AN ABSTRACT OF THE DISSERTATION OF

Jean-Christophe Domec for the degree of Doctor of Philosophy in Wood Science and Forest Science presented on March 13, 2002.
Title: Structure and Hydraulic Function of Xylem in Two Tree Species with Contrasting Amounts of Sapwood, *Pseudotsuga menziesii* and *Pinus ponderosa*.

Abstract approved: Signature redacted for privacy.

Barbara L. Gartner

Every wood anatomist knows that the wood near the center of a tree (juvenile wood) differs from the wood laid down at some distance from the pith (mature wood), and that the wood produced during the spring (earlywood) differs from the wood produced during the summer (latewood). There is a progressive increase in the dimensions of the cells from inner to outer growth rings. These differences affect the structure and function of the wood for water transport and mechanics. However, why do trees produce different wood quality as a function of cambial age? Is it as an adaptation to hydraulics or mechanical demands? No research has been undertaken in this area, because of the historic lack of communication between wood scientist and ecophysiologists, and because the hydraulic architecture field had few insights to offer until its recent wave of increasing sophistication. The chapters presented here are founded on these questions and provide new concepts and understandings of the trade-off between hydraulic properties and mechanical support in trees. We measured specific conductivity (k_s) and vulnerability to embolism (loss of k_s) to map tree hydraulic properties at different vertical and radial locations in the trunk and branches. In addition, field measurements, mechanical characteristics and anatomical features were determined. To investigate a wide range of wood properties, this research was

conducted in two conifer species with contrasting amount of sapwood Douglas-fir (*Pseudotsuga menziesii* Mirb.) and ponderosa pine (*Pinus ponderosa* Dougl) and within three different age-classes. In Douglas-fir, the differences in wood properties from the pith to the bark, from the bottom to the top of a tree, and within earlywood and latewood had more effect on hydraulic than on mechanical properties. In ponderosa pine, change in wood properties did not affect the hydraulic characteristics as much as in Douglas-fir. We showed that ponderosa pine sapwood has so much potential storage of water that it can compensate and level off the differences in water transport. Any change in wood density from pith to bark is more reflective of the need to alter hydraulic efficiency than the need to increase mechanical strength as trees grow.

Structure and Hydraulic Function of Xylem in Two Tree Species with Contrasting Amounts of Sapwood, *Pseudotsuga menziesii* and *Pinus ponderosa*

By
Jean-Christophe Domec

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented March, 13, 2002
Commencement June, 2002

Doctor of Philosophy dissertation of Jean-Christophe Domec presented on March 13, 2002.

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Jean-Christophe Domec, Author

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Structure and Hydraulic Function of Xylem in Two Tree Species with Contrasting Amounts of Sapwood, *Pseudotsuga menziesii* and *Pinus ponderosa*

Chapter I

Introduction
or Justification and Expected Accomplishments

The four manuscripts that comprise this thesis focus on different aspects of hydraulic versus mechanical roles of wood in Douglas-fir and ponderosa pine. Most researchers who study water relations think that the secondary xylem is developed by the cambium to maximize water transport in the trunk, whereas researchers in wood mechanics assume that it is to support the loads of the crown. These different interpretations of the role of wood in a tree must be made through the characteristics on which the selective pressures were large, and through a varied range of wood properties. No research has been undertaken in this area because the hydraulic architecture field had few insights to offer until its recent wave of increasing sophistication (e.g., Tyree and Sperry 1989), hypothesis (e.g., Ryan and Yoder 1997) and controversies (Meinzer *et al.* 2001*a*, 2001*b*).

Is there a tradeoff between mechanical and hydraulic function of wood (Gartner 1996)? The answer is almost semantic, and partly depends on how a tissue is organized. At the level of cell type, yes: cells that are specialized for high conductivity make up wood of lower density and stiffness (modulus of elasticity). At the level of the tissue, the answer depends on the cellular organization. In almost all cases, self-supported trees have lower water transport efficiency (or specific conductivity) and higher density and stiffness than the plants that do not have to provide their own support (lianas, vines; Gartner 1991*a*, 1991*b*). Hydraulically, a

young tree has a low ability to buffer its environment and it may experience highly negative water potentials (drought), so wood with low vulnerability to embolism (air blockage) would be adaptive. Young wood higher up the tree, such as on the leader, would have a larger system to buffer water deficits due to capacitance, so could survive with less-safe wood. Outer wood would best serve the plant with high conductivity; low safety would not be detrimental. Mechanically, the small change in stiffness relative to the large change in second moment of area (which scales as r^4), suggests that stiffness is relatively unimportant. Research on prediction of stresses in tapered (Gere and Carter 1963) or tapered and orthotropic bending members (Jayne and Tang 1970; Leichti and Yoo 1992), has shown that small tapers (< 10°) have little effect on normal bending stresses, but can have an enormous effect on the magnitude and position of shear stresses. In a cylinder, the maximum bending stress occurs at its base, but in a slightly tapered one, it occurs at 20-60% of its height (depending on basal anchorage, taper, and loading; Leichti and Yoo 1992).

Within a single tree, and between a chronosequence of trees, **it is therefore logical to hypothesize that seedlings, saplings, and leaders should require wood of very different structure to meet both water transport and mechanical needs**. Within one individual, woody plants have a large range of anatomical and mechanical properties, varying within the bole both radially and vertically, varying along a branch from the insertion with the stem outward to the tip, and in roots versus aboveground parts. Wood in all these compartments also varies within each growth ring that constitutes a trunk, branch or root. The radial variation across sapwood has been labeled "juvenile wood" (JW). The anatomical, chemical, and mechanical properties of JW are quite distinct from those in "mature wood" (MW), and for many applications JW is considered inferior. Limited data showed that in going from JW to MW in Douglas-fir there are changes by a factor of 1.7 in wood density, 4.5 in stiffness (Senft et al.1985*a*), 2.9 in tracheid length and 2.2 in tracheid width (Megraw 1985). Juvenile wood has received much attention from

forest products users, who discovered they must have different uses for JW and MW, and tree breeders, who assume a goal should be to decrease its severity or duration of formation (Senft et al. 1985*b*). With short rotation ages in use for forest trees, JW is becoming an increasingly large proportion of the resource base for solid wood products, composites, and paper. However, no one has asked the biological question, **"Why do trees produce different wood quality as a function of cambial age?"** or in other words: **Do trees make JW, MW as an adaptation to hydraulic or mechanical demands**?

