

How do water transport and water storage differ in coniferous earlywood and latewood?

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Abstract

The goal of this research project was to determine the water transport behaviour of earlywood versus latewood in the trunk of 21-year-old Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] trees. Specific conductivity (k_s) and the vulnerability of xylem to embolism were measured on a single growth ring and in a subset of earlywood and latewood samples within the same ring. Earlywood/latewood ratio, trunk water potential (Ψ) and relative water content (*RWC*) were used to predict differences in conductivities and vulnerability to embolism. Earlywood has about 11 times the k_s of latewood, and up to 90% of the total flow occurred through the earlywood. Earlywood's vulnerability to embolism followed the same trend as that of the whole wood, with 50% loss of conductivity at -2.2 MPa (P_{50}). Latewood was more vulnerable to embolism than earlywood at high Ψ , but as Ψ decreased, the latewood showed very little further embolism, with a $P_{50} < -5.0$ MPa. The lowest trunk Ψ estimated in the field was about -1.4 MPa, indicating that latewood and earlywood in the field experienced about 42% and 16% loss of k_s , respectively. The higher vulnerability to embolism in latewood than in earlywood at field Ψ was associated with higher water storage capacity (21.8% *RWC* MPa⁻¹ versus 4.1% *RWC* MPa⁻¹, latewood and earlywood, respectively). The shape of the vulnerability curve suggests that air seeding through latewood may occur directly through pores in the margo and seal off at lower pressure than earlywood pores.

Key words: Cavitation, earlywood, embolism, hydraulic conductivity, latewood, relative water content.

Introduction

There are two distinct zones of growth within a tree ring: earlywood and latewood. The early season growth in a tree, which produces earlywood (periclinal growth), accounts for 40–80% of a ring's growth in width for a year. As the growth rate slows and stops during autumn, the cells laid down are smaller, denser, and mechanically stronger (therefore appearing darker).

Water is the most limiting ecological resource for most tree and forest sites (Richter, 1976; Waring and Running, 1998). Change in earlywood/latewood growth patterns reflect, in part, the control of wood properties by water availability. Factors such as temperature, sunlight conditions, and the slope of the hillside also can affect the width of tree rings and the amount of earlywood or latewood (Larson, 1962). Numerous studies have shown that for conifers, in general, higher wood density, as a consequence of a greater proportion of latewood, is triggered by drought stress (see review by Zobel and Van Buijtenen, 1989). Latewood formation appears to be more sensitive to climate than earlywood formation (Bannan, 1967; Lebourgeois, 2000). In growing periods with lower precipitation than normal and excessively low temperatures, tree growth is diminished and the proportion of latewood is higher. Conversely, when growing conditions are ideal, tree growth is enhanced and the proportion of latewood reduced (Kennedy, 1961).

Although the significance of the outermost ring to the hydraulic conductivity and earlywood and latewood to xylem embolism of the whole stem have been quantified in ring porous trees (*Ulmus americana*, Ellmore and Ewers, 1986; *Quercus cerris*, Lo Gullo *et al.*, 1995), no study has investigated it in a conifer species or within the earlywood and the latewood of the same ring. Furthermore, there are no reports of a direct measurement of vulnerability to embolism within a single ring and within its components. It

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is logical to infer that earlywood and latewood would have very different hydraulic properties.

The differences in hydraulic conductivity and vulnerability to embolism between earlywood and latewood have been linked to differences in xylem anatomy (Zimmermann, 1983). Hydraulic conductivity is proportional to the fourth power of the radius of xylem conduits (Gibson *et al.*, 1985; Tyree and Ewers, 1991). Earlywood tracheids have wider lumen diameters than latewood tracheids (Panshin and de Zeeuw, 1980; Ewers *et al.*, 1997). The trade-off, however, is that conduits with high conductivity might be more vulnerable to embolism (Schulte and Gibson, 1988; Sperry and Saliendra, 1994; Hargrave *et al.*, 1994). These data suggest that earlywood can transport a large proportion of water to the main trunk when plant-water status is favourable, but might limit plant water use during drought. In hardwoods, the small-diameter latewood vessels and the small-diameter vasicentric tracheids near the larger vessels are thought to provide water transport once the earlywood and/or wider vessels have become air-filled (Carlquist, 1985; Cochard *et al.*, 1997). In softwoods, the question remains unsolved. Does latewood remain conductive after the earlywood becomes air filled, or does it not?

Embolism due to drought is thought to be caused by air seeding at inter-conduit pit membranes (Zimmermann, 1983; Crombie *et al.*, 1985). Air seeding in conifers occurs through inter-tracheid pit membrane when the torus becomes displaced from its normal sealing position (Sperry and Tyree, 1990). They found that non-sealing of bordered pits in latewood in conifers could account for 20% of the total hydraulic conductivity after the earlywood had sealed off at low water potential (Ψ). The shape of the vulnerability curves varies among and within species and it is thought that they reflect the water stress environment under which the plants grew (Tyree and Sperry, 1988; Tyree *et al.*, 1994; Matzner *et al.*, 2001).

Much less is known about earlywood versus latewood responses to embolism, and about how much embolism occurs in these two zones of a growth ring at field Ψ . The proportion of earlywood versus latewood within a ring and xylem anatomy might be adaptive hydraulic traits and not simply the consequences of water balance in the field. Earlywood and latewood might regulate water transport under stress, based on their influence on hydraulic conductivity, embolism vulnerability, and internal storage capacity. It is hypothesized that, on an anatomical basis, as predicted by the 'air-seeding' hypothesis, hydraulic functions are directly linked to bordered pit functioning and on the mechanical properties of the pit membrane structure proposed by Petty (1972). Embolism developing in earlywood tracheid would not spread to adjacent tracheids because the air-seeding tension created between a water-filled tracheid and an empty one would exceed the mechanical tension required to pull an air bubble through

the margo. The torus would seal off the chamber before air can be drawn through the pores. Therefore, reduction in hydraulic conductivity in earlywood would be linked to the mechanical properties of the membrane. Within the latewood, air would go through the pores before the torus can be sealed because of its high mechanical resistance to displacement. Thus, reduction in hydraulic conductivity in latewood will be more a function of the size of the pores through the margo. Because of their bordered pit structure, earlywood tracheids are therefore expected to be both more efficient and safer from embolism than latewood. If, as expected, embolism resistance is higher within earlywood, a safe xylem is not costly in term of carbon investment.

