

Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure

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Summary We do not know why trees exhibit changes in wood characteristics as a function of cambial age. In part, the answer may lie in the existence of a tradeoff between hydraulic properties and mechanical support. In conifers, longitudinal tracheids represent 92% of the cells comprising the wood and are involved in both water transport and mechanical support. We used three hydraulic parameters to estimate hydraulic safety factors at several vertical and radial locations in the trunk and branches: vulnerability to cavitation; variation in xylem water potential (Ψ); and xylem relative water content. The hydraulic safety factors for 12 and 88 percent loss of conductivity (S_{H12} and S_{H88} , representing the hydraulic safety factors for the air entry point and full embolism point, respectively) were determined. We also estimated the mechanical safety factor for maximum tree height and for buckling. We estimated the dimensionless hydraulic and mechanical safety factors for six seedlings (4 years old), six saplings (10 years old) and six mature trees (> 110 years old) of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).

Over the natural range of Ψ , S_{H12} decreased linearly from treetop to a minimum of 0.95 at the tree base. Young and mature trees had S_{H12} values 1.4 and 1.3 times higher, respectively, at their tips (juvenile wood) than at their bases (mature wood). Modeling analyses indicated that if trees were made entirely of mature wood, S_{H12} at the stem base would be only 0.7.

The mechanical safety factor was 1.2 times higher for the base of the tree than for the rest of the tree. The minimum mechanical safety factor—1.6 for the critical buckling height and 2.2 for the critical buckling load—occurred at the base of the live crown. Modeling analysis indicated that if trees were made only of mature wood, these values would increase to 1.7 and 2.3, respectively.

Hydraulic safety factors had values that were less than half those for mechanical safety factors, suggesting that wood structure in Douglas-fir has evolved primarily as a result of selection for hydraulic safety rather than mechanical safety. The results suggest that forest managers must consider the role of juvenile wood in tree physiology to avoid producing plantations vulnerable to drought.

Keywords: cavitation, hydraulic safety factor, juvenile wood, mature wood, mechanical safety factor, relative water content, trunk vulnerability curve, water potential.

List of symbols and abbreviations: *a*, vulnerability curve parameter; *b*, vulnerability curve parameter and pressure (MPa) at 50 PLC (Ψ_{50}); *I*, second moment of area (m^4); *k_s*, hydraulic specific conductivity (m^2); JW, juvenile wood; *L*, length of tree segment (m); *L_{cr}*, critical buckling length (m); MCS, maximum crushing strength (MPa); *M_d*, wood dry mass (g); *M_f*, wood fresh mass (g); MOE, modulus of elasticity (MPa); MOR, modulus of rupture (MPa); MW, mature wood; *P*, load (MN); *p*, branch distributed load ($MN m^{-1}$); *P_{cr}*, critical load (MN); *p_{cr}*, branch critical distributed load ($MN m^{-1}$); PLC, percent loss of conductivity; RWC, relative water content (%); RWC_{mid}, midday relative water content (%); RWC_{pd}, predawn relative water content (%); *s*, slope of the linear part of the vulnerability curve ($PLC MPa^{-1}$); S_{H12} , hydraulic safety factor for 12 PLC; S_{H88} , hydraulic safety factor for 88 PLC; S_{Mb} , buckling mechanical safety factor; S_{MBr} , branch mechanical safety factor; S_{Mh} , height mechanical safety factor; VC, vulnerability curve; *V_f*, wood fresh volume (cm^3); Ψ , xylem water potential (MPa); Ψ_{mid} , xylem midday water potential (MPa); Ψ_{pd} , predawn xylem water potential (MPa); Ψ_{12} , pressure at 12 PLC (MPa); Ψ_{88} , pressure at 88 PLC (MPa).

Introduction

Is there a tradeoff between the mechanical and hydraulic functions of wood (Gartner 1996)? The answer depends on the scale of observation. At the cellular level, there is a tradeoff. Cells specialized for high hydraulic conductivity usually have wide lumens, and thus lower density and stiffness (modulus of elasticity; MOE) than cells with narrow lumens. At the structural level, tradeoffs are apparent in the lower specific conductivity (*k_s*) and higher density and stiffness in self-supporting plants or plant parts than in lianas (Gartner 1991a, 1991b, Chiu and Ewers 1992, Rowe and Speck 1996) and by lower conductivity in compression wood than in opposite wood (Spicer and Gartner 1998a). At the tissue level, however, the hydraulic and mechanical functions of wood are not necessarily antagonistic. For example, if we examine how gymnosperm growth rings function from the pith outward, we find an

increase in both mechanical and hydraulic functions (Mencuccini et al. 1997), related to wider and longer earlywood cells, denser latewood and, often, a higher proportion of latewood near the bark (Panshin and de Zeeuw 1980, Pothier et al. 1989).

Wood produced near the pith is commonly called juvenile wood (JW), whereas wood external to JW is called mature wood (MW). An old conifer tree has a core of JW, about 10–30 rings wide from ground level to the apex, which is covered with MW in subsequent rings. Thus, at any time, the tree is producing JW at the tip and MW near the bottom. The anatomical, chemical and mechanical properties of JW are quite distinct from those of MW (see Megraw 1986 for a review). Among other features, MW is more dense, with much longer cells (Megraw 1986) and higher k_s than JW (Pothier et al. 1989, Sellin 1991, Mencuccini et al. 1997, Spicer and Gartner 2001). There are no reports comparing the vulnerability to cavitation of JW and MW.

We hypothesized that differences among parts of a tree (e.g., base, tip) in mechanical and hydraulic requirements are reflected in differences in wood structure. In particular, we suggest that large anatomical differences between JW and MW result primarily in differences in hydraulic, rather than mechanical requirements. Small differences in wood structure can result in large changes in hydraulic properties such as k_s , which scales with conduit r^4 , or vulnerability to cavitation, with little effect on mechanical properties such as structural stiffness, which is dominated by the second moment of area (I ; m^4), not material properties.

We employed a series of hydraulic experiments and hydraulic and mechanical models to test the hypothesis that trees have a higher safety factor for mechanical support than for water transport. We calculated the hydraulic safety factor from the seasonal ambient water potential inside the tree and the curves of vulnerability to cavitation. We also considered the relationship between water content and xylem embolism. We calculated the mechanical safety factor in three ways, all of which underestimated the true value. This paper represents a first attempt to combine hydraulic performance during water stress with mechanical performance to infer the selective pressures likely to have influenced the evolution of wood properties.

Materials and methods

Plant material and experimental site

We examined three age classes of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees (Table 1): 110-year-old mature trees, 10-year-old saplings and 4-year-old seedlings. The mature trees and saplings were located on the same site in the Coast Range of Oregon, USA (42°57' N, 123°21' W; elevation 220 m; mean annual precipitation 1080 mm, recorded 9 km from the study site). The seedlings, from a population of coastal-dry seed source, were grown in a well-watered outdoor nursery bed in Corvallis, OR. By felling or climbing mature trees, we obtained a vertical profile describing variation in vul-

nerability to cavitation, water storage and relative water content (RWC; %) and xylem water potential (Ψ ; MPa) with tree height.

Hydraulic specific conductivity, vulnerability and relative water content curves

We measured specific conductivity (k_s) in water-soaked samples. We expressed k_s as length squared (m^2). This unit is the direct consequence of separating the viscosity from the driving agent (water) in terms of a pressure difference. Thus, the expression is determined only by the structure of the wood and is entirely independent of the nature of the fluid. After measuring k_s in water-soaked samples, we induced embolism by applying progressively higher air pressures, each time measuring both k_s and weight (for calculation of RWC). Six 4-year-old seedlings harvested in April 1999 were sampled two nodes down from the top and the entire stem cross-section was used (note that we conducted the experiment on the wood between the nodes, not at the node itself). Six 10-year-old saplings harvested in March 1999 were sampled five nodes from the shoot apex and excised sections were used as described below. We sampled one branch per tree and used the wood > 5 cm from the branch–stem junction on the 5-year-old branch at Node 5. We selected a branch that appeared intermediate in diameter at that node. The trunks of six mature trees harvested in March 1998 (reported in Domec and Gartner 2001) were sampled at Nodes 5, 15 and 35 and at the base (Node 98) in the outer sapwood (adjacent to the cambium). We sampled Nodes 15, 35 and 98 in the inner sapwood (two growth rings from the heartwood–sapwood boundary). Three branches from each of the three mature trees (> 5 cm from the branch–stem junction) were sampled in mid-March 2000, on the 5-, 15- and 35-year-old branches at Nodes 5, 15 and 35 from the top, respectively. We collected the samples at 0600 h, immersed them in water and transported them to the laboratory. Bark was removed from small-diameter samples (all seedling and branch measurements), and samples were extracted from the larger pieces of wood with a chisel. We soaked samples under vacuum for 48 h to fill some of the embolized tracheids.