The radial ring variation, or the two distinct zones of growth within a tree ring, are earlywood (EW) and latewood (LW). Trees grow mostly during the springtime, when there is plenty of rain and sun to nourish them. They start their spring growth by dividing a layer of cells known as the cambium, that lay between the old wood and the tree's bark. In cold winter climate, when the frost from the winter has left the ground and water becomes available to the subsurface EW begins to develop. This process leads to the reactivation of the cambial growth (Bannan, 1962). As the growth rate slows and stops during fall, the cells laid down are smaller, denser and mechanically stronger (and therefore appear darker). This layer, called LW, marks the end of the growing season and is portion of an annual ring that is produced after the EW formation has ceased. The area from the beginning of the earlywood and end of the latewood periods represent one year of growth. However, no one has asked the biological question, **"Why do trees produce different wood quality as a function of ring age?"** or in other words: **Do trees make EW, LW as an adaptation to hydraulic or mechanical demands**?

My overall research goal was to infer whether trees have evolved the strategy of producing JW/MW and EW/LW, for hydraulic function or for mechanical support function. An alternative, that production of JW or MW, and EW or LW is a neutral trait, would be indicated by only small effects of radial change in wood structure on both hydraulics and mechanics. Such a result could suggest that forest managers must consider the role of JW and LW in management

and tree improvement in order to avoid, inadvertently, creating plantations that are vulnerable to stress such as wind or drought. If JW or LW produced by a tree allow it to survive a water stress, then any tree-breeding program that looks for altering their proportion or properties could produce drought-vulnerable plants, resulting in high economic and environmental costs. If the hydraulic function of JW or LW is important, then programs can proceed to select or manage for wood of desirable quality for users. To achieve my chalenging goal, I split it into two main objectives, related to pure hydraulic studies (Chapter II, IV and V) and a combination between hydraulic and mechanic (Chapter III, with some mechanical conclusions discussed in chapters IV and V).

My first objective was to assess whether trees produce wood with different hydraulic properties in different locations across the whole sapwood width (Chapter II, and IV for Douglas-fir and ponderosa pine species respectively), but also within a single ring (Chapter V, study done on Douglas-fir only). I adapted the pressure-bomb technique (Cochard *et al.* 1992) that is commonly used to measure vulnerability to cavitation in branches and roots (Sperry and Ikeba 1997) for measuring vulnerability to embolism in disk segments. The objective of this part of my work was to test whether it can be applied to pieces of wood as it can on branches or stems. After successfully developing this technique on pieces of trunk, I measured specific conductivity (k_s), vulnerability to cavitation (which was a novelty) in MW at breast height and in JW and in leaders (JW upper) as well as in EW and LW from a single growth ring.

My second objective was to explore whether change in wood properties are adaptive, or based on hydraulic or mechanical characteristics (Chapter III, and parts of chapters IV, and V). If one compares the function of a gymnosperm growth ring going from pith to bark, one finds lower mechanical and hydraulic efficiency in the pith area than toward the bark (Menuccini *et al.*, 1997). This pattern is due to the EW having larger cell dimensions from pith to bark and at the same time the LW becoming more dense. Likewise, a stem could increase its specific conductivity by

having a few large vessels or tracheids in EW but with unchanged mechnical properties by keeping wood density constant. In a series of experiments (hydraulic) and modeling efforts (hydraulic and mechanical), I sought to identify whether trees have a higher safety factor for water transport than for mechanical support (Chapter III). The safety factor could be defined as the rate of failure (hydraulic or mechanic) that still permits a tree to survive. Hydraulic failure occurs when a tracheid becomes embolized or air-blocked. Using the vulnerability to cavitation curves measured in laboratory on pieces of trunk and branches, and the minimum negative water potentials as a function of radial and vertical position in the tree, we mapped hydraulic failure of different parts of the tree. This study led me to determine the minimum loss of water efficiency (or loss of specific conductivity) of sapwood in spring (wet period) and more interestingly the maximum, at the end of summer (dry period).

Mechanical failure occurs when the bending stresses exceed those wood can support. We modeled trees as tapered beams with concentric shells of varied material densities. We hypothesized that trees have a higher safety factor for mechanical support than water transport, suggesting that trees have evolved the large radial changes in anatomy more for hydraulic than mechanical reasons. Trees would produce wood for hydraulic and not mechanical function: JW near the plant's base in young trees and higher up in older trees to buffer environmental pressure.

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Chapter II

Cavitation and Water Storage Capacity in Bole Xylem Segments of Mature and Young Douglas-fir Trees

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Domec, J.C. and B.L. Gartner. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. Trees, 15: 204–214.

II.1 ABSTRACT

Hydraulic specific conductivity, vulnerability to cavitation and water storage capacity of Douglas-fir sapwood was determined for samples from six young (1.0–1.5 m tall) and six mature trees (41–45 m tall). Measurements on samples from young trees showed there were no effects of two contrasting sample types (entire stem segments vs. sectors chiseled out of entire stems) on any of the calculated hydraulic parameters, for vulnerability to cavitation and water storage capacity. Measurements on mature trees were made on wood from four heights on the bole and from two sapwood depths. Outer and inner sapwood at the base of the tree had higher water storage capacities and were more vulnerable to cavitation than was sapwood from the tree top. At every height, old trees were more vulnerable to cavitation than at 1.0 m from the ground in young trees. The water storage capacities showed three distinct phases at the base of the trunk. Young trees had similar water storage capacity (per unit volume of sapwood) to the top of the mature trees, which was lower than the water storage capacity throughout the rest of the bole xylem. The way in which capacitance was calculated (on a volumetric basis vs. on a relative water content basis) affected the conclusion one would draw at the low water potentials (<–3 MPa). Within a tree, we found an apparent trade-off between having both hydraulic specific conductivity and stem water storage, and vulnerability to cavitation.

Key words Douglas-fir (*Pseudostuga mensiesii* (Mirb.) Franco) – Cavitation – Embolism – Trunk vulnerability curve – Water storage capacity

II.2 INTRODUCTION

Methods now exist to quantify the effect of embolism on hydraulic conductivity (Sperry et al. 1987). These methods consist of measuring the flux of water perfused under moderate pressure difference (5 kPa) and steady-state conditions across an isolated stem segment that has been subjected to a given degree of water stress. This conductivity is then expressed as a percentage of the maximum conductivity obtained before water stress was imposed. By repeating this procedure with different samples at different pressure potentials, a vulnerability curve (VC) can be established. A VC expresses the percentage loss of conductivity exhibited relative to the minimum water potential experienced by the sample.