The objectives of this study were to compare earlywood and latewood water transport capacities within a single growth ring in fast-growing Douglas-fir trees [*Pseudotsuga menziesii* (Mirb.) Franco]. Hydraulic parameters (conductivity, vulnerability to embolism, water storage capacity) were measured on entire wood samples, as well as within earlywood and latewood samples. Field data measurements of Ψ and relative water content were used to confirm laboratory results and to describe earlywood and latewood water transport and storage when water is under tension.

This research was designed to test the following three hypotheses: (1) sapwood conductivities are lower in latewood and in whole wood than in earlywood, (2) earlywood and latewood conductivities weighted by the proportion of earlywood/latewood explain the whole wood conductivity, and (3) vulnerability to embolism is higher for latewood than for earlywood.

Materials and methods

Plant material and sample preparation

The study was carried out in an even-aged (21-year-old) Douglas-fir stand (elevation 277 m, 44°43' N, 123°20' W) 15 km northwest of Corvallis, Oregon, growing on an inceptisol soil. The mean annual temperature and annual rainfall (1961–1996) are 12.4 °C and 1800 mm, respectively (Table 1; www.orst.edu/Dept/IPPC/wea/). Douglas-fir was chosen because of its fast growth, which gives wide growth rings with distinct latewood. In mid-June 2001 (before the start of the summer drought), five trees were selected randomly and felled. A disc 20 cm thick was cut at breast height from each tree and transported immediately in a wet plastic bag to the laboratory where blocks were prepared. From each cross-sectional disc, six blocks, at approximately 60° intervals around the circumference, were cut within the same single ring with a hammer and chisel (Domec and Gartner, 2001).

The samples were chiselled out of the wood with the long axis parallel to the grain, then submerged in water and put under vacuum for 48 h to refill some of the embolized tracheids. Their original dimensions were 150 mm (axial direction), 10 mm tangential direction, and 7–9 mm radial direction (the width of one growth ring). Samples were randomly designated as A–F. All hydraulic measurements on sample A were done on the entire sample, i.e. both the earlywood and the latewood were left intact. Before the final measurements, samples B–F were sawn in half, to 75 mm in the axial direction. One half was designated B₁–F₁ and the other half B₂–F₂.

Table 1. Tree and samples characteristics of the Douglas-firs studied (n=5)

	Mean ± SE	Minimum	Maximum
Tree properties			
Tree age (years)	21.4 ± 0.5	23	20
Tree height (m)	17.4 ± 0.6	20	16
Tree properties at height sampled (breast height)			
Tree age (years)	17.5 ± 0.6	15.2	18.8
Diameter (cm)	29.4 ± 0.8	28	31.7
Sapwood area (cm ²)	424 ± 31	374	518
Heartwood area (cm ²)	176 ± 10	133	199
Number of sapwood rings	9.4 ± 0.5	8	11
Ring properties			
Ring from bark used	4.4 ± 0.6	3	7
Ring width (mm)	8.6 ± 0.3	9.2 ± 0.3	7.4 ± 0.3
Percentage earlywood	66.6 ± 2.3	59.7 ± 1.9	74.5 ± 1.9

Using a chisel and razor blades, the latewood was removed from samples B₁–F₁, leaving just earlywood, and the earlywood was removed from samples B₂–F₂, leaving just latewood (Fig. 1).

Specific and hydraulic conductivities

Specific conductivity (k_s , in m²), is a measure of the hydraulic efficiency of the xylem in relation to the cross-sectional area of the wood and was calculated according to Darcy's law (Edwards and Jarvis, 1982). Initial specific conductivity ($k_{s(i)}$) was measured on each 130–150 mm segment (intact segments A–F, before they were sawn in half) using the membrane-lined pressure sleeve needed to ensure fluid did not leak from the sides of samples (Spicer and Gartner, 1998a). Samples were soaked in water, then $k_{s(i)}$ was measured at a pressure difference of 2.8 kPa, using filtered (0.22 µm) water adjusted with HCl to pH 2 to prevent microbial growth. The hydraulic pressure head has been preselected as low enough to avoid any refilling of the embolized tracheids. Efflux was collected in a 1 ml-graduated micropipette (0.01 ml graduation). When the flow was steady, the time required for the meniscus to cross six consecutive graduation marks was recorded. Hydraulic conductivity, k_h (in m⁴), which expresses the volume flow–pressure relationship, but not on an area basis (Tyree and Ewers, 1991), was defined as $k_h = A \times k_s$, where A is the cross-sectional area (m²) of the sample.

Vulnerability curves and water storage capacity

Vulnerability curves (VCs) of the wood samples were constructed by means of the air injection method (Salleo *et al.*, 1992; Sperry and Saliendra, 1994) adapted for samples taken directly from the trunk (Domec and Gartner, 2001). The air injection method is based on the theory that the negative water potential (Ψ) required to pull air into a conduit and cause embolism is equal to the positive air pressure required to push air into the conduit when Ψ is equal to the atmospheric pressure. The objective was to measure the percentage loss of conductivity (PLC) on segments by moving the sample alternately between the membrane-lined pressure sleeve for determining k_s and the double-ended pressure chamber for causing embolism. The segments were inserted into the air-injection chamber, with both ends protruding. The air-tight chamber was sealed with rubber gaskets at both ends, held in place by stainless end caps. Pressure was induced into the chamber stepwise, and held constant for 1 min. After each air injection k_s was remeasured and the percentage that $k_{s(i)}$ was below $k_{s(i)}$ gave the sample's PLC. The temperature of the solution, the fresh mass (M_f), the volume (V_f), determined by water displacement (Archimedes's principle), and the length of each sample were recorded before and after each conductivity measurement. The samples always weighed the same