We measured initial specific conductivity ($k_{s(i)}$) on 130- to 170-mm segments and used the method described by Domec and Gartner (2001) to construct vulnerability curves (VCs) for the 10-year-old saplings. This method involved measuring the percent loss of conductivity (PLC) on segments taken directly from the trunk and saturated in water. Samples were transferred alternately between the membrane-lined pressure sleeve, required to ensure fluid did not leak from the sides of samples (Spicer and Gartner 1998b), and the double-ended pressure chamber, used to cause embolism (Salleo et al. 1992, Sperry and Saliendra 1994). The pressure chamber was initially pressurized to 0.5 MPa, and the pressure was subsequently increased in steps of 1.0 MPa to more than 95 PLC.

We calculated PLC following each pressurization of the chamber as $PLC = 100[(k_{s(i)} - k_{s(\Psi)})/k_{s(i)}]$, where $k_{s(\Psi)}$ is specific conductivity at a given pressure. We fitted hydraulic vulnerability curves by the least squares method based on a sigmoidal

Table 1. Mean values (\pm SE, $n = 6$) for morphological characteristics of young and mature Douglas-fir trees. Mature trees and saplings were sampled from the same site.

	Height (m)	Age (years)	Diameter at breast height (cm)	Sapwood area at base (cm ²)	Leaf area per tree (m ²)
Mature trees	44.7 \pm 1.3	105 \pm 5	64 \pm 2	750 \pm 98	302 \pm 82
Saplings	5.6 \pm 0.3	10 \pm 1	3.5 \pm 2.4	41 \pm 7	17 \pm 3
Seedlings	1.2 \pm 0.1	4	0.96 \pm 0.20	0.92 \pm 0.06	0.20 \pm 0.01

function:

$$\text{PLC} = \frac{100}{1 + \exp(a(\Psi - b))}, \quad (1)$$

where a indicates the slope of the linear part of the vulnerability curve and b is the potential at which 50 PLC occurred (Ψ_{50}). The pressures at 12 PLC ($\Psi_{12} = 2/a + b$) and at 88 PLC ($\Psi_{88} = -2/a + b$) were determined as described by Domec and Gartner (2001). The value Ψ_{12} , termed the air entry point (Sparks and Black 1999), is an estimate of the xylem tension at which the resistance to air entry of pit membranes within the conducting xylem is overcome and cavitation and embolism begin (Sperry and Tyree 1988). Although only a linear approximation of the true air entry point, which as shown by the VCs starts close to $\Psi = 0$, this value is useful as a basis for comparing curves. Likewise, Ψ_{88} could be termed the full embolism point, interpreted as approximating the actual tension resistance of the xylem before it becomes non-conductive.

Relative water content is the mass of water in the sample divided by the potential maximum value of water in the sample. We calculated RWC for each type of sample used in this study, on excised samples taken from the trunks and branches used to determine a VC, and from cores obtained from the trees in the field (to infer in situ cavitation). To estimate the rate of change in RWC associated with cavitation, we determined RWC initially and after each applied pressure by recording the water displacement by volume (V_f ; cm³) and the fresh mass (M_f ; g) by weight and length. Following final pressurization, we recorded the dry mass (M_d ; g) and, by using the length, back-calculated the dry mass and then calculated RWC assuming a cell wall material density of 1.53 g cm⁻³ (Siau 1984):

$$\text{RWC} = \frac{M_f - M_d}{V_f - M_d / 1.53}. \quad (2)$$

We recorded in situ vertical profiles of RWC for cores obtained in mid-September 1999 and mid-March 2000, 1 h before sunrise and at midday between 1200 and 1800 h solar time.

Trunk and leaf water potential

We estimated PLC of trees in the field from water potential (Ψ) measurements and vulnerability curves constructed in the laboratory. To estimate trunk Ψ at the base of the trees, we used temperature-corrected stem psychrometers (Dixon and Tyree 1984; PWS Instruments, Guelph, ON, Canada) installed

on the three mature trees 1.8 m above ground. The sensors were pressed tightly against the sapwood to prevent loss of contact from diurnal swelling of bark and cambium. We used a CR7X data logger (Campbell Scientific, Logan, UT) to record measurements every half hour for four consecutive days during summer (September 10–13, 1999) and three consecutive days during winter (March 15–17, 2000).

On the same three trees, we measured leaf and trunk Ψ within the crown at three heights, corresponding to Nodes 5, 15 and 35 from the top (determined from cores taken with an increment borer). We used a pressure chamber (PMS Instruments, Corvallis, OR) to measure three foliage-bearing branch cuttings per tree and per height every 15 min for 2 h at predawn (Ψ_{pd}) and 3 h at midday (Ψ_{mid}). We estimated trunk Ψ on leaves bagged in aluminum foil to prevent transpiration (Begg and Turner 1970).

From March 1998 to March 2000, we periodically measured Ψ of foliage-bearing branches with the pressure chamber. Every 4 to 6 weeks, we measured Ψ_{pd} from six randomly selected young (about 10 years old) and six mature (about 110 years old) trees from the same site and of the same general size and form as the harvested trees used to develop the VCs. We also measured the seasonal change in Ψ_{pd} and Ψ_{mid} (taken at 1300 h solar time) in the trunks and branches of six 10-year-old saplings. From March 1999 to May 2000, we used the bagged leaf techniques described previously (Begg and Turner 1970) to collect data points at Node 5. We measured Ψ_{pd} and Ψ_{mid} on the 4-year-old seedlings only once in March, June, August and September 2000, to avoid disturbing the whole plants by reducing their leaf areas.

Trunk relative water content

From wood samples tested in the laboratory, we determined the relationship between the negative of the applied air pressure and RWC. Then, based on the measured Ψ of standing trees, we estimated RWC and compared it with RWC in the field.

We determined the actual RWC of trunk wood from increment cores (12 mm in diameter) on the same days (winter and summer) and on the same three trees on which we measured trunk Ψ values. For the lowest three heights (base, Nodes 35 and 15), we split the sapwood portion of the core into two segments of equal length. We determined the heartwood–sapwood boundary visually. For the top core (Node 5), we used the entire sapwood for one measurement. We wrapped each core in plastic film and put it in a vial while we were in the tree, but we split and weighed each core (M_f) within 10 min of har-

vest. At the laboratory, we determined V_f and M_d for the cores and then calculated RWC (Equation 2). We collected the cores at predawn (RWC_{pd}) and between 1300 and 1500 h solar time (RWC_{mid}).

Because of the small diameter of their trunks, we could take increment cores only 5 mm in diameter from the 10-year-old saplings. We collected the cores on the same days we measured Ψ_{pd} and Ψ_{mid} and determined RWC as described for the mature trees. The stems of the 4-year-old seedlings were too small to core, so we harvested entire trees to measure RWC. We cut 15 trees on September 14–15, 2000. For each sample, we determined RWC on a 50-mm section of the main trunk at Node 2, counting down from the top. We determined RWC on five trees immediately after measuring Ψ_{pd} , on five trees immediately after measuring Ψ_{mid} , and on the last five trees one full day after dehydration on the laboratory bench caused Ψ to drop below -3.5 MPa. In addition, we determined the seasonal change in RWC at the base of the mature and 10-year-old sapling trunks at breast height with increment borers 12 and 5 mm in diameter, respectively. We collected cores at predawn about every 4 to 6 weeks from March 1998 to March 2000 and calculated RWC as described previously.

Wood density and the derived properties

We determined the wood density (g cm^{-3}) of each sample tested hydraulically (trunks and branches from the mature trees, saplings and seedlings):

$$\text{Density} = M_d/V_f, \quad (3)$$

where M_d is oven dry weight (dried at 105 °C) and V_f is fresh volume.