The vulnerability curves published for woody plants in general and for Douglas-fir (*Pseudostuga mensiesii* (Mirb.) Franco) in particular have been for small seedlings or branches and roots (Cochard 1992; Sperry and Ikeba 1997; Kavanagh et al. 1999), but the crucial information for the trunk is unknown. Current techniques to quantify the vulnerability to embolism (e.g., Holbrook et al. 1995; Alder et al. 1997) are limited to small-diameter (<2-cm) roundwood (that necessitate the use of the entire xylem cross section), so absolutely no information on trunks or indeed any plants >2-cm diameter has been assembled. Spicer and Gartner (1998a) developed a conductivity apparatus that allows determination of the hydraulic specific conductivity (k_s) of wood samples that are smaller than an entire stem cross-section. This apparatus allows measurements of k_s of trunks, branches, and roots. This paper represents the first attempt to use this method in conjunction with the air-injection method to determine the VCs as well as the water storage capacity of mature tree trunks.

Within an individual, woody plants have a large range of anatomical and mechanical properties, varying within the bole both radially and vertically. Because of the differences in wood anatomy and density (Gartner 1995), it is logical to hypothesize that the top and the bottom of a tree would be characterized by wood

of very different hydraulic properties. We test the hypothesis that the top of the tree is less vulnerable to cavitation than the bottom because of smaller tracheid diameters (Panshin and De Zeeuw 1980), which are harder to embolize (Tyree et al. 1994), and that inner sapwood has lower resistance to cavitation than outer sapwood because it has "aged", or accumulated more damage to the conducting system. In addition, we tested whether the sample geometry affects VCs and values of water storage by comparing the air injection methods on entire cross sections of roundwood versus excised chunks from young trees. Finally it is surprising that among numerous studies on vulnerability to cavitation, there is still a lack of a simple method to analyze the VCs that can be compared between studies. We present coefficients that have a physiological significance, then use these coefficients to compare VCs between and within individual trees.

II.3 MATERIALS AND METHODS

II.3.1 Sample shapes test

Trunk segments were collected from six young (4-year-old) Douglas-fir trees from a nursery bed ranging from 1.0 to 1.5 m in height. Long stem segments were removed from the third year of growth where the diameter under bark was small enough to fit entirely into a 1-cm-diameter double-ended pressure chamber. The whole segments were long enough to be divided into two smaller segments of 13 cm. The bottom segment was split in two parts along the grain with a chisel whereas the top segment was left intact, and the ends of all segments were recut with razor blades. Only one of the split segments was used from each tree.

The principle of the method was to measure the loss of conductivity on the prepared samples of trunk wood by alternately measuring conductivity in one apparatus and applying air pressure in a second apparatus. The first apparatus was a double-ended chamber (made of PVC) with a latex membrane that was pushed

against the sample sides with a small positive pressure to keep fluid from leaving by the samples sides rather than ends (Spicer and Gartner 1998a, b). The second apparatus was a double-ended pressure chamber that is used for the air-injection method (Salleo et al. 1992; Sperry and Saliendra 1994). We measured the initial hydraulic conductivity $k_{s(i)}$, then imposed a small positive air pressure (Ψ) on the sample to induce cavitation in the most vulnerable tracheids. Segments were then removed from the pressure chamber and submerged in water for about 15–35 minutes to permit diffusion of air bubbles into tracheids. The samples were freshly recut at each end after each pressurization, the hydraulic conductivity at Ψ, $k_{s(\Psi)}$, was re-measured, and a larger pressure was then imposed. The pressure bomb was first pressurized to 0.5 MPa and stabilized with a valve regulator for 1 min, and then 1.0 MPa steps were used until >95% loss of $k_{s(i)}$ was reached. We established the vulnerability curves (VCs) by graphing the proportion of saturated $k_{s(\Psi)}$ as a function of applied air pressure. We conducted several tests to assess whether there was a difference between the loss of conductivity for 1-min duration of pressurization and that for 10 min, but could detect none, which was consistent with what was found by Kavanagh et al. (1999) on branches and roots for the same species. For the split segments, the conductivity apparatus as well as the method of measurement were taken from Spicer and Gartner (1998b). One end of the pressure sleeve was attached to tubing filled with filtered (0.22μm) water adjusted with HCl to pH 2 in order to prevent microbial growth. The temperature of this solution was recorded before and after each hydraulic conductivity measurement. The distal end was attached to a 1 ml micropipette (0.01 ml graduation) and the flow through the segment was induced by a hydraulic head of pressure of 0.0052 MPa. We recorded the time for 5 consecutives intervals, observing the meniscus in the pipette as it passed successive tick marks. After measurements, sample lengths were measured (mm) then the cross-sectional area of each end was estimated by using the two tangential widths and one radial width. The solution was passed through 13 cm long trunk sections ranging from 0.7 to 0.9 cm^2 in transverse area.

For the whole, intact segments, the two differences in the methodology were the following: the conductivity measurements were made without surrounding the sample in the membrane-lined pressure sleeve, and transverse area was estimated with two perpendicular diameters.

II.3.2 Mature trunk measurements

Six Douglas-fir (*Pseudostuga mensiesii* (Mirb.) Franco) trees from the Cascade Range, Oregon, USA (42°57N, 123°21W) located at 220-m elevation were selected from the stand for experiments in late March 1998, before the spring growth had started. The trees were selected to have no major forks or injury and to be of similar size and dominance. The trees averaged 43.7 ± 1.3 m tall and were 100–120 years old. The morphological characteristics of the trees are shown in Table II.1. Within hours of harvesting (on 27 March and 1 April), we cut four disks from each tree with an approximate thickness of 22 cm from the following internodes (counting from the top of the tree): 5, 15, 35, and from 1-meter height above the ground (which represented 102–113 internodes, Fig. II.1). These disks were transported in wet plastic bags then stored at 5°C until blocks were prepared. From each disk, four blocks were cut within three days of felling the trees, two from the inner sapwood and two from the outer sapwood. Preparation of these specimens made from the blocks followed the procedures outlined by Spicer and Gartner (1998a, b). The specimens were split with a chisel along the grain then stored in the dark at 5°C in water that was changed daily, until they were used within three weeks of preparation. After each measurement the number of days (ranging from 1 to 21) was computed to determine the effect of time storage. Determination of the VCs for each segment from the six trees followed the same method as that described above for the young trees. The storage time was unavoidable because trees had to be harvested in one trip, and then it required about 6 hours to produce a vulnerability curve on each sample, once it was already prepared.

