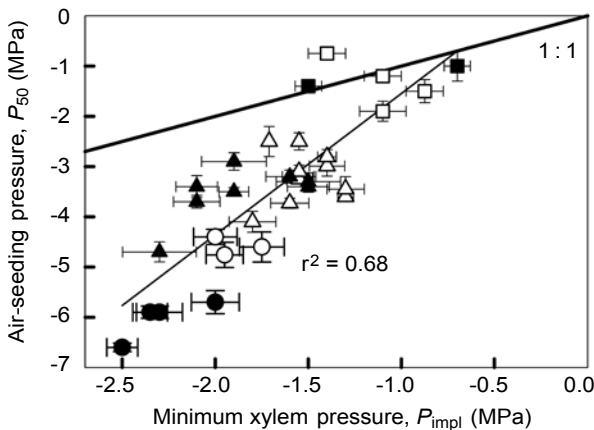


Figure 6. Pressure causing 50% loss of conductivity (P_{50}) versus mean minimum in situ xylem pressure (P_{min}). Symbols are as in Fig. 1. All measurements are mean \pm SE.

Table 3. Safety factors for hydraulic failure by cell wall implosion ($P_{\text{impl}}/P_{\text{min}}$) and by air-seeding (P_{50}/P_{min}) in root, trunk and branch samples of Douglas-fir and ponderosa pine trees. For roots and branches, values represent the mean of the different sampling depths or heights, respectively ($n = 5-6$).

	Douglas-fir		Ponderosa pine	
	$P_{\text{impl}}/P_{\text{min}}$	P_{50}/P_{min}	$P_{\text{impl}}/P_{\text{min}}$	P_{50}/P_{min}
Roots				
young trees: juvenile wood	2.3 ± 0.3	0.9 ± 0.1	1.4 ± 0.1	0.5 ± 0.1
old trees: juvenile wood	3.8 ± 0.4	1.4 ± 0.3	3.1 ± 0.3	1.2 ± 0.3
Trunk				
young trees: juvenile wood	4.8 ± 0.6	2.0 ± 0.1	5.4 ± 0.2	2.4 ± 0.2
old trees: juvenile wood	4.9 ± 0.7	2.1 ± 0.2	4.5 ± 0.3	2.2 ± 0.1
old trees: mature wood	3.5 ± 0.5	2.0 ± 0.1	3.6 ± 0.3	2.3 ± 0.1
Branches				
young trees: juvenile wood	8.6 ± 1.0	2.6 ± 0.1	8.3 ± 0.7	2.6 ± 0.2
old trees: juvenile wood	9.5 ± 1.3	2.5 ± 0.2	7.9 ± 0.2	2.4 ± 0.2

Safety factors

Within trees, actual minimum values of xylem pressures (P_{min}) experienced in field conditions were more negative in branches than in trunks, which were more negative than roots (Table 1). The relationship between P_{50} and P_{min} was similar across both species and across roots, branches, and trunks (Fig. 6). There was a linear decrease of P_{50} with decreasing P_{min} . Extrapolation to the 1:1 relationship yielded a predicted maximum P_{min} of -0.7 MPa at which point the roots would have lost 50% conductivity, which also coincided with the maximum extrapolated implosion pressure (Fig. 5b).

Within young and old trees of each species, average safety factors for implosion ($P_{\text{impl}}/P_{\text{min}}$) increased significantly ($p = 0.03$) from roots to trunk to branches (Table 3; Fig. 7a). The safety factors for implosion in the trunk wood and in the branches had similar values in Douglas-fir and ponderosa pine trees ($p < 0.04$; Fig. 7a). However, roots from young and old Douglas-fir trees exhibited higher safety factors for implosion than roots from old ponderosa pine trees ($p = 0.01$). Within each species, trunk juvenile wood safety factors for implosion did not differ significantly between young and old trees ($p > 0.3$) (Table 3). For both species, the safety factors for implosion in the trunk wood of the young trees (juvenile wood) were significantly higher ($p < 0.01$) than the ones from the base of the old trees (mature wood), but not significantly different ($p > 0.2$) than the ones at the top of the old trees (juvenile wood) (Table 3). For both species the safety factors for implosion in the branches of the young trees were not significantly different than the ones from the old trees ($p < 0.01$).