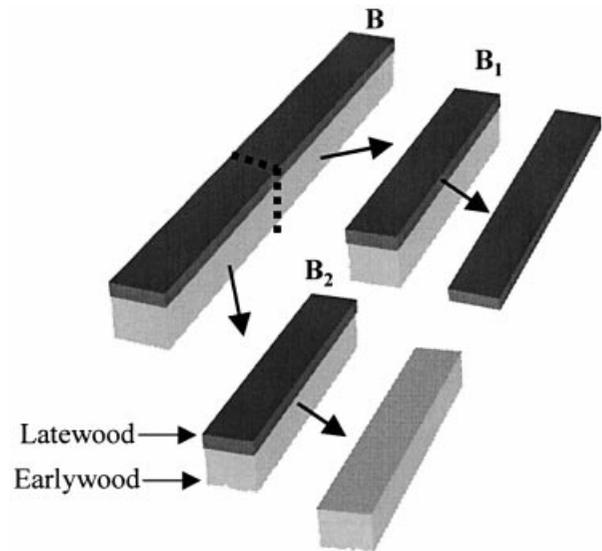


Fig. 1. Sample preparation. Six samples within rings 3–7 were removed from the tree disc taken at breast height. From the six samples prepared, one sample (sample A) was randomly used to determine hydraulic properties in the entire ring ('whole-wood'). The other five samples (samples B–F) were split into two equal segments to determine hydraulic properties within earlywood and latewood (B₁, B₂...F₁, F₂). For clarity, only sample B is shown.

before and after, giving no evidence of refilling. VCs were determined by means of plotting PLC versus Ψ , where Ψ is predicted as the negative of the applied air pressure (Pockman and Sperry, 2000).

After $k_{s(i)}$ had been measured on intact samples A–F, VCs were constructed in two ways. First, sample A was used to construct an entire VC, subjecting it to air pressures ranging from 0.5–5.0 MPa. Second, different samples B–F were used for different air pressures to construct one curve (Fig. 2). After k_s had been determined for samples B and C, they were sawn in half to prepare samples B₁ and C₁ (only earlywood) and B₂ and C₂ (only latewood), and k_s was measured again (samples B, C, B₁, B₂, C₁, and C₂) were used as replicates for k_s at full saturation). After k_s had been determined for sample D, it was pressurized to 0.5 MPa, its k_s was remeasured, then it was sawn in half to prepare samples D₁ and D₂, on which k_s was measured. Likewise, after k_s had been determined for samples E and F, they were pressurized to 1.0 and 3.0 MPa, respectively, their k_s was remeasured, then they were sawn in half to prepared samples E₁, E₂, F₁, and F₂, on which k_s was measured. For earlywood and latewood samples, PLC was determined by means of the paired segments methods, which compared $k_{s(i)}$ of samples D₁, D₂, E₁, E₂, F₁, and F₂ to the average $k_{s(i)}$ of samples B₁, B₂, C₁, and C₂ from the same disc (Fig. 2). To test for differences between the paired segment method and the regular method (consisting of measuring PLC within the same samples at different Ψ), a comparison was made at each Ψ between samples A and intact samples B–F.

Embolized area estimated by the staining method

Following each final conductivity measurement, each sample was perfused with filtered (0.22 µm) safranin-O (0.5% aqueous solution) under 15 kPa pressure head for 20 min while still enclosed in the pressure sleeve apparatus. The hydraulic pressure head has been preselected as high enough to allow safranin-O to flow without refilling any of the embolized tracheids. For the initial measurements, the samples always stained completely, giving no evidence of embolism. The percentage of unstained wood area of each sample

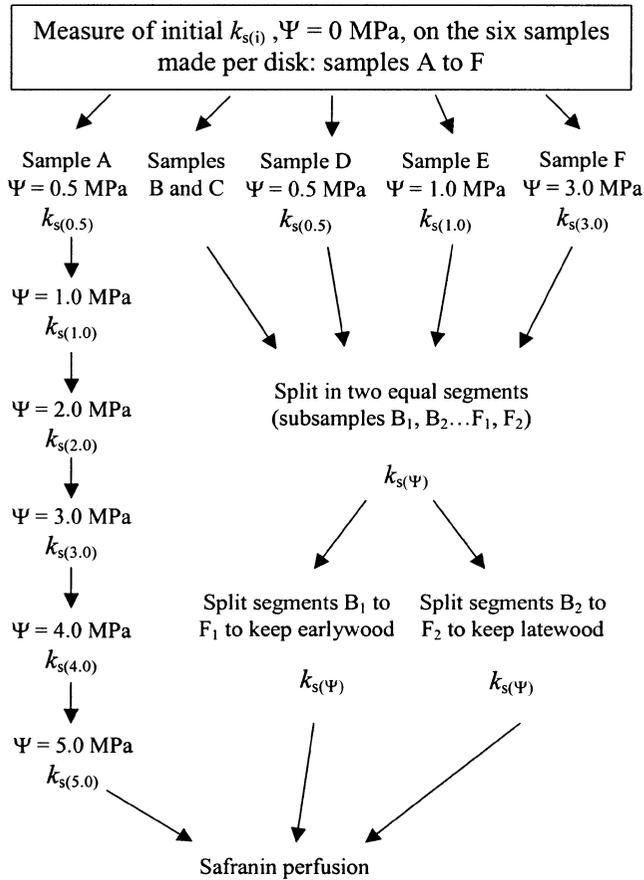


Fig. 2. Summary of procedures used to assay the specific conductivity (k_s) and the vulnerability curves within on single ring or whole sample (A) and earlywood and latewood samples (B–F).

used for the VCs was analysed with an image analysis system consisting of a compound microscope, a video camera, a computer, and the software NIH Image (v. 1.60, Rasband, 1996).