Figure II.1: Preparation technique for Douglas-fir samples. (a) Four disks were cut perpendicular to the trunk of the tree. One disk at node 5 counting down from the top of the tree, one at node 15, one at node 35 and one at 1-meter height (corresponding to node 105). (b) For the first three disks, four samples were removed from two perpendicular sides in order to determine the hydraulic specific conductivity, the vulnerability to cavitation, and the water storage capacity. Two samples were taken in the inner part of the sapwood (two rings before the sapwood-heartwood transition), and two other samples in the outer part (youngest rings formed). For the upper disk (node 5), only two samples were taken in the outer part. The disk represented as an example is from node 15.

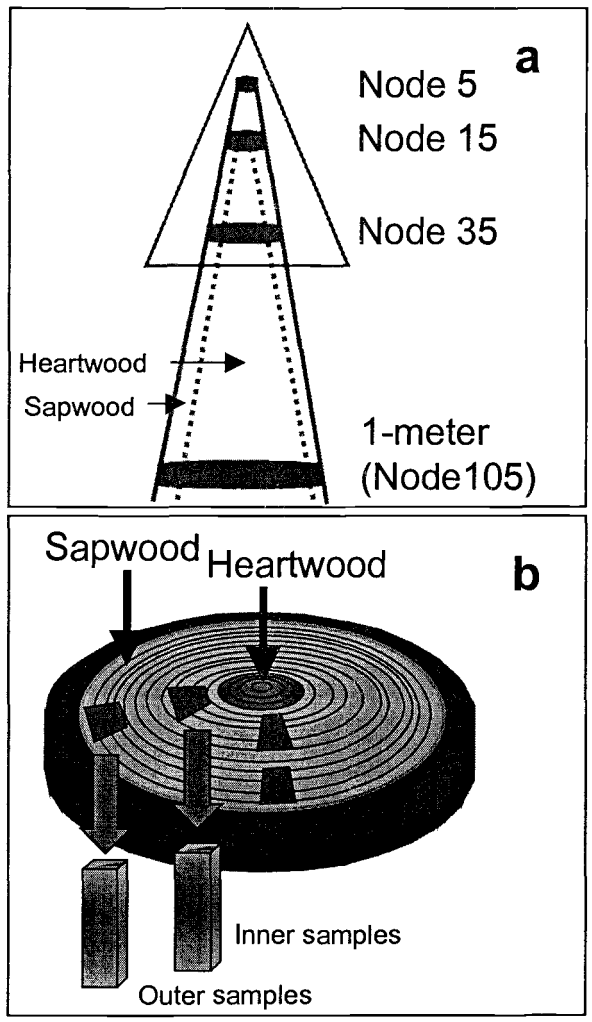


Table II.1. Mean values (± SE, n=6) for morphological characteristics of mature Douglas-fir trees by height position (node) counting down from the top of the tree, at 1 m from the ground, and at the base (about 30 cm). The base of the live crown was located a few nodes below node 35 at a mean height of 29 ± 1 m. The whole sapwood width has been divided in two parts to determine the outer sapwood shell (comprised between the outer part of the sapwood and the middle of the sapwood width) and the inner sapwood shell (comprised between the middle of the sapwood width and the heartwood-sapwood boundary). The proportion of outer sapwood (%) has been calculated in dividing the outer sapwood shell by the total sapwood area.

Height position	Mean height (m)	Diameter (cm)	Sapwood area (cm^2)	Heartwood area (cm^2)	Proportion of outer sapwood (%)	Number of sapwood rings (no.)
Node 5	42 ± 2	3.5 ± 0.5	7 ± 1	0	100	4.8 ± 0.2
Node 15	39 ± 1	9.5 ± 1.1	55 ± 6	50 ± 1	64 ± 1	8.9 ± 0.4
Node 35	35 ± 1	20 ± 1	222 ± 2	61 ± 12	60 ± 1	15 ± 1
1 meter	1	64 ± 2	760 ± 10	1766 ± 117	52 ± 1	29 ± 2
Base	0.33 ± 0.03	67 ± 2	808 ± 10	1915 ± 123	52 ± 1	30 ± 2

II.3.3 Calculation of specific conductivity

Sapwood specific conductivity was calculated according to Darcy's law (Edwards and Jarvis 1982):

$$k_s = \frac{V \cdot L \cdot \eta}{t \cdot A \cdot \Delta P} \quad (1)$$

where V is the volume of water that went through the sample (m^3), L is the sample length (m), η is the viscosity of water at the temperature at which the experiments were conducted (N s m^{-2}), t is the time (s), A the cross section area (m^2) of the sample and ΔP is the pressure difference (Pa) between ends of the sample. The entire cross-section of each sample was assumed to be functional sapwood and was calculated from the average of the cross-sectional areas of the two ends.

II.3.4 Calculation of coefficients from vulnerability curves

The percentage loss of conductivity at a given pressure was calculated using the following equation (Sperry and Tyree 1988):

$$\%loss\_k_{s(\Psi)} = \frac{\left(k_{s(i)} - k_{s(\Psi)}\right)100}{k_{s(i)}} \quad (2)$$

In this equation $k_{s(i)}$ is the initial specific conductivity and $k_{s(\Psi)}$ is the conductivity measured after air had been injected at a positive pressure, Ψ. A plot of these data is called a VC (vulnerability curve). The relationship between loss of conductivity and the applied pressure can be described by the following sigmoidal equation (e.g., Pammenter and Vander Willigen 1998):

$$\%loss\_k_{s(\Psi)} = \frac{100}{\left(1 + e^{a(\Psi - b)}\right)} \quad (3)$$

The coefficient "a" is an indicator of the slope and the coefficient "b" represents the tension at which 50% loss of conductivity occurred (denoted as $b=\Psi_{50}$).

We analyzed these data further by looking at the values from the derivative of Eq. 3. In this manner, more information could be gleaned and compared between different VCs. The derivative of Eq. 3 is:

$$\frac{d(\%loss\_k_{s(\Psi)})}{d\Psi} = \frac{-a\left(e^{a(\Psi - b)}\right)100}{\left(1 + e^{a(\Psi - b)}\right)^2} \quad (4)$$

The derivative gives us the slope of each tangential line at an applied pressure, Ψ. If one calculates the derivative for the point on the curve where the loss of k_s is 50% ($\%loss\_k_{s(b)}=50\%$), one can then calculate the intercepts of the derivative at $\%loss\_k_{s(\Psi)} = 0\%$ as (Fig.II.2):

$$\Psi_e = 2/a + b \quad (5)$$

and $\%loss\_k_{s(\Psi)} = 100\%$ as:

$$\Psi_{max} = -2/a + b \quad (6)$$

The values Ψ_e is termed the air-entry point (Sparks and Black 1999) and it is an estimate of the xylem tension at which pit membranes are overcome within the conducting xylem and when cavitation starts. Of course, it is only a linear approximation of the true air entry point, which may start very close to $\Psi = 0$ (as in

Figure II.2: Method of determining xylem air-entry point (Ψ_e) and full embolism point (Ψ_{max}) based on vulnerability curves data. The vulnerability curves are calculated using both parameters a and b (Eq. 3). The percent loss of hydraulic conductivity plotted versus the pressure applied results in a linear phase where the cavitation jump occurs. The air entry point and the full embolism point represent 12% and 88% loss of xylem hydraulic conductivity respectively (Eqs. 5 and 6). The slope of the dashed line tangential to the point (Ψ_{50}=b, 50) is equal to a.100/4 (Eq. 7).