We used the density values and two sets of equations to calculate the modulus of elasticity (MOE; MPa), modulus of rupture (MOR; MPa) and maximum crushing strength (MCS; MPa). First, we calculated the lowest safety factor (the most risky) for mechanics (Niklas 1992), multiplied by 0.4 to take account of the difference between dry and green wood (Bodig and Jayne 1982; Equations 4a, 5a and 6a). Second, we used the standard equations from the Wood Handbook (Forest Products Laboratory 1987) relating mechanical properties of green wood to density (Equations 4b, 5b and 6b):

$$\text{MOE} = (5.4 \times 10^3) \text{Density}, \quad (4a)$$

$$\text{MOE} = (6.7 \times 10^3) \text{Density}^{0.81}, \quad (4b)$$

$$\text{MOR} = 39.5 \text{Density}, \quad (5a)$$

$$\text{MOR} = 44.4 \text{Density}^{1.04}, \quad (5b)$$

$$\text{MCS} = 15.6 \text{Density}, \quad (6a)$$

$$\text{MCS} = 21.1 \text{Density}^{1.02}. \quad (6b)$$

We used transverse sections stained with safranin-O to determine the latewood proportion of each sample used for the VCs. We analyzed each section (one line scan through each

sample) by means of a compound microscope, a video camera, and the image analysis software package, NIH Image Version 1.60 (W. Rasband, NIH, Bethesda, MD). We calculated the mean latewood proportion for all growth rings analyzed in a sample.

Hydraulic and mechanical safety factors

We determined the hydraulic safety factors for 12 and 88 PLC (S_{H12} and S_{H88} , representing the hydraulic safety factors for the air entry point and full embolism point, respectively) for each height:

$$S_{H12} = \Psi_{12}/\Psi, \quad (7)$$

$$S_{H88} = \Psi_{88}/\Psi, \quad (8)$$

for each time point for which we had a value of Ψ . These two safety factors represent the margin of safety at Ψ values corresponding to the onset and culmination of catastrophic xylem dysfunction. Both Ψ_{12} and Ψ_{88} are from the VCs, and Ψ was measured in the field.

To calculate the mechanical safety factor for the trunk (considered as a tapered column) of the mature trees, saplings and seedlings in buckling under their own weight (S_{Mb}), we applied the dimensionless ratio:

$$S_{Mb} = P_{cr}/P, \quad (9)$$

where P_{cr} is the critical load (MN), or maximal loading before the tree buckles or becomes structurally unstable, calculated with the Euler column formula adapted to a linearly tapered cone (Niklas 1992; see Figure 1a for details), and P is the load above each height considered (MN).

We estimated P as the sum of the fresh mass of the branches, trunk and leaves. We estimated total leaf mass by weighing one quarter of the total leaf biomass of the six mature trees harvested for our previous study (Domek and Gartner 2001), the six saplings, and the 15 seedlings used to determine RWC and Ψ . To estimate the mass of the branches, we applied a linear relationship, determined from the branches used for the vulnerability curves, between leaf fresh weight and branch fresh weight (Table 2). To calculate the dry mass of the trunk, we used the wood density and the cross-sectional area, considering a linear taper (of radius) between heights (Table 2). We calculated the mass of water as the difference between the trunk volume and the pure cell wall material volume, assuming a constant density for the cell wall material of 1.53 g cm^{-3} (Siau 1984) and void volumes of 50 and 10% for heartwood and sapwood, respectively.

We calculated a second mechanical safety factor, the height safety factor (S_{Mh}), by the dimensionless ratio:

$$S_{Mh} = L_{cr}/L, \quad (10)$$

where L_{cr} is the critical buckling length (m), or maximum height likely to be achieved before the tree buckles (Gere and Carter 1963, Niklas 1994; see Figure 1a for details), and L is

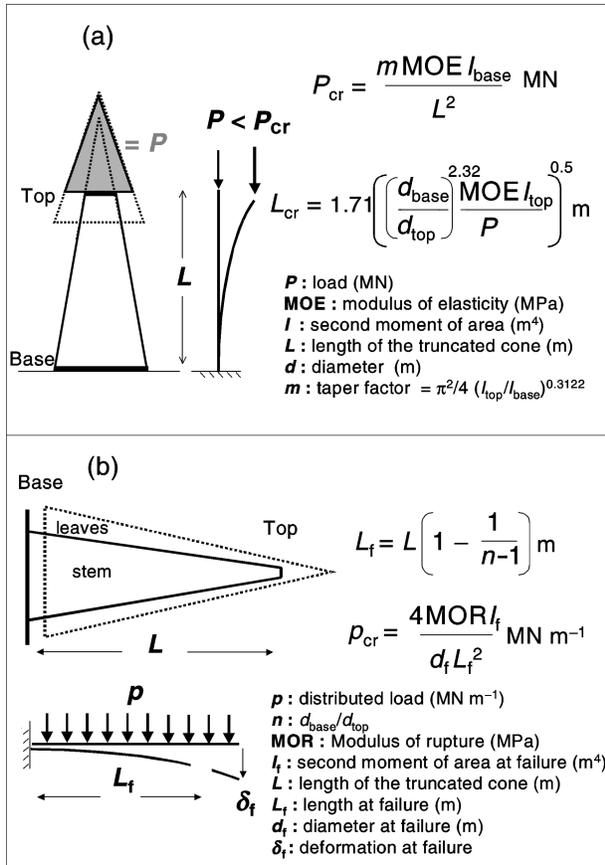


Figure 1. (a) Critical load (P_{cr}) and critical length in buckling (L_{cr}) for the trunk of mature trees and (b) critical distributed load (p_{cr}) of branches. The calculation of load (P) was corrected for the actual load of the trunk (after Bodig and Jayne 1982, Gere and Timoshenko 1984, Niklas 1992). The second moment of area for a solid circular cross section is expressed as $I = 0.25\pi r^4$.

the length (m) of the linearly tapered tree determined below each height considered. We estimated critical values P_{cr} and L_{cr} for the lowest permissible values (ranging from 63 to 73) of the slenderness ratio (height/radius) above which (calculated to be a height of 14–15 m) the Euler curve applies (Bodig and Jayne 1982, Gere and Timoshenko 1984). For the lower part of the trunk, we based critical values on the maximum load

Table 2. Parameters used to estimate branch weight, radius and the density load at each height in the tree based on six mature Douglas-fir trees sampled at four heights. Relationships used were polynomial, with either three (quadratic) or two (linear) parameters as: $ah^2 + bh + c$, where h is height in m. The relationship for the branches holds for heights above 30 m (live crown boundary). Mean branch weight was 0.98 ± 0.05 times mean leaf weight (mean of 15 branches).

	<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²
Branch weight (N)	-2.41	141.40	1611.20	0.99
Radius (cm)	0.00	-0.60	29.24	0.99
Density (g cm ⁻³)	2.18×10^{-1}	-10.91	5.30×10^2	0.99

(MCS × area) before collapse of the tree, which does not affect the conclusions, because critical values are higher in compression than in buckling.

To estimate the mechanical safety factor for individual branches subjected to their own weight (S_{MBr}), we used a third equation, the dimensionless ratio:

$$S_{MBr} = p_{cr}/p, \tag{11}$$

where p_{cr} is the critical distributed load that the branch can sustain before failure (MN m⁻¹) and p is the actual distributed load along the branch (MN m⁻¹). Because of freezing air temperatures in winter, we added an ice load (distributed over the branch length) of 3.1 g cm⁻¹ (Cannell and Morgan 1989). Using the normal stresses that occur in the cross-section of a linearly tapered beam under load (Gere and Timoshenko 1984; see Figure 1b for details) and assuming that the branches were horizontal, we calculated the failure points to be at 13 ± 2 and $55 \pm 5\%$ of the total length from the tip of the branches for the mature and sapling trees, respectively.

In a further comparison of the hydraulic and mechanical properties of JW and MW, we calculated the safety factors that would result if a tree were composed of pure JW (properties equal to those at Node 5 of the mature trees) or pure MW (properties equal to the average sapwood at the base of the mature tree). We changed the JW properties of the seedlings and saplings to the properties of the MW found at the base of mature trees.

Statistical analysis

We used least squares methods to fit relationships between hydraulic parameters and applied pressure, as well as linear and nonlinear relationships between hydraulic parameters. We determined differences in hydraulic parameters, field measurements and mechanical properties between mature trees, saplings and seedlings by means of a one-way ANOVA. To assess the difference between outer and inner sapwood at each date, we used a two-way ANOVA with one repeated measure factor. We applied paired *t*-tests specifically to compare hydraulic parameters of the branches within the mature trees. We performed all statistical procedures with Statistical Analysis Systems software (1996, SAS Institute, Cary, NC).