Safety factors for air-seeding (P_{50}/P_{min}) were on average half the value of safety factors for xylem implosion (Table 3). Values of safety factors for air seeding were similar between species and overall increased from the roots (values of 0.5 to 1.4) to the trunk (2.0–2.4) to the branches (2.4–2.6) (Table 3). The base of the old trees

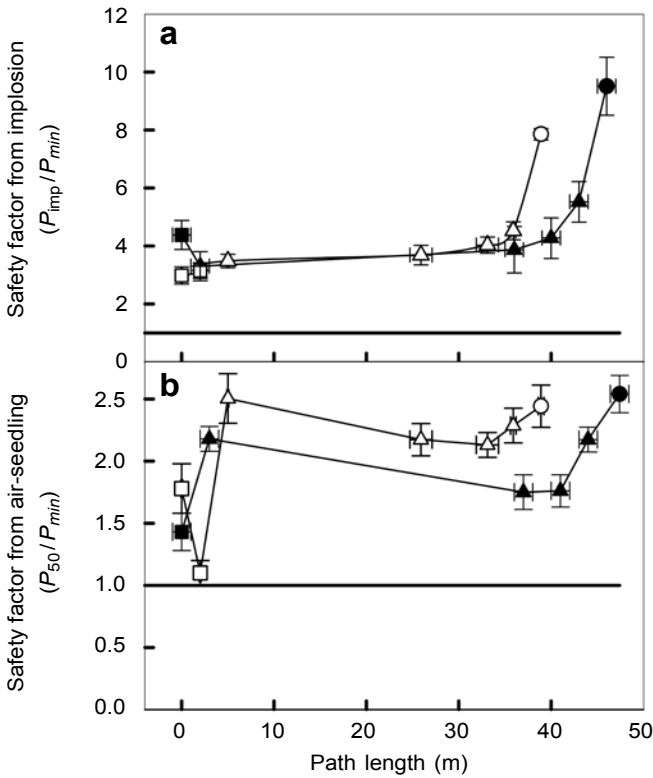


Figure 7. **a**: Safety factor for tracheid implosion (P_{impl}/P_{min}) versus path length and **b**: safety factor for air-seeding (P_{50}/P_{min}) versus path length in roots, trunk and branches from young and old Douglas-fir and ponderosa pine trees. Symbols are as in Fig. 1. The thick horizontal line corresponds to a safety factor of 1. All measurements are mean \pm SE.

(mature wood) had similar safety factors for air-seeding as the top (juvenile wood) in both species (Table 3; Fig. 7b). The hydraulic safety factors for air-seeding were significantly higher in the branches than anywhere else in the trees ($p < 0.02$), but did not differ statistically between the branches of old trees and those of young trees ($p > 0.4$, species pooled). In a comparison of young to old trees, safety factors for air-seeding did not differ significantly for trunk wood for either species ($p < 0.07$), but for root wood, the young trees had significantly lower safety factor values than did the old trees ($p < 0.02$). Safety factors for air-seeding of trunks were similar in the juvenile wood of young trees and old trees.

DISCUSSION

The results showed that from roots to branches, changing cell wall properties had predictable effects on resistance to embolism (P_{50}). This study for the first time links the variation in P_{50} to variation in the structure of tracheids among different locations

within trees of different ages for two conifer species. The structural and hydraulic demands imposed on different plant parts (roots, trunks and branches of different ages and positions) appear to affect the degree to which these different plant parts exhibit tradeoffs of xylem efficiency against safety. Moreover, the study identified safety factors for two modes of hydraulic failure that are physiologically significant over a broad range of tree size and age. The two safety factors followed similar axial trends from roots to terminal branches and had similar values for both species studied.

Structure-function relationships in juvenile wood versus mature wood

In the present study, trunks tended to differ from roots and branches in their relationships among xylem anatomical features and hydraulic and mechanical characteristics (Table 2). Similar to results of Rosner *et al.* (2008), we found that despite anatomical and structural differences with position in the trunk, there were few differences in vulnerability to embolism with increasing percent latewood, wood density or tracheid mean hydraulic diameter. However, tracheid mean hydraulic diameters in the trunk increased significantly with increasing percent latewood and wood density. One hypothesis is that the mature wood cambium produces earlywood with wide tracheids to optimize hydraulic function and also with thick latewood to optimize structural support or water storage (Domec & Gartner 2002a; Rosner *et al.* 2007). Therefore, the xylem of the trunk appears to be constructed in response to both mechanical and hydraulic demands (Gartner 1995; Jagels & Visscher 2006).