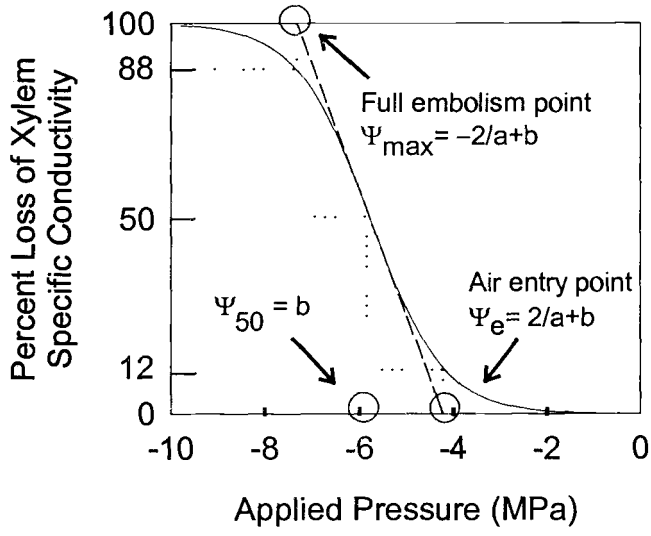


Fig. II.2), but it provides a very useful way to compare different curves. Likewise, we termed Ψ_{max} the full embolism point and it is interpreted as approximating the actual maximum tension of the xylem before failing and becoming non-conductive. The applied pressures at air entry point and at full embolism point represent respectively 11.92 and 88.08% loss of xylem hydraulic conductivity. Finally, one can also derive the actual slope (s) of the linear part of the vulnerability curve from Eq. 4 (Fig. II.2) as:

$$s = a \cdot 100/4 \quad (7)$$

where s is in % loss_k_s MPa^{-1} and can be used as an estimate of the slope of the conductivity loss versus xylem water potential. As suggested by Sperry (1995), the steeper the slope, the more conservative the evolved strategy of the xylem due to a smaller safety margin between Ψ_e and Ψ_{max}.

II.3.5 Water storage capacity

For each conductivity measurement, the mass and the volume of the specimens were measured. Mass was determined on a balance after samples were dried using paper towel, and volume was determined from mass displacement of the specimen in a beaker of water on a balance (Borghetti et al. 1991). After the last cycle, the specimens were reweighed after drying at 104°C. Relative water content (RWC) was calculated as follows:

$$RWC = \frac{M_f - M_d}{(V_f - V_s)D_{H2O}} \quad (8)$$

where D_{H2O} is the density of water (g cm^{-3}); M_f and M_d are the fresh and dry mass of the wood (g), respectively; V_f is the fresh volume of the sample (cm^3); and V_s is the volume of solid material (cm^3) (pure cell wall material, without air or water).

The volume of solid material was calculated from the dry mass assuming that dry cell-wall material has a density of 1.53 g cm^{-3} (Siau 1984).

Water storage capacity can be defined as the amount of water withdrawn from the stem at given water potential (Holbrook 1995). Most of the time and for comparative reasons, capacitance is expressed as the change in water mass relative to the sample volume per unit change in water potential. The volumetric capacitance (C_V) between 0 and 5 MPa was determined after each conductivity point as follows (Running 1980; Edwards and Jarvis 1982; Tyree et al. 1991):

$$C_V = \frac{d\left(\frac{(M_f - M_d)}{V_f}\right)}{d\Psi} \qquad \text{in kg } l^{-1}\,\text{MPa}^{-1} \qquad (9)$$

Because wood is a porous material of variable density, we also expressed the capacitance as the change in RWC per unit change in water potential. This latter expression allows us to compare differences in storage capacities for samples differing both in total water volume and wood density. The RWC-based capacitance (C_{RWC}) between 0 and 5.0 MPa can be defined as:

$$C_{RWC} = \frac{dRWC}{d\Psi} \qquad \text{in RWC MPa}^{-1} \qquad (10)$$

For the mature trunk measurements, to determine whether the slope of the dehydration curve was constant throughout its range, we also computed capacitance values for three phases in each dehydration curve (Tyree and Yang 1990): a phase from 0 to 0.5 MPa ($C_{0-0.5}$), a phase from 0.5 to 3.0 MPa ($C_{0.5-3}$) and a phase from 3.0 to 5.0 MPa (C_{3-5}). According to Tyree and Yang (1990), these three phases dealt with water released by capillaries, water released by both capillaries and cavitation events, and water released by cavitation events only, respectively.

II.3.6 Statistical Analysis

For the sample shapes test, paired *t*-test were used to test differences in hydraulic parameters, a, b, Ψ_e, Ψ_{max}, and the slopes of the dehydration curves, between split and whole seedling trunks.

For the mature tree trunks, the vulnerability curves were fit by the least square methods on the empirical model described in Eq. 3 conducted with Sigma Plot 5.0 for Windows (1999, Jandel Scientific Software, San Rafael, CA). Each sample was used as a single replicate that gave a single value of each a and b. The values of a, b, Ψ_e, and Ψ_{max}, were compared among locations (two radial and four height positions) by carrying out an analysis of variance (ANOVA) and covariance (ANCOVA) using a strip-plot randomized complete block design (trees as block) with radial position and height position being the strip plots factors. In the strip plot design, which is a modification of the split plot design, observations are made on sets of "whole units". Unlike the split plots design, there are no split plots within whole (main) plots. Rather, the subunit treatments are applied in strips across an entire replication of main plot treatments. This arrangement facilitates mathematical manipulations concerning the subunits (there are easier to apply) but sacrifices precision in comparing the main effect of a treatment (SAS 1996). We used ANCOVA specifically to test for the significance of a covariate, the number of days of running the sample after preparation and initial RWC, while controlling for the effect of k_s.