Results

Vulnerability and relative water content curves

Vulnerability to cavitation varied among organs and tree age classes. At applied pressures between 0 and 2 MPa, the trunks of 10-year-old saplings were less vulnerable to cavitation than the bases of mature trees. They became more vulnerable, however, at more negative applied pressures, as indicated by the slope of the curve and the xylem water potential at which 50 PLC occurred (Figure 2a, Table 3). The trunks of 10-year-old saplings and mature trees were more vulnerable to cavitation than their branches. Branches from saplings were less vulnerable to cavitation than branches from mature trees (Table 3).

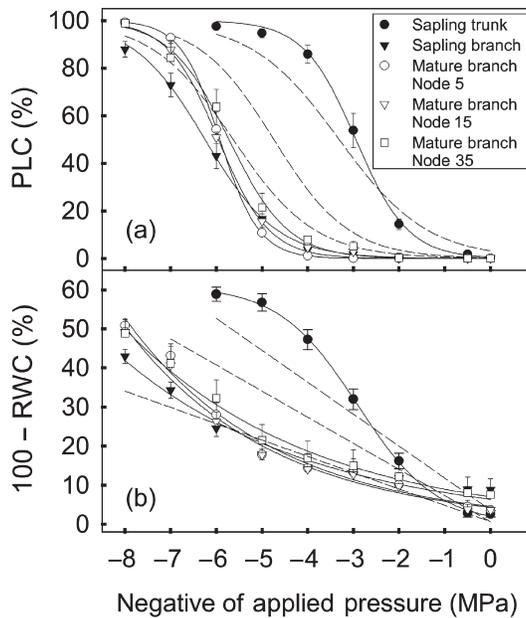


Figure 2. Relationship between the negative of air pressure used in air injection experiments and: (a) vulnerability curves for trunk and branches of 10-year-old saplings and branches of mature trees at the three nodes showing the percentage loss of xylem hydraulic conductivity (PLC); and (b) sapwood water deficit ($100 - \%RWC$). Error bars = ± 1 SE. For comparison, from left to right, the first dotted line is for the fitted trunk curve of six 4-year-old seedlings (from a nursery bed), the second dotted line is for the tops of six mature trees, and the third for the bases of six mature trees (from the same site as the 10-year-old saplings; Domec and Gartner 2001).

However, none of the parameters of vulnerability to cavitation for the three types of branches of the mature trees differed significantly from one another ($P > 0.1$). For all types of branches

combined, mean Ψ_{12} (12 PLC) and Ψ_{88} (88 PLC) were -4.7 ± 0.1 and -7.2 ± 0.2 MPa, respectively.

For 10-year-old saplings, RWC decreased sigmoidally (in the trunk) or exponentially (in the branches) as the applied pressure increased. For all but sapling trunks, RWC decreased with no associated percent loss in conductivity at applied pressures from 0 to at least -2 MPa (Figure 2b). The RWC–applied pressure relationships did not differ significantly between branches of mature trees and branches of 10-year-old saplings ($P > 0.1$) (Table 3).

Field measurements and hydraulic safety factors

In mature trees, trunk water potential (Ψ) decreased linearly from base to apex (Figure 3a). For the winter predawn measurements, the slope of the curve of Ψ versus height did not differ significantly from the hydrostatic slope ($P = 0.51$). There was no significant difference between the winter slopes taken at predawn and those taken at midday ($P = 0.36$). In summer, the slopes for the predawn and midday values were 39 and 46% higher than the hydrostatic gradient, respectively ($P < 0.04$), but did not differ significantly from one another ($P = 0.82$).

Like Ψ , RWC decreased seasonally from tree base to apex, but unlike Ψ , the decrease was nonlinear (Figure 3b). The mean daily change in RWC ($8.2 \pm 0.4\%$) for the summer measurements was comparable with the total change ($7.2\% \pm 0.5\%$) between winter and summer predawn values (Table 4). Estimated RWC (Figure 3b), based on water potential measurements and the relationships between PLC and RWC (Table 3), fit well with the measured summer predawn water potential. For midday, the estimated RWC values fit well only for the base of the trees. For the tops of the trees, the values underestimated measured RWC by 11–12% for Nodes 5, 15 and 35. For the saplings and seedling trees, estimated RWC based

Table 3. Mean parameters (\pm SE) describing the percent loss of conductivity (PLC), sapwood water deficit ($100 - \%RWC$) and function type used to fit the sapwood water deficit parameters in trunk and branches in three age classes of Douglas-fir. The vulnerability parameters were fit using the least squares method based on a sigmoidal function (see Equation 1 and text for details). Parameter s represents the slope of the linear portion of the vulnerability curve ($s = a25$) and b is the potential at which 50 PLC is reached (Ψ_{50}). Values with different letters within a column are significantly different at $P < 0.05$.

Sample type	Nodes from top	Vulnerability curves		RWC curves		
		s (PLC MPa ⁻¹)	b (MPa)	α	β	Function type
<i>Trunks</i>						
Four-year-old seedlings ¹	2	29.7 \pm 3.2 ab	-5.6 \pm 0.2 a	-4.2 \pm 0.3 a	14.7 \pm 1.7	$\alpha\Psi + \beta$
Ten-year-old saplings	5	43.7 \pm 4.7 cd	-2.9 \pm 0.1 b	1.2 \pm 0.1	-2.9 \pm 0.1	$61/(1 + e^{\alpha(\Psi-\beta)})$
Mature trees ¹	5	30.4 \pm 4.4 ab	-4.7 \pm 0.2 c	-6.7 \pm 0.3 b	0.6 \pm 1.4	$\alpha\Psi + \beta$
Mature trees ¹	15	33.7 \pm 3.9 ab	-3.6 \pm 0.2 d	-8.7 \pm 0.5 c	0.5 \pm 1.8	$\alpha\Psi + \beta$
Mature trees ¹	35	33.0 \pm 3.9 ab	-3.3 \pm 0.2 d	-9.4 \pm 0.6 c	0.3 \pm 1.9	$\alpha\Psi + \beta$
Mature trees ¹	98 (base)	25.9 \pm 3.9 a	-3.3 \pm 0.2 bd	-7.8 \pm 0.3 d	3.9 \pm 1.3	$\alpha\Psi + \beta$
<i>Branches (4-year-old)</i>						
Ten-year-old saplings	5	31.8 \pm 4.4 a	-6.3 \pm 0.2 e	-2.3 \pm 0.1 e	6.4 \pm 0.5	$\beta e^{\alpha\Psi/10}$
Mature trees	5	57.9 \pm 6.8 c	-5.9 \pm 0.1 a	-3.1 \pm 0.1 f	4.5 \pm 0.7	$\beta e^{\alpha\Psi/10}$
Mature trees	15	41.8 \pm 3.2 cd	-5.9 \pm 0.1 a	-3.1 \pm 0.2 f	4.3 \pm 0.6	$\beta e^{\alpha\Psi/10}$
Mature trees	35	35.7 \pm 3.0 bd	-5.8 \pm 0.2 a	-2.5 \pm 0.1 e	7.0 \pm 0.5	$\beta e^{\alpha\Psi/10}$

¹ Parameters taken from Domec and Gartner (2001).

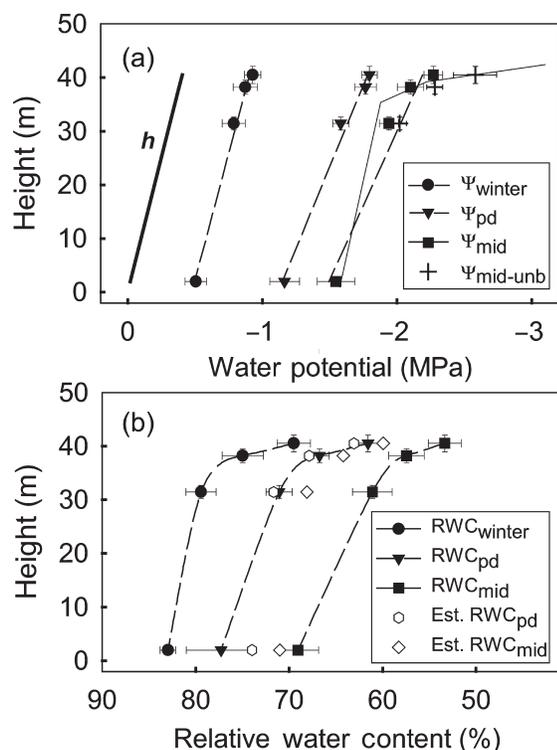


Figure 3. Height in mature Douglas-fir trees versus (a) trunk water potential and (b) relative water content (mean of outer and inner sapwood). Values are for winter (Ψ_{winter} , $\text{RWC}_{\text{winter}}$), summer predawn (Ψ_{pd} , RWC_{pd}) and summer midday (Ψ_{mid} , RWC_{mid}). In (a), the thick solid line, the thin solid line and the crosses represent the theoretical hydrostatic gradient ($h = 0.01 \text{ MPa m}^{-1}$, plotted through the origin), the potential at which 12 PLC occurred and the water potential for summer midday data of unbagged leaves ($\Psi_{\text{mid-unb}}$), respectively. In (b), the open hexagons (Est. RWC_{pd}) and open diamonds (Est. RWC_{mid}) are for estimated RWC based on the summer predawn and summer midday water potential data, respectively, and the relationships described in Table 3. Error bars = $\pm 1 \text{ SE}$.

on Ψ was within 5% of the measured RWC (data not shown).