Earlywood and latewood proportion

Total widths of the earlywood, latewood, and total ring were determined for each sample before its halves were cut down to just latewood or just earlywood. These measurements were made with the tree-ring measuring device as follows. The sample was placed on a moving Velmex measuring table equipped with an AcuRite ENC 150 linear encoder and a QuickCheck-1000 digital measuring device and display. By watching the image of the growth ring on a monitor projecting the sample's magnified video image, and then by moving the stage, one can read out the growth ring width to 0.01 mm precision. Average earlywood proportion for each sample was then calculated.

Moisture content, relative water content and water storage

Moisture content (MC) is defined as the mass of water present in a piece of wood expressed as a percentage of the mass of oven-dry wood (M_d):

$$MC(\%) = \left(\frac{M_f}{M_d} - 1 \right) 100 \text{ (dimensionless)} \quad (1)$$

Relative water content (RWC) is the mass of water in the sample divided by the potential maximum values of water in the sample. To

get a rate of change in RWC associated with cavitation, RWC was determined for each sample used to construct a VC, initially and after each pressure, by recording V_f (cm³) and M_f (g). Following final pressurization, M_d (g) was recorded after drying at 104 °C. Length was used to back-calculate the volume of cell wall material (V_s , cm³) and M_d (g) at each given pressure. RWC can then be calculated as follows:

$$RWC = M_f - \frac{M_f - M_d}{(V_f - V_s)D_{H_2O}} \text{ (dimensionless)} \quad (2)$$

where D_{H_2O} is the density of water (g cm⁻³). V_s was calculated from M_d assuming that latewood and earlywood dry-cell-wall material has a density of 1.53 g cm⁻³ (Kennedy and Warren, 1969; Kellog *et al.*, 1975; Siau, 1984).

Water storage capacity, defined as the amount of water withdrawn from the stem at given water potential (Holbrook, 1995), was expressed as the change in RWC per unit Ψ . This definition of capacitance made it possible to compare differences in storage capacities that are related to a difference not only in total water volume, but also in tissue density (Domec and Gartner, 2001). The volumetric RWC-based capacitances (C_{RWC}) for a given range of pressures were determined after each conductivity point as follows (Edwards and Jarvis, 1982):

$$C_{RWC} = \frac{dRWC}{d\Psi} \text{ in } RWC \text{ MPa}^{-1} \quad (3)$$

Capillary water changes cannot be estimated accurately by using the pressure chamber, because positive pressure cannot displace capillary water (Zimmermann, 1983; Tyree and Yang, 1990). The hypothesis of capillary water storage states that water storage comes from the change in the radius of the meniscus between the cell wall and the gas space (Zimmermann, 1983). If this hypothesis is correct, then maximum capillary water storage is released at a pressure close to zero, and stops before 0.6 MPa (Holbrook, 1995; Tyree and Yang, 1990). Therefore, to determine whether the slope of the dehydration curve was constant throughout its range, and to avoid underestimating capillary water at low applied pressure, capacitance values were computed for three phases in each dehydration curve: a phase from 0–0.5 MPa ($C_{0-0.5}$), a phase from 0.5–1.0 MPa ($C_{0.5-1.0}$) and a phase from 1.0–3.0 MPa ($C_{1.0-3.0}$).

Wood density and volume occupied by cell wall material, by water and by gas

Wood density values were determined for each sample tested hydraulically:

$$\text{Density} = \frac{M_d}{V_f} \text{ in } g \text{ cm}^{-3} \quad (4)$$

For each type of sample, the volume occupied by water, cell wall material, and gas (on a fresh volume basis) was calculated as:

$$V_{H_2O}(\%) = \frac{(M_f - M_d)}{V_f} 100 \quad (5)$$

$$V_{\text{cell wall}}(\%) = \frac{M_f}{1.53V_f} 100 \quad (6)$$

$$V_{\text{gas}}(\%) = (1 - V_{\text{cell wall}} + V_{H_2O}) 100 \quad (7)$$

Field measurements

To examine the RWC in earlywood and latewood, eight dominant trees were cored with a 12 mm increment borer during winter (10–15

March 2001, before the growing season), and during summer (25–30 September 2001, before the rain started). Cores were wrapped in plastic wrap immediately after removal and placed in a cooler. They were returned to the laboratory the same day and processed. The last growth ring was removed and the next two growth rings were divided into earlywood and latewood. As described previously, V_f , M_f , and M_d were measured and RWC was calculated. The same days and on the same trees, trunk Ψ at breast height was estimated (on leaves bagged in aluminium foil to prevent transpiration) with a pressure chamber (PMS Instrument Company, Corvallis, Oregon). Three foliage-bearing branches per tree were measured. The relationship between the negative of the applied pressure and RWC and PLC was determined from samples tested in the laboratory, then PLC was estimated, based on the measured Ψ and RWC of standing trees in the field.

Statistical analysis

Least squares methods were used to fit relationships between the hydraulic parameters and the applied pressure, as well as the linear and non-linear relationships between hydraulic parameters. Analysis of variance (ANOVA) was used to determine differences in hydraulic parameters between the entire samples and the subset of samples, with tree as a blocking factor. Paired t -tests were used specifically to test the difference in hydraulic parameters between earlywood and latewood. All statistical procedures were conducted with Statistical Analysis Systems software ((SAS Institute Inc, 1997).

Results

Sample shape, staining tests

The average latewood made up 33% of the ring ($\pm 2\%$; ranged from 26% to 40%) (Table 1). The sum of the measured k_s in earlywood and latewood, weighted by the proportion of earlywood/latewood, was a good estimate of k_s measured within the whole samples (Fig. 3a). The slope of the regression line was not significantly different from 1 ($P=0.26$). Neither the hydraulic parameters nor the estimated capacitances differed between the whole samples (B–F) and the subsample pieces (B₁, B₂ to F₁, F₂; $P > 0.62$, data not shown). Whole long samples (A) and small subsample pieces (D–F) had similar PLC at 0.5, 1.0, and 3.0 MPa (Fig. 3b). There was a strong relationship between the estimated PLC based on the unstained part of the samples (non-functional wood) and the actual PLC measured (Fig. 4). The slope of the regression line, however, was significantly lower than 1 ($P=0.04$).