The values of capacitance for a given range of pressures were compared among position with an analysis of variance (ANOVA) using a strip-plot randomized complete block design (trees as block) with radial position and height position as the strip plots factors and with repeated measures in the procedure (repeated measures being the three different capacitances because they are inter-dependent and correlated over the range of applied pressures). The experiment was designed to assess values at both inner and outer sapwood, but for height position,

we were interested in an estimate of the entire sapwood. Therefore, the effect of height position on the vulnerability parameters and on both measures of capacitances (C_v and C_{rwc}) was made by weighting the values by the proportion of the total sapwood area occupied by the outer and inner sapwood shells (Table II.1). The inner shell represented the area from the third growth ring exterior to the heartwood/sapwood boundary to the middle of the sapwood zone, and the outer shell represented the area from the middle of the sapwood zone to the cambium.

Least square (LS) means were generated from a PROC MIXED procedure, and multiple comparisons among means were calculated using least square differences (LSD). All statistical procedures were conducted with Statistical Analysis Systems software (1996; SAS Inc., Cary, NC).

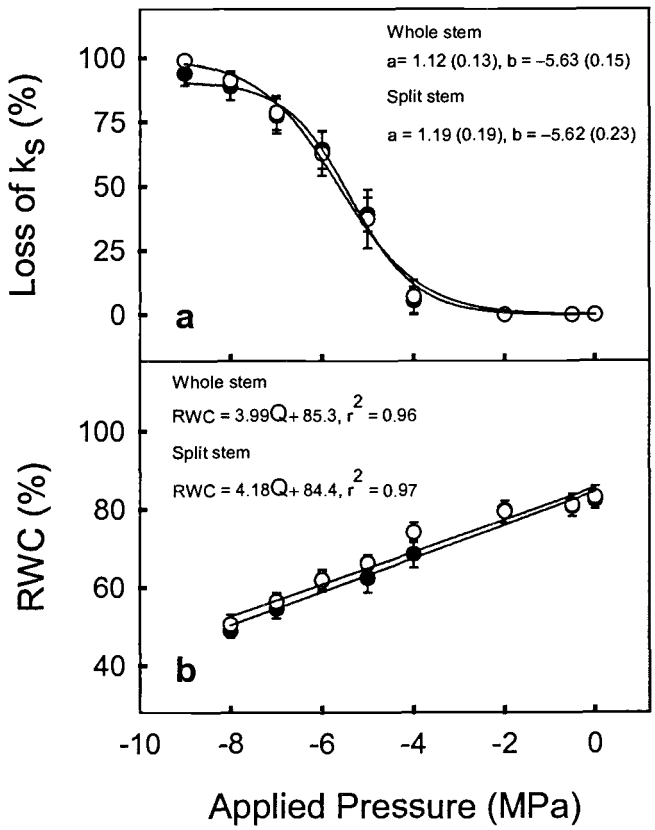
II.4 RESULTS

II.4.1 Sample shapes test

Whole stems and pieces of stems taken from Douglas-fir seedlings had similar VCs (vulnerability curves) (Fig. II.3), with respective values *s* (slope of the linear part of the VCs) of 28.0 and 29.8% loss_k_s MPa^{-1}. Neither the vulnerability parameters, nor the estimated capacitances differed between the whole and split stems ($P>0.31$, paired t-test, data not shown). The values of Ψ_e (the air-entry point) for the whole and split stems were –3.4 and –3.2 MPa respectively. The values of Ψ_{max} (the full embolism point) for the whole and split stems were –7.9 and –8.0 MPa respectively.

The mean C_V (capacitance on a volumetric basis) was 0.037 and 0.036 kg l^{-1} MPa^{-1} for whole and split stems respectively. The minimum capacitances were between 0.5 and 2.0 MPa. The minimum C_V was 0.021 and 0.017 kg l^{-1} MPa^{-1} for the whole and split stems respectively. The minimum C_{RWC} (capacitance on the basis of

Figure II.3: Relationship between (a) vulnerability curves and (b) relative water content (RWC) for Douglas-fir seedlings showing the percentage loss of xylem hydraulic conductivity versus the negative of air pressure used in air injection experiments (n=6 for each injection mean; error bars are standard errors, vulnerability parameters from Eq. 3 and stem capacitances are shown in the figure with the SE in parentheses). Filled symbols are for split stem and open symbols are for the whole stem.



relative water content) was 1 and 2% RWC MPa^{-1} for the whole and split stems respectively.

II.4.2 Trunk vulnerability to cavitation

For both measures of RWC and percent loss of conductivity, blocking on trees was effective: the estimate of variation between trees was more than zero. This difference means that the variation of our experimental units (height and radial positions) was greater between the trees than within the trees. By accounting for these intrinsic differences among our experimental units, we obtained a smaller experimental error and improved the precision with which we estimated the effects of height and radial positions (Newman et al. 1997). Specific conductivity (k_s) was neither related to the number of days after preparation nor the RWC of the sample (P>0.05, ANCOVA).

The tips of old trees were more vulnerable to cavitation than the tips of young trees (compare Fig. II.3a and top panel, Fig. II.4a). Additionally, for the outer sapwood, the top of the tree (node 5) had a significantly higher resistance to cavitation than node 35 and 1 meter for all 3 parameters Ψ_e, Ψ_{50} (the tension at which 50% of conductivity is lost) and Ψ_{max} and than node 15 for the 2 parameters Ψ_{50} and Ψ_{max} (Table II.2). For the inner sapwood, there was no significant difference between the base, node 35, and node 15 for any of the parameters calculated from the VCs. There was, however, a marginally significant interaction between disk position and the sapwood radial position for the first three heights for both Ψ_e ($F_{2,10}$=4.14, P=0.0491) and Ψ_{50} ($F_{2,10}$=4.12, P=0.0497).

In an ANOVA with height and radial position as fixed effects for the lower three heights, there was no significant difference between the overall inner and outer sapwood for either Ψ_e ($F_{1,5}$=6.47, P=0.052) or Ψ_{max} ($F_{1,5}$=2.77, P=0.16). There was a significant difference for Ψ_{50} between the overall inner and outer sapwood ($F_{1,5}$=6.98, P=0.041). This effect resulted from the significant difference between the outer and inner samples at node 35. Indeed, by position inner sapwood

was only significantly less resistant to cavitation ($P<0.0045$) than outer sapwood at node 35 (approximately base of the live crown) where Ψ_e and Ψ_{50} are respectively 0.9 MPa and 0.6 MPa higher than the outer sapwood measurements (Fig. II.4a and Table II.2). This pattern is not observed at the base of the tree ($P>0.75$) or at node 15 ($P>0.075$).