Seasonal predawn water potentials (Ψ_{pd}), measured at breast height, showed a 1.0 MPa change between the least negative values (winter) and the most negative values (after 2 months without rain) in both mature and young trees (Table 4). The minimum leaf water potential ($\Psi_{\text{mid-unb}}$) measured on young trees never fell below -2.2 MPa , and the difference between $\Psi_{\text{mid-unb}}$ and estimated trunk water potential (Ψ_{mid}) remained constant at around -0.3 MPa (Figure 4). Relative wa-

ter content was always lower for the inner sapwood of the mature trees than for the outer sapwood ($P < 0.035$, Figure 4). The sapwood water deficit ($100 - \% \text{RWC}$) was related linearly to Ψ for all sample types (Table 5), which included outer and inner sapwood samples of mature trees, young saplings and seedlings.

For the mature trees, the base and Node 35 were more vulnerable to cavitation than Nodes 15 and 5 (Figure 5a). The vulnerability curves and measured Ψ implied that large variations in trunk xylem embolism occurred throughout the season for both the base and the base of the live crown (Node 35). At Node 35, estimates of maximum (late September) and minimum (mid-March) xylem embolisms during the season were 32 and 10 PLC, respectively (data not shown). The tops of mature trees never experienced more than 6 PLC; the 10-year-old saplings and 4-year-old seedlings never experienced more than 9 and 3 PLC, respectively.

The hydraulic safety factor for 12 PLC ($S_{\text{H}12}$) at the top of a mature tree was 41% higher than at the base of the live crown ($P < 0.05$) and 33% higher than at the stem base (Figure 5b, Table 6) ($P < 0.05$). The $S_{\text{H}12}$ was significantly higher in the branches than in the trunk ($P < 0.05$), but did not differ statistically between the branches of mature trees and those of 10-year-old saplings ($P > 0.16$).

The pooled data from the 4-year-old seedlings, the 10-year-old saplings and the four heights in the mature trees (for both inner and outer samples) showed an increase in k_s with mean number of rings from the pith (cambial age) for both inner and outer sapwood (Figure 6a).

Mechanical safety factors

Wood density increased by 18% from the pith to the outer growth rings, corresponding to a decrease of 18% between the bottom and the top of the mature tree (Figure 6b). There was a strong linear relationship between percent latewood and wood density for trunks of mature trees (Figure 6b):

$$\text{Percent latewood} = 123.54\text{Density} - 32.46 \quad (12)$$

$$(r^2 = 0.95, P < 0.001).$$

By combining all sample types (mature trees, saplings, seedlings and branches), we obtained the relationship:

$$\text{Percent latewood} = 162.18\text{Density} - 47.9 \quad (13)$$

$$(r^2 = 0.93, P < 0.001).$$

Table 4. Mean ($\pm \text{SE}$) water potential (Ψ) and relative water content (RWC) in the trunks of 4-year-old seedlings, 10-year-old saplings and mature trees at breast height. Winter and summer values were measured in mid-March and mid-September, respectively.

	Winter ¹		Summer predawn		Summer midday	
	Ψ (MPa)	RWC (%)	Ψ (MPa)	RWC (%)	Ψ (MPa)	RWC (%)
Four-year-old seedlings	-0.67 ± 0.04	86.7 ± 0.5	-1.90 ± 0.10	75.8 ± 4.4	-2.35 ± 0.15	64.9 ± 4.2
Ten-year-old saplings	-0.54 ± 0.04	81.4 ± 3.5	-0.87 ± 0.07	70.6 ± 4.0	-1.58 ± 0.09	63.0 ± 3.7
Mature trees	-0.51 ± 0.08	83.9 ± 0.9	-1.16 ± 0.11	77.3 ± 3.7	-1.55 ± 0.14	69.1 ± 2.3

¹ Because predawn and midday winter values were not significantly different ($P < 0.05$), the mean of the two measurements is given.

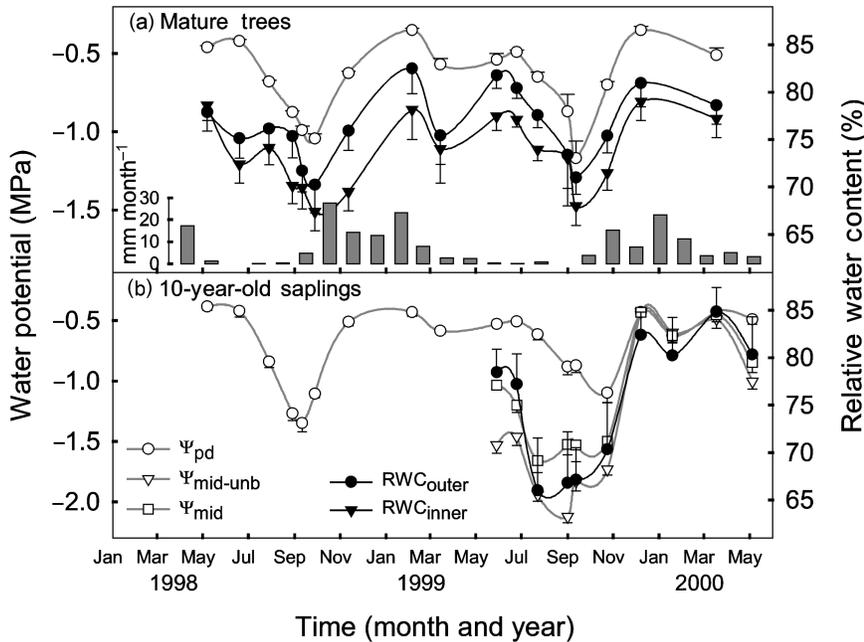


Figure 4. Temporal change in water potential and relative water content (RWC) for (a) mature and (b) young Douglas-fir trees over two consecutive years at breast height. Symbols: ● = RWC for the outer sapwood; ▼ = RWC for the inner sapwood; ○ = water potentials for predawn unbagged leaves (Ψ_{pd}); □ = water potentials for midday bagged leaves (Ψ_{mid}); and ▽ = water potentials for midday unbagged leaves ($\Psi_{mid-unb}$). Histograms represent the monthly precipitations recorded 9 km from the study site. Error bars = ± 1 SE.

Because MOE and MOR both scaled by a factor of about 1 (Equations 4 and 5), they followed similar patterns (data not shown). This decrease in wood density, along with the actual taper and load distribution with height, was associated with a 19% decrease in minimum S_{Mh} (mechanical safety factor for height) calculated along the trunk (Figure 7).

Minimum S_{Mh} ranged from about 1.5 in mature trees to 5.0 in 10-year-old saplings (Table 7). Minimum S_{Mb} (mechanical safety factor in buckling for trunk) ranged from about 2.0 in mature trees to 10.0 in 10-year-old saplings. Minimum S_{MBr} (mechanical safety factor for branch) ranged from 3.2 in 10-year-old saplings to 4.8 in mature trees under their own load and from 2.0 in 10-year-old saplings to 3.5 in mature trees under ice load. For mature trees, the lowest values of S_{Mh} and S_{Mb} were found between heights of 29 and 31 m (71% of tree height; Figure 7).

Tradeoffs between juvenile wood and mature wood

All sample types (trunks and branches from 4-year-old seed-

Table 5. Slopes (a) and intercepts (b) of the linear regressions of sapwood water deficit (100 - %RWC) versus the water potential (Ψ) measured in the field for mature trees, 10-year-old saplings and 4-year-old seedlings (100 - %RWC = $a\Psi + b$, $P < 0.001$ in every case).

	a	b	r ²
Mature trees			
Outer sapwood	-10.13	13.58	0.76
Inner sapwood	-10.20	16.48	0.73
Ten-year-old saplings	-13.85	9.65	0.90
Four-year-old seedlings	-5.19	10.74	0.84

lings, 10-year old saplings and mature trees) showed an inverse relationship between low values of k_s ($< 4 \times 10^{-12} \text{ m}^2$), which represent branches and JW, and S_{H12} (Figure 8). At higher values of k_s , S_{H12} was constant at about 1, meaning that the plant parts with high k_s , or MW, operate at the point of incipient xylem cavitation.