Hydraulic parameters within earlywood and latewood

Earlywood had significantly higher k_s than latewood ($P < 0.001$, Table 2). Latewood had less than 9% of the k_s of earlywood and 13% of the k_s of whole wood. At the ring scale, latewood (accounting for 33% of the surface area) provided only 5% of the total k_h (Table 2).

Vulnerability to embolism varied among wood type samples. Latewood samples were more vulnerable to embolism than earlywood samples at 0.5 MPa and 1.0 MPa, but not a 3.0 MPa (Table 2; Fig. 5a). Earlywood samples were not significantly different from the whole wood

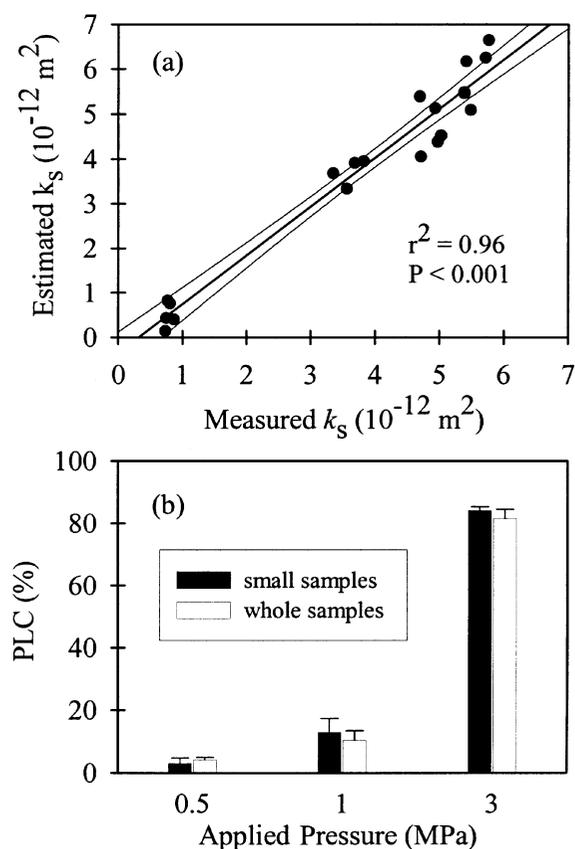


Fig. 3. (a) Measured specific conductivity (k_s) in the whole sample versus k_s estimated as the sum of the measured k_s in earlywood and latewood weighted by the proportion of earlywood and latewood found in the ring ($n=20$). The regression line and the 95% confidence intervals are represented. The slope of the regression line was not significantly different from 1 ($P=0.26$). (b) Comparison of the percentage loss of conductivity (PLC) at the three applied pressures between the small and whole samples.

sample ($P > 0.21$), and followed the same trend. The xylem pressures causing 50 PLC (P_{50}) for the entire VC and earlywood were -2.3 ± 0.1 and -2.1 ± 0.2 MPa, respectively (Fig. 5a). At any applied pressure, whole wood samples and earlywood samples were significantly different from latewood samples ($P < 0.04$).

Water deficit ($100-RWC$) showed a sigmoidal change with applied pressure within whole wood samples. The steepest slope occurred between 2.0 and 3.0 MPa (Fig. 5b). For latewood, water deficit increased exponentially with higher applied pressures to reach a maximum at 40% (Fig. 5b). Earlywood had a smaller decrease in water deficit at 0.5 and 1.0 MPa than latewood, but it had a much greater decrease and was significantly different than latewood at 3.0 MPa ($P=0.03$). Earlywood samples had water deficit similar to that of whole-wood samples at 0.5 and 1.0 MPa, but they had significantly lower values at 3.0 MPa ($P < 0.01$). Latewood had significantly different values in water deficit than whole-wood samples for the three different applied pressures ($P < 0.05$, Fig. 5b).

Latewood had a much higher water storage capacity than earlywood between 0.5 and 1.0 MPa (22 versus 4% $RWC\ MPa^{-1}$, latewood and earlywood, respectively). This trend was reversed between 1.0 and 3.0 MPa (5% versus 23% $RWC\ MPa^{-1}$, latewood and earlywood, respectively; Table 3). There was no significant difference between earlywood and latewood for $C_{0-0.5}$ (Table 3). There was no significant difference between whole sample and latewood for $C_{0.5-1.0}$, but there was a significant difference between the whole sample and earlywood and between the whole sample and latewood for $C_{0-0.5}$ and $C_{1.0-3.0}$ ($P < 0.05$). Within the earlywood samples, there was a significant difference in water storage capacity between $C_{0-0.5}$, $C_{0.5-1.0}$ and $C_{1.0-3.0}$ ($P < 0.006$). Water storage capacities were not significantly different between the first two phases for the latewood samples ($P=0.9$) and between the last two phases for the whole wood samples ($P=0.7$)

Latewood and earlywood composition

Percentages of air and RWC at full saturation were the same within both types of wood, however all other wood properties were statistically different ($P < 0.01$; Table 4). The latewood had a higher percentage of cell wall and a

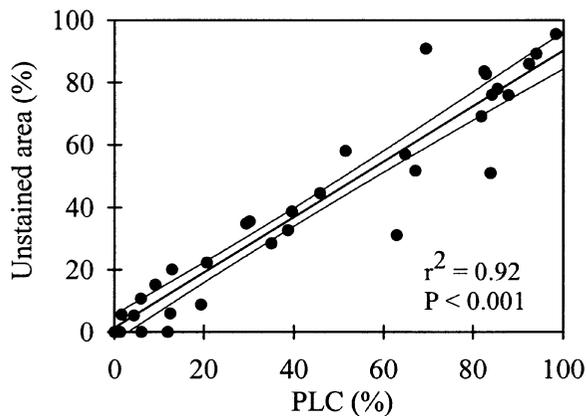


Fig. 4. Embolized tracheids measured by the percentage loss of conductivity (PLC , equation 3) in the whole sample and in earlywood and latewood subsamples versus the embolized area estimated by the staining method (% unstained area). The regression line and the 95% confidence intervals are represented ($n=80$). The slope of the regression line was significantly different from 1 ($P=0.04$).

lower percentage of water. At 3.0 MPa, latewood had a lower percentage of air, but the same percentage of water. Latewood had more than twice the density of earlywood ($0.26\ g\ cm^{-3}$ versus $0.60\ g\ cm^{-3}$).