For the lower three disks, there was no evidence (Table II.3) of a position effect for either Ψ_e ($F_{2,10}=2.11$, $P=0.17$) or Ψ_{50} ($F_{2,10}=1.29$, $P=0.32$). However, if we include the top of the tree (node 5), the difference between positions becomes highly significant for both parameters Ψ_e ($F_{3,14}=13.06$, $P=0.0002$) and Ψ_{50} ($F_{3,14}=10.10$, $P=0.0023$). There was no evidence of a position effect on s for the four disks ($F_{3,14}=2.23$, $P=0.15$). Node 5 was significantly different than the other three heights ($P<0.05$) for any of three parameters calculated. Between the other positions, the parameter Ψ_e at node 15 and 35 was significant lower than at the base of the tree ($P=0.04$).

Using the data from the four disks in the tree, we asked whether there was a relationship between k_s and Ψ_e, Ψ_{50}, and Ψ_{max} (Fig. II.5a). The slopes of straight lines were significantly different from zero at the 5% confidence level and were not statistically different from one another ($P=0.76$, ANOVA). There was a significant positive correlation for both Ψ_e and Ψ_{50} but not for Ψ_{max}.

Using the data from the four disks in the tree, we asked whether there was a relationship between sampling height and calculated parameters of the VCs (Ψ_e, Ψ_{50}, and Ψ_{max}, Fig. II.6). For Ψ_e, the slope of the portion of the line between the first two heights (the unbranched parts of the trunk between 1-meter and node 35) was –0.0101 MPa m^{-1} and was parallel to the theoretical hydrostatic gradient shown by the dotted line (–0.0100 MPa m^{-1}). This slope was zero for Ψ_{50} and positive for Ψ_{max} (0.0141 MPa m^{-1}). Within the crown (from nodes 35 to 5), the

Figure II.4: (a) Loss in conductivity and (b) relative water content (RWC) vs. applied air pressure in six mature Douglas-fir trees at four heights in the trunk (node 5, node 15, node 35 from the top and 1-meter from the base) and two radial positions (outer and inner sapwood). Within the tree, the base had a higher water storage capacity than the top (see first column, Table 4 for the linear regression coefficients and statistical comparisons among height and radial positions) and was more vulnerable to cavitation than the top. Error bars are standard errors. Filled symbols are for the outer sapwood and open symbols are for the inner sapwood.

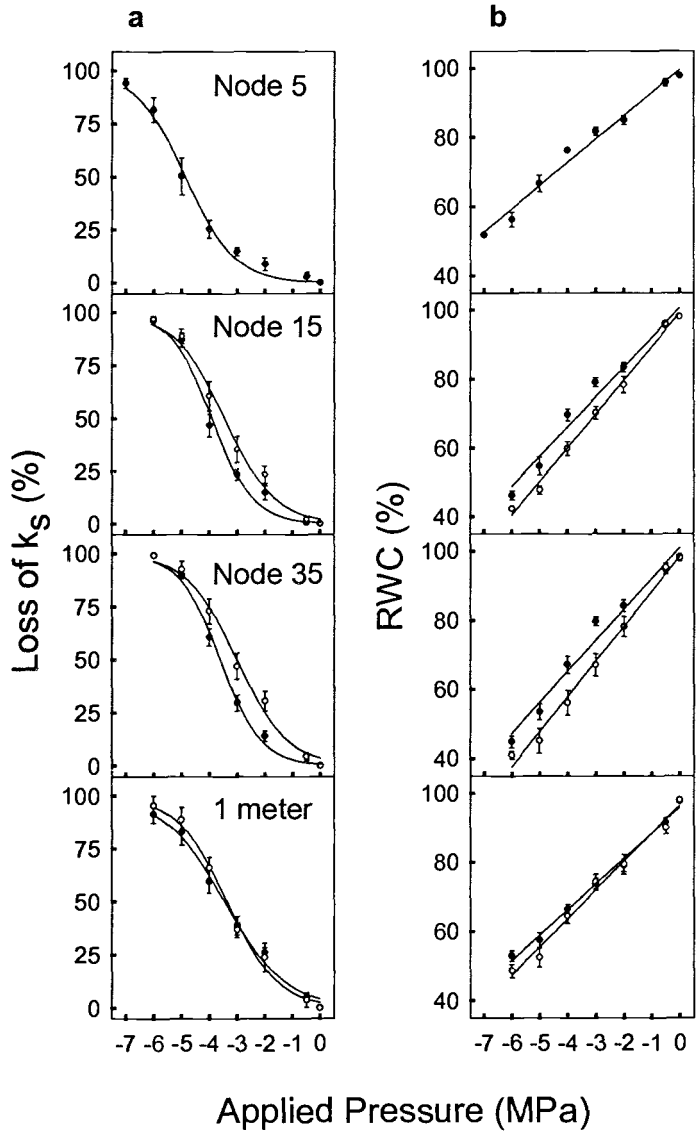


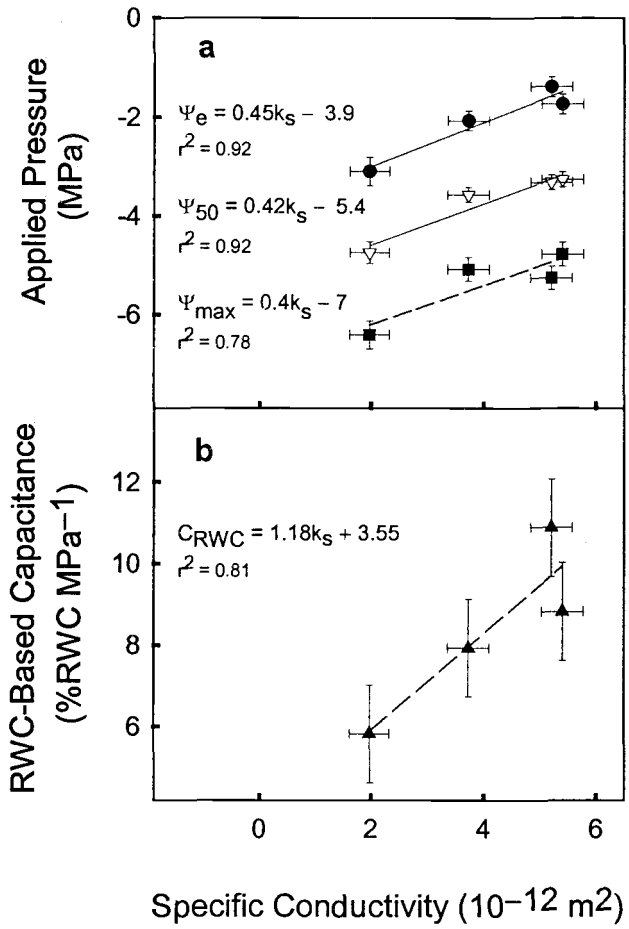
Table II.2. Effect of height and radial position in the tree on the slope of the linear portion of the vulnerability curve (*s*), the potential (b) at which 50% loss of k_s is reached, the air entry point (Ψ_e) and the full embolism point (Ψ_{max}). The loss of xylem conductivity at Ψ_e and Ψ_{max} are 12% and 88% respectively. The initial relative water content (RWC) of the samples is also given. Values with different letters within a column are significantly different ($P<0.05$). LS means (±SE, n=6) were generated from the PROC MIXED procedure, and multiple comparisons among means were calculated using LSD.