Calculations showed that trunk hydraulic safety factors were not different in juvenile and mature wood. Juvenile wood fulfills a different functional role in trees than mature wood, and apparently, below threshold P , juvenile wood maintains a higher proportion of its water transport for a given P (Mayr 2002; Domec & Gartner 2003; Rosner *et al.* 2006). In the trunk, the decrease in earlywood $(t/b)^2$ from juvenile wood to mature wood (Table 2; Fig. 4b) results from an increase in lumen diameter at an earlier cambial age than cell wall thickness (data not shown). This relative increase in cell wall thickness to cell lumen diameter in juvenile wood is consistent with why juvenile wood has lower specific conductivity (*i.e.*, Spicer & Gartner 2001) but also why juvenile wood is more resistant to air-seeding than is mature wood. Thicker secondary cell wall in the juvenile zone is associated with thicker pit chamber depth. A concomitant change is that pit membranes in juvenile wood are less flexible (more resistant to air-seeding) and less conductive than are membranes in mature wood (Domec *et al.* 2006a, 2008). As a consequence, juvenile wood has higher resistance to cell wall implosion and air-seeding but as a tradeoff has lower conductivity than mature wood (Domec *et al.* 2006a; Rosner *et al.* 2006).

Our measurements showed that the hydraulic diameter of xylem conduits decreased from roots to trunk to branches (Table 2; Fig. 2b): this general trend is in agreement with many other reports (Gartner 1995; Zobel & Sprague 1998; Spicer & Gartner 2001), although one study showed that hydraulic diameter in branches can increase with increasing height (Burgess *et al.* 2006).

The increase in sapwood conductivity attained by increasing the lumen diameter of xylem conduits in mature wood at the stem base is consistent with trees having evolved

in a manner that minimizes total hydraulic resistance for a given vascular volume (McCulloh & Sperry 2005). At the base of trees, the high conductivity associated with large conduit lumen diameter (Spicer & Gartner 2001) and very permeable pits (Dunham *et al.* 2007; Domec *et al.* 2008) partly compensates for the negative hydraulic impact of tree height, and contributes to the maintenance of leaf-specific conductivity as crown leaf area increases (Ewers & Zimmermann 1984; McDowell *et al.* 2002; Delzon *et al.* 2004). However, in contrast to studies by Martínez-Vilalta *et al.* (2002) and McElrone *et al.* (2004) but consistent with others (Dunham *et al.* 2007, 2008; Peterson *et al.* 2007) our study did not show that diameters of xylem conduits are wider in roots than at the base of the stem of the same tree. Differences in axial trends of tracheid diameter may reflect our choice of sampling locations within the trunk. When comparing root wood to trunk wood from the top of the stem, root tracheid mean hydraulic diameter is indeed larger, but if we sample lower in the trunk there is no significant difference. This result implies once again that at the base of the tree trunk, tracheid diameter can be as high as in the roots despite a lower P_{50} in the trunk than the roots.

Tradeoffs within root, trunk, and branch

In the present study, several tradeoffs between structural and functional attributes became apparent. The positive relationship between percent latewood and $(t/b)^2$ is explained by the fact that rings with lower percent earlywood (or higher percent latewood) were narrower and had fewer earlywood tracheids that were made of thicker cell walls relative to their lumen. Although wood density varied both among and within species, it was highly correlated with latewood percentage across roots to branches and in the same manner independent of species. Wood density is an integrated average of earlywood and latewood densities weighted by their respective proportion within a ring, whereas the hydraulic characteristics of the whole sample (earlywood and latewood combined) are mostly a reflection of earlywood hydraulic properties. Therefore high wood density may not necessarily be correlated with high resistance to air-seeding and to cell wall implosion. For example, Rosner *et al.* (2007) showed that in Norway spruce clones, an increase in resistance to air-seeding can be accompanied by a decrease in overall wood density and mechanical strength if the latewood percentage decreases. We propose that in conifers with a distinct earlywood to latewood transition, percent latewood (100-percent earlywood) is much more relevant than wood density for prediction of resistance to embolism and cell wall implosion because it reflects the section of the wood sample that would embolize and implode first under field conditions.

Tracheids in the roots had higher mean hydraulic diameters and lower safety factors than in the stem and branch locations studied (Table 2), and thus we predict that in these two species, variation in tracheid diameter along the tree's axis also has adaptive consequences. Between trunks and branches, and between roots and branches, tradeoffs existed such that the more distal parts were more resistant to air-seeding and to cell wall implosion (Pittermann *et al.* 2006), but at the cost of lower mean hydraulic diameter and consequently lower xylem conductivity (Domec & Gartner 2002b, 2005; Choat *et al.* 2005).