A change from JW to MW at the top of the tree would decrease S_{H12} by 49% and result in values lower than unity (Table 6). A change from JW to MW would lower the S_{H12} of the 10-year-old saplings and 4-year-old seedlings by 13 and 60%, respectively. The minimum values for mechanical safety factors were relatively insensitive to whether a tree is composed of juvenile or mature wood. The minimum values of S_{Mh} and S_{Mb} for pure MW were 10 and 16% higher, respectively, than for pure JW (Table 7). The change from MW to JW at the base of the tree would decrease the minimum mechanical safety factor by 14%, but would increase the minimum hydraulic factor by 98% (Tables 6 and 7).

By limiting each modeling analysis to one type of wood, we determined strong relationships between wood density and hydraulic parameters (Table 8). Within JW, the relationship was strong for k_s , S_{H12} and S_{H88} . Within MW, the relationship was strong for S_{H88} only.

Discussion

Tradeoffs between hydraulic and mechanical properties of wood

We conclude that large radial variation in the wood anatomy of trees is primarily an adaptation to hydraulic rather than mechanical requirements for the following three reasons. First, hydraulic safety factors for 12 PLC (S_{H12}), which represents the point of air entry described by Sparks and Black (1999),

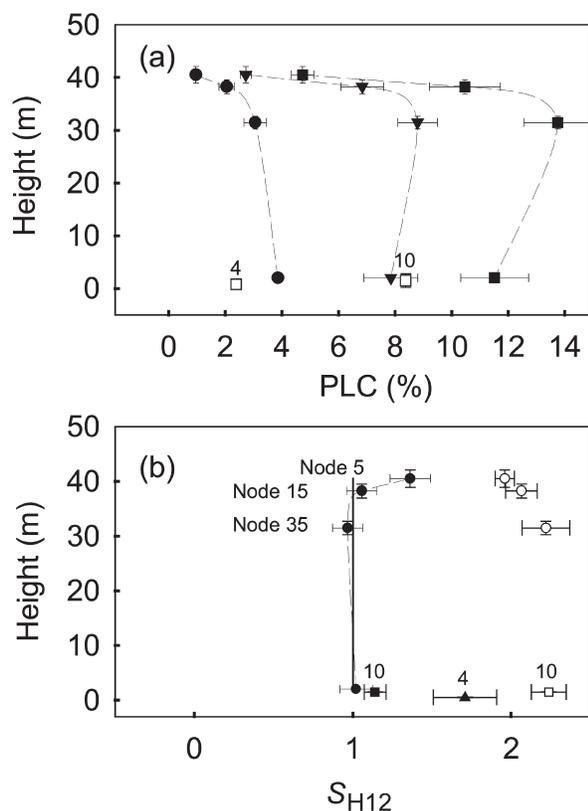


Figure 5. (a) Height in mature Douglas-fir trees versus (a) percent loss of conductivity (PLC), and (b) hydraulic safety factor for 12 PLC (S_{H12}). The vertical line represents $S_{H12} = 1$. The numbers 4 and 10 denote the 4-year-old seedlings and 10-year-old saplings, respectively. Symbols: (a) ●, ▲ and ■ = winter, summer-predawn and summer-midday values, respectively, for trunks of mature trees, and □ = summer-midday values for saplings and seedlings; (b) ▲, ■ and ● = trunks of seedlings, saplings and mature trees, respectively, and □ and ○ = branches of saplings and mature trees, respectively. Error bars = ± 1 SE.

were lower than mechanical safety factors. Second, the hydraulic safety factor was close to unity, indicating that variation in this parameter will likely impact survival. Third, reciprocal modeling of JW and MW properties showed much larger changes with wood type in hydraulic safety factors than in mechanical safety factors; in particular, S_{H12} would be < 1 at the treetop if the tree were composed only of MW (Tables 6 and 7).

The inverse relationship between hydraulic safety and k_s shows that JW, which is best able to buffer water deficits, has a lower k_s than MW (Figure 8). Thus, if trees had JW throughout their trunks, they would need a larger sapwood area to maintain the same water flux for a given water potential gradient. Increased sapwood area would mean an increase in the number of parenchyma cells (Gartner et al. 2001) and, hence, respiration (Pruyn et al. 1999).

Trees cannot produce MW throughout their trunks, however, because this would cause them to fail hydraulically at the tip (Table 6). Mature wood located at the treetop would experience a Ψ sufficiently low to cause embolism (Figure 3a). Ap-

parently, however, this high negative Ψ does not result from the hydrostatic gradient alone or from resistance of the water path. Eventually, in an older taller tree, MW occurs at the height of the JW discussed previously. In addition, resistance would be lower, not higher, if the wood were MW rather than JW (Figure 6a). The high negative Ψ in the wood at the treetop therefore must result from the dynamics of water flow. The delivery of water during periods of high transpiration cannot always keep up with demand at the top of the tree (Phillips et al. 2002).

The tradeoffs between hydraulic and mechanical properties of wood indicate that, within JW (also true if we include the branches), high density is associated with low k_s , and also with high S_{H12} and S_{H88} (Table 8); i.e., JW can be safe hydraulically and mechanically at the same time. In theory, high values of k_s and stiffness could result simultaneously from changes in both percentage of latewood (De Kort 1993) and tracheid diameter of earlywood (Calkin et al. 1986). Therefore, within JW, if there is a tradeoff, it might not be found in the maintenance of high k_s . In the field and during a drought, young seedlings and leaders of mature trees must react rapidly to changes in evaporative demand and water availability, so the ability to buffer the environment through low vulnerability to embolism is an adaptive trait. If JW allows a tree to resist low water potentials, then selection for early MW production could make trees more vulnerable to drought. Eliminating JW formation by over-watering in a nursery could result in increased mortality of planted stock.

Water storage capacity of the trunk

In winter, the slope of the relationship between water potential (Ψ) and trunk height of the mature trees followed the hydrostatic gradient (Scholander et al. 1965, Zimmermann 1983) both at predawn and at midday when there was no transpiration, but the slope was steeper than the hydrostatic gradient during the summer at predawn and midday when there was transpiration. This result contrasts with observations made in summer in Douglas-fir trees at Wind River, Washington, where Ψ returned to values predicted from the hydrostatic gradient by the predawn measurements (Bauerle et al. 1999). We note that the trees studied by Bauerle et al. (1999) were older (average age > 450 years old) than the trees we studied and their site was wetter than ours (2000 versus 1000 mm precipitation per year). At our site, cuticular water loss and water movement in the trunk could have occurred at night during the summer.

Water potential at the top of the trunk was 0.25 MPa (predawn) and 0.34 MPa (midday) more negative than the hydrostatic gradient alone (Figure 3a). Considering overnight friction and the difference between both intercepts of the slope with abscissas (Figure 3a), only 0.45 MPa accounted for the actual transpiration of the tree, which gives a gradient of about 0.01 MPa m^{-1} , comparable with data from studies described by Hellkvist et al. (1974). The steeper predawn slope compared with the hydrostatic slope could explain why estimated Ψ based on RWC did not coincide with Ψ measured at predawn at the bases of mature trees and with Ψ measured during the

Table 6. Percent loss of hydraulic conductivity (PLC), the potential at which 12 PLC occurred (Ψ_{12}), and hydraulic safety factors (S_{H12} and S_{H88}), modeling only one type of wood for each type of Douglas-fir tree trunk (either pure juvenile or pure mature wood). For the mature trees, we also modeled the difference between the top and the bottom of the tree. Values in boldface represent measured values in natural conditions; all other values are modeled.