Comparisons between field measurements and laboratory estimates

Minimum trunk Ψ measured at the end of the summer never dropped below $-1.4 \pm 0.2\ MPa$, for a calculated minimum RWC of $69 \pm 3\%$ for the whole ring. Latewood RWC was significantly lower than earlywood RWC ($P=0.002$). There were 4% and 8% seasonal decreases in

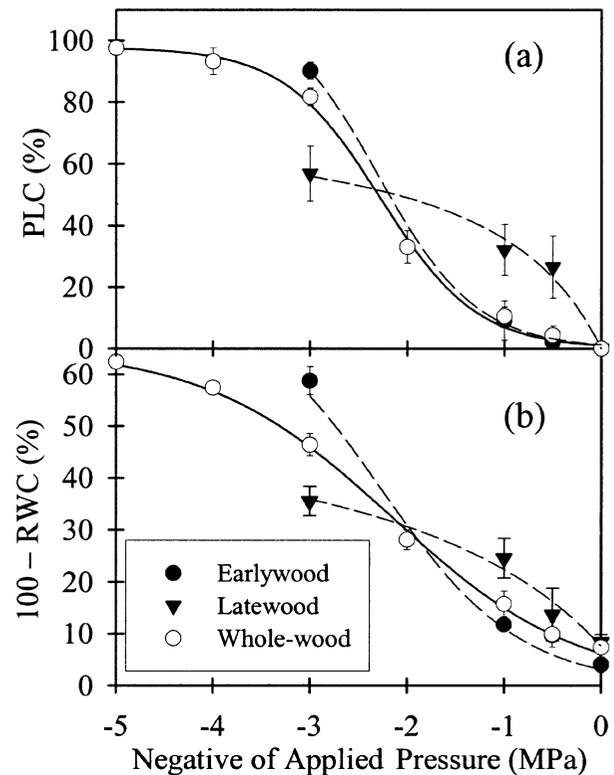


Fig. 5. (a) Vulnerability curves showing the percentage loss of xylem hydraulic conductivity (PLC) and (b) water deficit ($100-RWC$) for Douglas-fir whole-wood, earlywood, and latewood of 21-year-old trees at breast height versus the negative of air pressure used in air-injection experiments. The error bars are standard errors ($n=5$).

Table 2. Specific conductivity (k_s), hydraulic conductivity (k_h) and percentage loss of conductivity (PLC) at three negatives of applied pressures in whole-wood, earlywood and latewood samples

Mean \pm SE ($n=5$). Values within a column sharing the same letter are not significantly different at $P=0.05$.

	$k_s\ (m^2)$	$k_h\ (m^4)$	$PLC\ (\%)$		
			-0.5 MPa	-1.0 MPa	-3.0 MPa
Whole-wood	$5.0 \pm 0.3 \times 10^{-12}\ a$	$3.8 \pm 0.3 \times 10^{-16}\ a$	$2.9 \pm 1.7\ a$	$12.8 \pm 4.5\ a$	$84.1 \pm 1.1\ a$
Earlywood	$7.3 \pm 0.5 \times 10^{-12}\ b$	$3.4 \pm 0.1 \times 10^{-16}\ a$	$2.1 \pm 1.9\ a$	$10.3 \pm 6.4\ a$	$90.2 \pm 2.8\ a$
Latewood	$6.4 \pm 0.9 \times 10^{-13}\ c$	$2.0 \pm 0.5 \times 10^{-17}\ a$	$26.5 \pm 9.1\ b$	$32.1 \pm 8.3\ b$	$56.8 \pm 8.9\ b$

RWC in earlywood and latewood, respectively (Table 5). The calculated PLC values from summer trunk Ψ were 16% and 42% in earlywood and latewood, respectively (Table 5). There was close agreement between the estimated PLCs from the measured Ψ and RWC for earlywood, but not for latewood.

Discussion

Methodological issues

Using small or long samples gave statistically inseparable results for k_s or vulnerability to embolism (Fig. 3b). Cutting the samples in two pieces (one to be used for earlywood, the other for latewood) did not affect the degree of embolism, which made it possible to continue with the data analysis. This finding shows that damage to sample edges has no significant effect on k_s or vulnerability to embolism, validating the appropriateness of this method (Domec and Gartner, 2001).

Table 3. Effect of wood type on RWC-based capacitances (water storage capacity, % MPa⁻¹) for the three phases $C_{0-0.5}$ (between 0 and 0.5 MPa), $C_{0.5-1.0}$ (between 0.5 and 1.0 MPa), and $C_{1.0-3.0}$ (between 1.0 and 3.0 MPa)

Means (\pm SE) are shown ($n=5$). Values within a column sharing the same letter are not significantly different at $P=0.05$.