Tracheid implosion

Because $(t/b)^2$ is proportional to embolism resistance, tracheid anatomy can be used as an index of drought resistance (Hacke *et al.* 2001; Rosner *et al.* 2007). The hydraulic safety and efficiency of conifer xylem is linked strongly to the structural and mechanical properties of tracheid bordered pits (Hacke *et al.* 2004; Domec *et al.* 2006a). Pit structural features responsible for lowering P_{50} will also cause higher flow resistance and therefore steeper pressure gradients and more negative xylem pressures at a given height, assuming no other adjustments (such as stomatal closure or lower leaf area per sapwood area). These features that lowered P_{50} would then require stronger cell walls to avoid collapse. The safety factors for implosion in this research were high, up to almost 10. One interpretation of such high safety factors is that there has been strong selection pressure to avoid implosion (Pittermann *et al.* 2006), probably because contrary to air-seeding, cell wall implosion would cause irreversible hydraulic failure. The lower safety factors for air-seeding suggest that this mode of hydraulic failure is more relevant than hydraulic failure by implosion.

Trunk segmentation in relation to safety factors: trends with height

In this paper we showed that roots and trunks of young and old trees operate close to their critical point of losing half of their hydraulic conductivity by air-seeding under field conditions. In addition, the bases of the trees had significantly lower safety factors for hydraulic failure through both tracheid implosion and air-seeding than the top parts. Thus, the bottoms of the trees operate under conditions that are closer to those that will cause hydraulic failure (both by implosion and by air-seeding) than the tops.

When safety factors are defined in the manner described here as the ratio of a threshold value (*e.g.*, P_{50}) to the worst-case field value (*e.g.*, P_{\min}), the root system emerges as potentially the most vulnerable component for maintenance of xylem transport. Roots can also become hydraulically discontinuous with the soil during drought, increasing the likelihood of hydraulic failure (Sperry *et al.* 1998). However, in actuality, different plant parts in different locations will have different likelihoods of experiencing values that are closer to the threshold value than the worst-case field value. For example, roots and trunk bases are unlikely to develop the more negative xylem pressures that would cause embolism because of various buffering mechanisms related to water storage and redistribution in the soil and plant tissues (Meinzer 2003; Meinzer *et al.* 2003). In both Douglas-fir and ponderosa pine trees, hydraulic redistribution of water from deep to shallow roots mitigates seasonal increases in embolism in shallow roots (Domec *et al.* 2004), and trunk water storage plays an adaptive role in preserving whole-tree hydraulic integrity by dampening fluctuations in xylem pressure (Phillips *et al.* 2003; Domec *et al.* 2005). Alternately roots are less persistent and may regrow based on resource availability in soil. Therefore, the interpretation of 'safety factors' must be done with an understanding the likelihood of reaching the threshold values at which failure will occur.

The biomechanical demands placed on wood for support of the tree itself rather than for its role in maintaining an intact water-conducting system may also contribute to some of the observed anatomical differences found in different plant parts. In above-

ground tissues, wood density and hydraulic architecture often vary with biomechanical demands (Gartner *et al.* 1990; Gartner 1991; James *et al.* 2006), and these demands are quite different at the bottom and tops of trees. At the level of the branch and upper canopy, the stem has to resist much wind-loading (Morgan & Cannell 1987; Niklas 2006). Therefore, the overbuilding of tracheid walls to resist mechanical stresses may contribute to more negative values of P_{50} higher in the tree. In contrast, the bases of trees and their roots are not subjected to the same magnitude of mechanical stress. Bending, in particular, causes much lower surface strains near the base of the tree because of the large stem diameter, and the stiffness of the structure is also much greater simply by virtue of the large radius resulting in a large second moment of area (Gartner 2006). On the other hand, the smallest stems can bend many degrees before reaching the critical strain needed to cause snapping, but larger stems may need extra mechanical strength (Gartner 2006). These demands for bending could be related to other aspects of how cell walls are built in juvenile vs. mature wood.

We could also argue that in branches smaller tracheids with thicker walls may be the result from branch cells being subjected to lower xylem pressures and therefore lower turgor during their expansion phase (Hejnowicz 1997). It could also seem paradoxical and maladaptive that roots have a higher vulnerability to embolism causing them to operate at the threshold of xylem dysfunction by air-seeding and implosion (Fig. 6 & 7b). However, highly vulnerable roots may provide signals that cause stomata to begin conserving water, and recent studies suggest that root embolism may be more easily reversed than stem embolism (McCully 1999; Domec *et al.* 2004, 2006b).

The trends in the safety factors with height are in agreement with whole-tree safety factors for mechanical failure under realistic loading conditions (Mattheck *et al.* 1993). The safety factor for mechanical instability has been shown to decrease with tree height and several studies have reported trunk safety factors for mechanical instability of about 4 (Niklas 1989; Domec & Gartner 2002b; Peltola 2006), similar to the values reported here for the safety factor for tracheid implosion. These published values as well as our values for tracheid implosion suggest that trees are mechanically overbuilt. Ecologically, this ensures long-term persistence through varied environmental conditions to ultimately allow reproductive success.

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