		PLC (%)	Ψ_{12} (MPa)	$S_{H12} = \Psi_{12}/\Psi$	$S_{H88} = \Psi_{88}/\Psi$
<i>Mature trees</i>					
Pure juvenile wood	Top of the tree	3.45	-3.09	1.36	2.81
	Base of the tree	2.01	-3.09	2.00	4.13
Pure mature wood	Top of the tree	23.75	-1.57	0.69	2.25
	Base of the tree	13.90	-1.57	1.01	3.30
<i>Ten-year-old saplings</i>					
Pure juvenile wood		8.37	-1.80	1.14	2.59
Pure mature wood		12.88	-1.57	0.99	3.21
<i>Four-year-old seedlings</i>					
Pure juvenile wood		2.68	-3.93	1.71	3.17
Pure mature wood		30.72	-1.57	0.68	2.21

day at the tops of mature trees, whereas these values fit well for the small trees (Figure 3b). Nightly recharge of the trunk would cause RWC to fall below the value expected for the tree-top during the day and exceed the value expected for the base during the night (Waring and Running 1978). Such an over-

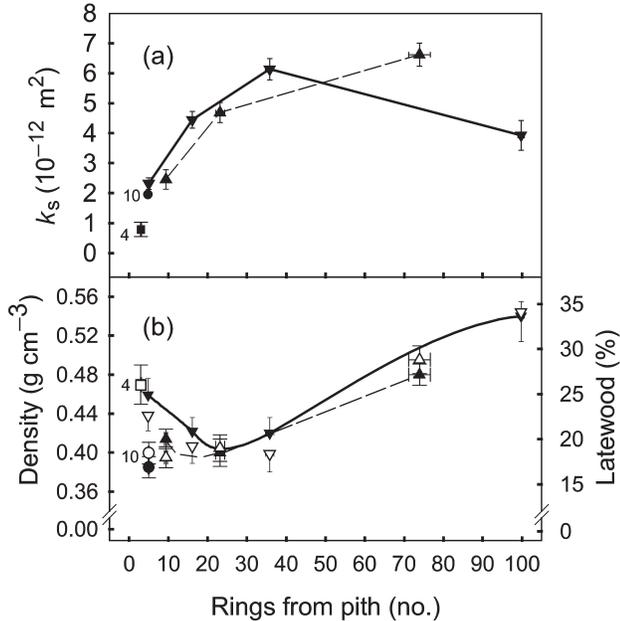


Figure 6. (a) Hydraulic specific conductivity (k_s) of Douglas-fir trees measured at full water saturation versus the number of rings from the pith in the outer (∇) and inner (\blacktriangle) samples of trunks of mature trees and from trunks of 10-year-old saplings (\bullet) and 4-year-old seedlings (\blacksquare). (b) Wood density and % latewood versus the number of rings from the pith. Open symbols = wood density, closed symbols = % latewood; outer (∇ , \blacktriangledown) and inner (Δ , \blacktriangle) samples from trunks of mature trees and from trunks of 10-year-old saplings (\circ , \bullet) and 4-year-old seedlings (\square , \blacksquare). The numbers 4 and 10 denote the 4-year-old seedlings and 10-year-old saplings, respectively. Error bars = ± 1 SE.

night gradient could help recharge the upper branches and the trunk. Predawn Ψ at the base of the mature tree was 0.30 MPa lower than that in the 10-year-old saplings (Table 4), indicating that some water movement took place at the base of the trunk (assuming that the young trees were in equilibrium with the soil Ψ). The daily change in RWC of the trunk also indicates that studies measuring water storage and the time constant for water transport by instantaneous difference between the total sap flow recorded at the base and at the top of the tree could underestimate the global capacitance of the tree bole (Loustau et al. 1996, Phillips et al. 1997), because these studies assume a complete nightly recharge of the trunk and no diurnal hysteresis.

The seasonal change in RWC was about 20% in both mature

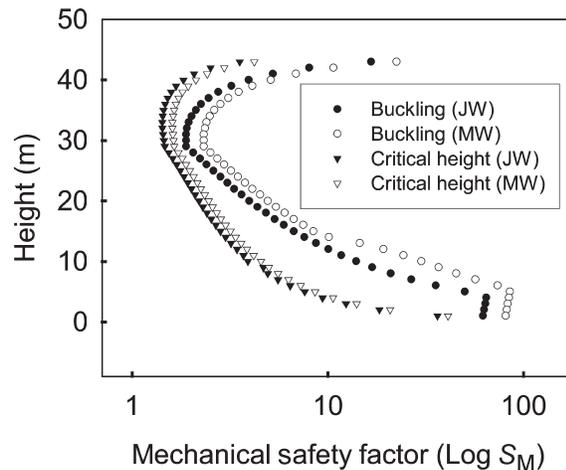


Figure 7. Mechanical safety factors by height for the critical height (∇ , \triangledown) and for the critical buckling load (\bullet , \circ) on a logarithmic scale. A 45-m tree was modeled either as pure juvenile wood (JW) or pure mature wood (MW); the actual case (a mixture of JW and MW) would lie between the open and closed symbols.

Table 7. Wood density (g cm^{-3}) and minimum, mechanical safety factors expressed on a height basis (S_{Mh}), on a buckling basis (S_{Mb}) for the trunks, and on a bending basis (S_{MBr}) for the branches under static loading. For the trunks, values are listed for wood modeled as pure juvenile wood or pure mature wood. Values in boldface represent measured values in natural conditions; all other values are modeled.

Type of wood modeled	Density (g cm^{-3})	S_{Mh}^1	S_{Mb}^1	S_{MBr}^2
<i>Mature trees</i>				
Pure juvenile wood	0.42 ± 0.01	1.54 (1.86)	2.01 (2.93)	
Normal	0.42–0.51	1.55 (1.87)	2.17 (3.17)	
Pure mature wood	0.51 ± 0.02	1.68 (1.98)	2.33 (3.25)	
<i>Ten-year-old saplings</i>				
Normal	0.39 \pm 0.03	4.31 (5.31)	9.88 (11.96)	
Pure mature wood	0.51 ± 0.01	5.01 (5.91)	9.97 (13.87)	
<i>Four-year-old seedlings</i>				
Normal	0.47 \pm 0.03	1.81 (2.17)	3.94 (5.52)	
Pure mature wood	0.51 ± 0.02	1.88 (2.22)	4.27 (5.98)	
<i>Branches</i>				
Mature tree, Node 35	0.56 ± 0.01			4.81 (3.46)
Mature tree, Node 15	0.56 ± 0.02			4.25 (3.25)
Mature tree, Node 5	0.51 ± 0.01			3.46 (2.80)
Ten-year-old saplings, Node 5	0.55 ± 0.02			3.23 (2.02)

¹ The most risky (lowest) values calculated with Equations 4–6. Values in parenthesis were calculated with equations from the Forest Products laboratory (1987).

² Values in parenthesis are for branches carrying ice load.

trees and young saplings, comparable with findings by Waring et al. (1979), but only half the values reported in most studies on the same species from wetter sites (Chalk and Bigg 1956, Waring and Running 1978). The outer sapwood of mature trees had higher RWC than the inner sapwood on most dates. That RWC decreases toward the pith suggests that the older sapwood becomes, the harder it is to refill following cavita-

tion. This interpretation is consistent with the steeper slopes found between Ψ and RWC for the lower parts of the trunks (base and Node 35) compared with the young trees and the tops of the mature trees (coefficient α in Table 3). A structural basis for this hypothesis could be related either to tracheid morphology or to the lower wood density in JW than in MW (Abdel-Gadir and Krahmer 1993).

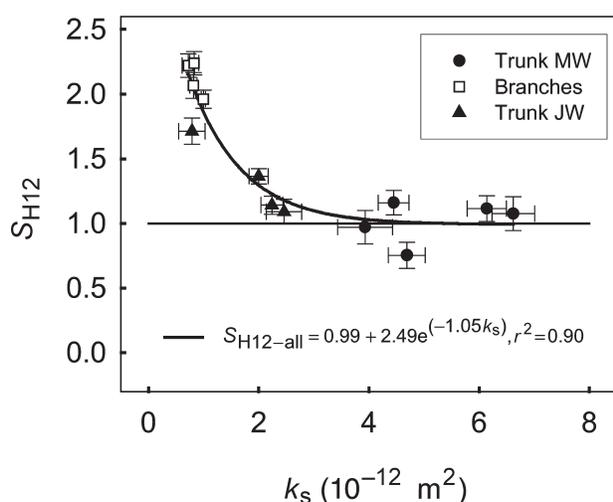


Figure 8. Hydraulic safety factor for the air entry point (S_{H12}) versus the hydraulic specific conductivity (k_s) for all types and for the three age classes of trees sampled (branches of 4-year-old seedlings, 10-year-old saplings and mature trees). The best fitted regression ($P < 0.01$) for all samples combined ($S_{H12-all}$) is shown. The horizontal line represents $S_{H12} = 1$. Error bars = ± 1 SE.