	$C_{0-0.5}$	$C_{0.5-1.0}$	$C_{1.0-3.0}$
Whole-wood	5.1 \pm 1.2 a	11.3 \pm 0.1 a	15.3 \pm 0.2 a
Earlywood	11.3 \pm 4.3 a	4.1 \pm 2.5 b	23.5 \pm 1.1 a
Latewood	10.5 \pm 8.3 a	21.8 \pm 7.1 a	5.5 \pm 1.4 b

Table 4. Wood density (dry mass/green volume), moisture content (MC), volume occupied by cell wall material (V_{cellwall}), volume occupied by water ($V_{\text{H}_2\text{O}}$), volume occupied by gas (V_{gas}), and relative water content (RWC) at full saturation (after 48 h under vacuum) in whole-wood, earlywood and latewood samples

Means (\pm SE) are shown ($n=5$). Values within a column sharing the same letter are not significantly different at $P=0.05$.

	Density (g cm ⁻³)	MC (%)	V_{cellwall} (%)	$V_{\text{H}_2\text{O}}$ (%)	V_{gas} (%)	RWC (%)
Whole-wood	0.39 \pm 0.02 a	182 \pm 12 a	25.3 \pm 1.2 a	69.3 \pm 2.1 a	5.4 \pm 1.4 a	93 \pm 2 a
Earlywood	0.26 \pm 0.02 b	316 \pm 18 b	16.7 \pm 1.0 b	79.9 \pm 1.0 b	3.4 \pm 1.3 a	96 \pm 2 a
Latewood	0.60 \pm 0.01 c	92 \pm 3 c	39.6 \pm 0.7 c	55.4 \pm 1.1 c	5.1 \pm 1.0 a	92 \pm 2 a

Table 5. Measured earlywood and latewood relative water content (RWC) and estimated percentage loss of conductivity (PLC) from summer measured field RWC and trunk water potential (Ψ_{trunk}) taken at midday

Field value of winter Ψ_{trunk} was -0.5 ± 0.1 MPa. Minimum field values of summer Ψ_{trunk} at predawn and midday were -1.0 ± 0.1 MPa and -1.4 ± 0.1 MPa, respectively. The corresponding summer Ψ_{leaf} at midday was -1.7 ± 0.1 MPa ($n=6$).

	Measured RWC winter	Measured RWC summer	Estimated PLC from measured RWC	Estimated PLC from measured Ψ_{trunk}
Earlywood	79 \pm 2	75 \pm 4	22 \pm 8	16 \pm 3
Latewood	65 \pm 2	57 \pm 1	56 \pm 3	42 \pm 2

Earlywood/latewood segmentation to conductivity and vulnerability to embolism

As expected, latewood had much lower k_s than earlywood. The very low k_s found in latewood can be explained by the small tracheid diameter of its cells compared to earlywood cells. Hagen–Poiseuille’s law predicts that the large earlywood tracheids are responsible for most of the water flow within a single ring (Zimmermann, 1983). Earlywood k_s exceeded latewood k_s 11-fold, which would correspond to a 1.8-fold increase in tracheid diameter (Hagen–Poiseuille’s law), all other factors being equal. This result agrees with the ratio of tracheid diameters described in the literature for conifers (McMillan, 1968; Cown, 1975).

The results supported the hypothesis that earlywood transports water more efficiently and is less vulnerable to embolism than latewood at Ψ occurring in the field under normal conditions (Tables 2, 5). This result contrasts with that reported in a ring-porous species ((Lo Gullo *et al.*, 1995). Using the staining method, they showed that latewood vessels of young trees of *Quercus cerris* were narrower, shorter and less vulnerable to embolism than earlywood ones.

Within a growth ring, there was a positive relationship between k_s and safety, and there is no trade-off between the two. However, the margin of safety between the measured Ψ in the field and the beginning of embolism was less than 0.5 MPa. This study confirmed that wood from the trunk base of Douglas-fir trees may operate close to the edge of hydraulic safety because of the high vulnerability to embolism of earlywood below -2.0 MPa ((Domec and Gartner, 2002a).

Embolism formation is thought to be related not to conduit size, but rather to pore size at the interface of two

tracheids through the bordered pits (Tyree *et al.*, 1994). Indeed, the low resistance to embolism is correlated with structural features of the bordered pit membrane (Petty, 1972; Bolton and Petty, 1978; (Domec and Gartner, 2002*b*). The small and thick torus and strands of the bordered pits found in latewood might not allow the margo to act as a valve, preventing air bubbles from spreading from one embolized tracheid to another. It has been reported that in *Pinus sylvestris* (L.), latewood membranes were more rigid than earlywood ones and that they could not seal off completely at field Ψ values (Gregory and Petty, 1973). Pores between the strands of the membrane are smaller in latewood than in earlywood (Petty and Puritch, 1970; Fengel, 1972), suggesting that air-seeding occurs directly through these pores. The mechanical resistance of the torus would exceed the mechanical tension required to pull an air bubble through the membrane. The mechanism of water-stress-induced embolism in latewood would then be similar to that of vessel-bearing plants (Sperry and Tyree, 1988). The resistance of embolism in latewood would then be proportional to the size of the pores in latewood, which can explain the observed decrease of conductivity commencing immediately at 0 MPa and below. The shape of the curve before reaching the plateau (0–1.0 MPa, Fig. 5*b*) might reflect the pore size distribution within the strands of the membrane in latewood. The membranes were probably completely deflected at $\Psi < -1.0$ MPa and the sealed torus probably created a closed system, protecting the tracheids responsible for the remaining 40% of conductivity. Regarding the earlywood, it has been reported that the porosity of the membrane that holds the torus is too large to prevent the air meniscus passage at Ψ values lower than -0.1 MPa, but it is elastic enough to be completely deflected and to seal off the torus (Sperry and Tyree, 1990). The slippage of the torus from its sealed position created gaps big enough to develop cavitation in adjacent tracheids. This result might explain why there was a complete loss of conductivity for lower applied pressures in earlywood but not in the latewood (Fig. 5*a*). The thicker torus of latewood would prevent it from slipping off from its sealed position (Domec and Gartner, 2002*b*).