Patterns in, and structural basis for, differences in hydraulic properties among plant parts

The JW in young trees had the same k_s as same-aged tips of mature trees (Figure 6a). We know of no other data comparing these locations. Within individual trees, JW had lower k_s than MW. If we define JW as samples with ≤ 20 rings from the pith and MW as samples with ≥ 35 rings from the pith (Abdel-Gadir and Krahmer 1993), the k_s of JW was $11 \pm 1\%$ lower than that of MW ($P < 0.001$). Comparable differences in k_s between JW and more mature wood have been reported in 28-year-old radiata pine (*Pinus radiata* D. Don) (Booker and Kininmonth 1978) and 34-year old Douglas-fir (Spicer and Gartner 2001). The same pattern is also suggested by studies comparing k_s at the same height in the trunk of trees of different ages (Pothier et al. 1989, Mencuccini et al. 1997).

Following the same pattern as k_s , S_{H12} and S_{H88} in JW of young trees was the same as in same-aged tips of mature trees (Table 6). Within individual trees, JW had higher S_{H12} than MW, with the lowest value at the base of the live crown. The low S_{H12} values under the live crown were strongly correlated with high k_s (Figure 8). Between the base of the live crown and the tree base, S_{H12} was close to unity, suggesting that the main trunk of the tree was functioning close to the point of cata-

Table 8. Slopes and intercepts (in parenthesis) of the linear regressions of hydraulic conductivity (k_s), the hydraulic safety factors for 12 PLC (S_{H12}) and the hydraulic safety factors for 88 PLC (S_{H88}) versus wood density. Based on the number of rings by which the wood was separated from the pith (or cambial age), data are presented for juvenile wood (JW or samples ≤ 20 rings from the pith including branches), mature wood (MW or samples with ≥ 35 rings) or all wood (MW + JW).

	Density JW (g cm^{-3})		Density MW (g cm^{-3})		Density JW + MW (g cm^{-3})	
k_s (m^2)	-9.26 (5.88)	$r^2 = 0.76^{**1}$	-9.66 (8.42)	$r^2 = 0.11$ ns	-15.49 (10.17)	$r^2 = 0.29$ ns
S_{H12}	7.17 (-1.81)	$r^2 = 0.90^{**}$	0.62 (0.78)	$r^2 = 0.09$ ns	5.99 (-1.39)	$r^2 = 0.56^{**}$
S_{H88}	5.75 (-0.19)	$r^2 = 0.61^*$	8.35 (-1.01)	$r^2 = 0.92^{**}$	6.79 (-0.30)	$r^2 = 0.78^{**}$

¹ Significance levels refer to the slope of the regression; ns = not significant ($P > 0.05$); * = $P < 0.05$; and ** = $P < 0.01$.

strophic xylem dysfunction (Tyree and Sperry 1988, Sperry and Pockman 1993). We hypothesize that S_{H12} is inversely related to the size of earlywood tracheids, because smaller earlywood cells are harder to embolize. Within individual trees, S_{H88} followed the trend in wood density, which was high at both the apex and the base of the tree (Table 8). Hacke et al. (2001) found a strong correlation between wood density and cavitation resistance for 50 PLC in branches within a wide range of species. We hypothesize that cavitation resistance at high negative pressure, like S_{H88} , is determined largely by the proportion of latewood, which is highly correlated with wood density (Equations 12 and 13, De Kort 1993). It is well known that latewood pits are less apt to aspirate than earlywood pits (Meyer 1971) because latewood pit membranes are less flexible (Petty 1972).

For branches, 50 PLC occurred at a mean water potential of -5.9 MPa (Table 3), which is close to the value of -5.3 MPa reported by Sperry and Ikeba (1997) and Kavanagh et al. (1999), but 2.5 MPa lower than the value reported by Cochard (1992) for the same species. For the branches and top, there was a 10% drop in RWC between 0 and 2.0 MPa, with no loss in conductivity (Figure 2), or less than 5 PLC (Figure 5), respectively, which is a common measurement for branches in field conditions (Bond and Kavanagh 1999).

Our results indicate that the highest resistance to xylem cavitation was in the branches and near the pith. In part, the explanation may lie in the anatomical structure of these samples (short narrow tracheids in the earlywood), which might allow some water loss without loss of conductivity (segmentation and redundancy of the hydraulic pathway at the cell level). The drop in RWC without effect on PLC could also result from water release by living cells (elastic storage due to radial parenchyma cells) or by the pith area, but not by capillary spaces, because a pressure chamber cannot generate sufficient pressure to displace capillary water (Zimmermann 1983, Domek and Gartner 2001). In our study, applied air pressure versus xylem water deficit in the laboratory gave slopes (Figure 2) comparable with field data (Table 5). By fitting a sigmoidal curve to the field values for the 10-year-old saplings, to make them comparable with the laboratory curve, we estimated a slope coefficient equal to 1.0 (close to the value of 1.2 shown in Table 3).

Although a relationship between k_s and wood RWC has been reported (cf. Jackson et al. 1995, Phillips et al. 1996), our study shows that this relationship is not always maintained.

We found that PLC and RWC responded differently to applied air pressure, with RWC changing sigmoidally or linearly. Other researchers have shown an exponential, rather than sigmoidal, decrease in k_s with decreasing RWC for mature trees (Tesoro et al. 1974, Waring and Running 1978, Edwards and Jarvis 1982, Pothier et al. 1989, Sellin 1991). An exception in our study was the 10-year-old sapling trunks, which showed a linear decrease in k_s with decreasing RWC. This trend is in contrast to that at the treetops, located on the capacitor comprising the entire stem. These results suggest that the nonlinear response seen at the base as well as at the tip of mature trees at low Ψ is related to a capacity for water storage that is lacking in saplings. During a drought, the trunk acts as a resistor/capacitor system at low Ψ , making it more efficient to use stored water (N.G. McDowell, Oregon State University, Corvallis, OR, unpublished data). The nonlinear decrease could also result from the wider range and distribution in tracheid lumen diameter at the base of the tree than at the tip (Panshin and de Zeeuw 1980), which would increase the deviation from a linear pattern.

Mechanical safety factors

The mechanical safety factors were relatively insensitive to wood type (JW or MW), because the differences between JW and MW in MOE or MOR (depending on the safety factor) were only about 18%. However, the second moment of area, I , increases as a function of stem radius to the fourth power. Thus, even slight differences in stem radius are far more important than differences between JW and MW in MOE and MOR.

We intended our estimates of the indices of mechanical safety to be conservative (i.e., prone to underestimate mechanical safety). Even though the models we used were under static load conditions, the values obtained for S_{Mh} , S_{Mb} and S_{MBr} are consistent with published values (Holbrook and Putz 1989, Milne and Blackburn 1989, Spatz and Bruechert 2000). The data indicated that branches and trunks have safety factors greater than unity, meaning that these structures are mechanically reliable (Niklas 1998). Minimum mechanical safety factors in branches were higher, because of higher wood density and thus strength (Table 7). With respect to mechanical performance, we assumed that critical buckling load governs tree mechanical behavior. This may be true if we compare trees to vines (Gartner 1991b), or as we did, one value of wood density to another in a single tree. The limitation with buckling load as

the mechanically controlled feature is that buckling is led by stiffness, not strength, and further, by definition, the ratio of $P_{cr}/P > 1$ (otherwise the tree is a vine). It could be, however, that tree mechanics are governed by the combined stress of bending and tension, or by the bending and compression resulting from environmental disturbance (e.g., wind). Under dynamic constraints, the values would decrease, but in the same order of magnitude, which would not change the conclusions drawn in this paper (Morgan and Cannell 1987, Kerzenmacher and Gardiner 1998). Although not considered here, tree mechanical behavior is also tied to root structure and the foundation strength of the ground (Coutts 1986, Niklas and Spatz 2000). The use of real MOE values at the tree and branch level could change the pattern within a tree (Mattheck et al. 1993) and affect the differences between young and mature trees. Real values are unlikely, however, to change the magnitude of our results, because we used the lower density–MOE relationships available from the literature (Niklas 1992).

Conclusion

We have presented hydraulic coefficients for three tree age classes, that can be applied in other studies. We demonstrated that the trunk of a mature tree functions near the point of catastrophic xylem disfunction under field conditions, whereas the trunk of a young tree operates hydraulically with a greater margin of safety. Trees appear to produce juvenile wood higher up the trunk to maintain hydraulic safety rather than to meet mechanical requirements. Because juvenile wood is inferior to mature wood for many commercial applications, there is an incentive to raise trees that produce less of it. However, if tree breeders reduce the amount of juvenile wood that trees produce, they may inadvertently create plants that are susceptible to drought. Our research raises many questions about the hydraulic function of sapwood.

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