Back-calculation of the part of latewood in the remaining k_s at -3.0 MPa (Fig. 5*a*) indicated that non-sealing of latewood bordered pits in Douglas-fir appeared to account for 30% of the total hydraulic conductivity that remained. With its very low k_s and proportion (33%) in a ring, however, fully conductive latewood can account for only 5% of the initial conductivity at full saturation, although it can account for 16% of the remaining conductivity at -3.0 MPa. This remaining conductivity in latewood represents only 2% of the initial conductivity, which is far from the 20% calculated by Sperry and Tyree (1990). By taking a mature tree with small growth rings and a higher proportion of latewood (close to 55%) (De Kort,

1993), latewood would still account for only 11% of the total ring conductivity at -3.0 MPa (during severe drought). To account for 50% of the whole ring conductivity, latewood would have to represent 90% of the whole ring area at full saturation, and 75% at -3.0 MPa. Such a high proportion of latewood within a growth ring is unlikely to be found in normal conifer wood, but it can often occur in compression wood, which forms on the lower sides of branches or in leaning trunks (Westing, 1968; Timell, 1986).

Compression wood of stems has wide annual rings and is much denser than normal wood because of the elevated proportion of latewood (Park, 1984; Yoshizawa *et al.*, 1987). It has been shown that compression wood in branches and seedlings of Douglas-fir had significantly lower k_s than normal wood (Spicer and Gartner, 1998*b*). It can be hypothesized that compression wood in trunks would be more vulnerable to embolism than normal wood at high Ψ . On the other hand, it might be more resistant to severe drought because of the higher latewood resistance to embolism at low Ψ . Old growth trees also have a generally higher proportion of latewood than young or mature trees, which could limit their water transport but increase their resistance to embolism at very low Ψ . A higher latewood/earlywood ratio could be a strategy for species such as Douglas-fir growing in wet conditions during the spring and dry conditions during the summer. It could also explain why vulnerability to embolism in mature Douglas-fir trees was higher at the base of the trunk than at the top of the trunk (under the crown), whereas its k_s was lower (Domec and Gartner, 2001).

Differences in water storage capacities between earlywood and latewood

The high water storage capacity observed at high Ψ (-0.5 MPa) has been described as capillary water (Tyree and Yang, 1990) and has no adaptive implication because it occurs before the plant becomes water stressed. Therefore, even though the first values of capacitance were not explained between 0 and 0.5 MPa, the other two estimated capacitance values ($\Psi = 0.5$ – 1.0 , and 1.0 – 3.0 MPa) were suitable.

The research described in this paper showed that within a growth ring, latewood had a higher water storage capacity than earlywood (Fig. 5*b*) and was more vulnerable to embolism at field Ψ under normal conditions (> -2.0 MPa). For earlywood, the low capacity storage found for the functioning range of potentials (between 0–1 MPa) suggests that its water uptake would be related linearly to the water loss by the leaves (Table 3; Fig. 5*b*). The advantage of maintaining this steady-state flow is stressed by the fact that few embolism events occur at Ψ less negative than -2.0 MPa (Fig. 5*a*). Therefore for earlywood, the trade-off associated with low vulnerability to embolism and high k_s is low water storage capacity

(Goldstein *et al.*, 1998; Stratton *et al.*, 2000). These characteristics might be important in old trees with a higher percentage of latewood, and it can be hypothesized that for the natural range of Ψ , earlywood would best serve the tree by conducting water efficiently and safely and latewood by providing an important amount of stored water. On the other hand, under dry conditions (< -2.0 MPa), earlywood would be more likely than latewood to use water storage that could represent an important fraction, but then latewood would keep a minimum level of k_s through better resistance to embolism. This hypothesis could explain why there was a bigger difference in *RWC* in latewood than in earlywood between winter and summer (Table 5). This hypothesis could also explain why trees with higher wood density and higher percentage latewood are related to arid areas (Polge, 1973; Megraw, 1985; Barajas-Morales, 1985) and are more resistant to cavitation (Alder *et al.*, 1996; Hacke *et al.*, 2001).

Trade-off between hydraulic and mechanical properties of latewood and earlywood

Latewood had a density 2.3 times higher than earlywood (Table 4), similar to other findings for the same species (Lutz, 1964; (Takjima, 1967). The overstated controlling factor for wood strength among trees is the varying latewood percentage for most species (Zobel and Van Buijtenen, 1989). Douglas-fir trees grow mostly during the springtime, when there is plenty of rain and sun to support the growth (Waring and Running, 1998). The change from earlywood to latewood is closely related to the availability of soil moisture, because a high moisture stress decreased auxin production (Gilmore *et al.*, 1966). The regulation of cell diameter is hormonal and is mediated by an auxin originating in the buds of growing shoots. High auxin production triggers the production of earlywood (reviewed in Larson, 1994; Aloni, 2001).

For a given amount of carbon stored as sapwood, changing the growth ring latewood/earlywood ratio from 0.5 (ratio found in the trees studied) to 2, for just 1 year, would enhance the overall wood density by 34%, which would also give an increase in Young's modulus (E or wood stiffness) in the same range (Biblis, 1969; Mott *et al.*, 2002), because wood density and E are correlated by a factor close to 1 (Bodig and Jayne, 1982). Mechanical performance (as judged by structural stiffness) increases greatly as the sample diameter gets larger, but this change is dominated by the increase in the second moment of area (I that scales as a function of stem radius to the fourth power), which almost entirely erases the contribution of E . The key quotient is then $E \times I$ (structural stiffness) and a change in latewood/earlywood to 2 would increase $E \times I$ by only 26% (with an average growth rate of 8.6 mm year⁻¹, Table 1), because for a given amount of wood stored, a higher latewood/earlywood ratio would also mean a

narrower growth ring. On the other hand, k_s would be reduced by 46%, but the overall sapwood $C_{0.5-1.0}$ would be increased by 55%. Therefore, changing the proportion of latewood/earlywood for only 1 year would have more impact on hydraulic parameters than on mechanical resistance of the sapwood. The trade-off and the advantage would be that, because of an increase in capacitance, more stored water would then be available for the trees.

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