Radial position	Height position	s = a.100/4 (%loss k_s MPa^{-1})	Ψ_e (MPa)	b = Ψ_{50} (MPa)	Ψ_{max} (MPa)	RWC (%)
Outer sapwood	Node 5	30.4 ± 4.7 ab	−3.1 ± 0.3 a	−4.7 ± 0.2 a	−6.4 ± 0.3 a	97.8 ± 0.4 a
	Node 15	40.2 ± 4.4 a	−2.3 ± 0.3 ab	−3.7 ± 0.2 b	−5.1 ± 0.3 bc	97.9 ± 0.4 a
	Node 35	37.1 ± 4.4 ab	−2.1 ± 0.3 b	−3.5 ± 0.2 b	−4.9 ± 0.3 bc	98.1 ± 0.4 a
	1 meter	27.0 ± 4.4 b	−1.3 ± 0.3 c	−3.3 ± 0.2 bc	−5.4 ± 0.3 b	97.6 ± 0.4 a
Inner sapwood	Node 15	32.5 ± 4.4 ab	−1.7 ± 0.3 bc	−3.4 ± 0.2 bc	−5.0 ± 0.3 bc	97.9 ± 0.4 a
	Node 35	35.0 ± 4.4 ab	−1.2 ± 0.3 c	−2.9 ± 0.2 c	−4.6 ± 0.3 c	97.8 ± 0.4 a
	1 meter	30.3 ± 4.5 ab	−1.5 ± 0.3 c	−3.3 ± 0.2 bc	−5.1 ± 0.3 bc	97.8 ± 0.4 a

Table II.3. Effect of height position in the tree on the slope of the linear portion of the vulnerability curve (*s*), the potential (b) at which 50% loss of k_s is reached, the air entry point (Ψ_e) and the full embolism point (Ψ_{max}). The loss of xylem conductivity at Ψ_e and Ψ_{max} are 12% and 88% respectively. Values with different letters within a column are significantly different ($P<0.05$). LS means (±SE, n=6) were generated from the PROC MIXED procedure, and multiple comparisons among means were calculated using LSD.

Height position	s = a.100/4 (%loss k_s MPa^{-1})	Ψ_e (MPa)	$b = \Psi_{50}$ (MPa)	Ψ_{max} (MPa)
Node 5	30.4 ± 4.4 a	−3.1 ± 0.3 a	−4.7 ± 0.2 a	−6.4 ± 0.3 a
Node 15	33.7 ± 3.9 a	−2.1 ± 0.2 b	−3.6 ± 0.2 b	−5.1 ± 0.2 c
Node 35	33.0 ± 3.9 a	−1.8 ± 0.2 b	−3.3 ± 0.2 b	−4.8 ± 0.2 b
1 meter	25.9 ± 3.9 a	−1.4 ± 0.2 c	−3.3 ± 0.2 b	−5.2 ± 0.2 c

Figure II.5: (a) Trunk xylem hydraulic safety versus trunk xylem hydraulic efficiency of Douglas-fir trees. Xylem safety is represented by mean air entry tension (Ψ_e, filled circles), mean cavitation tension (Ψ_{50}, open triangles) and maximum cavitation tension (Ψ_{max}, filled squares). Xylem efficiency is represented by the mean specific conductivity. (b) RWC-based capacitance versus mean specific conductivity. Xylem water storage capacity is represented by the mean RWC-based capacitance from 0 to 5 MPa (filled triangles). Error bars are standard errors.



relationship between VC parameters and the heights had steeper slopes (–0.19, –0.21 and –0.23 MPa m^{-1} respectively for Ψ_e, Ψ_{50}, and Ψ_{max}).

II.4.3 Trunk water storage capacity

Relative water content (RWC) showed a linear change with applied pressure, with significantly steeper slopes from the top to the bottom of the tree ($P<0.05$, Fig. II.4b, Table II.4). The overall trunk water capacitance was higher for the unbranched (below node 35) than for the branched part of the trees (Table II.5). The top of the mature trees had similar water storage capacity to the young trees. Note that capacitance as discussed here is on a tissue volume basis, not to be confused with water storage capacity, which takes into account the capacitance and the quantity of a tissue.

Even though there was a strong linear relationship between the RWC and the applied pressure for the whole ranges of pressure (Table II.4), we separated the dehydration curves into three different phases ($C_{0-0.5}$, $C_{0.5-3}$, and C_{3-5}, Tables II.4–II.6) corresponding to the three phases described by Tyree and Yang (1990). At the base of the tree, there was no significant difference in outer and inner sapwood for a given phase (Table II.4). In an ANOVA with height and radial position as fixed effects, there was no significant difference between the overall inner and outer sapwood for either $C_{0-0.5}$ ($F_{1,5}$=0.56, P=0.60) or C_{3-5} ($F_{1,5}$=–2.01, P=0.10). There was, however, a significant difference in $C_{0.5-3}$ between the overall inner and outer sapwood ($F_{1,5}$=5.07, P=0.039). For the first three disks, this effect is due to the significant difference between the outer and inner samples at node 35 and 15 (Table II.4).

For the four disks in the tree, we asked whether there was a global relationship between $C_{0-0.5}$, $C_{0.5-3}$, and C_{3-5}. There was a significant difference in water storage capacity between $C_{0-0.5}$ and C_{3-5} ($F_{2,74}$=–3.59, P=0.006) and between $C_{0.5-3}$ and C_{3-5} ($F_{2,74}$=–4.82, $P<0.001$). Dehydration isotherms did not show

Figure II.6: Hydraulic safety of trunk xylem vs. height in mature Douglas-fir. Xylem safety is represented by mean air entry tension (Ψ_e, filled circles), mean cavitation tension (Ψ_{50}, open triangles) and maximum cavitation tension (Ψ_{max}, filled squares). The theoretical hydrostatic gradient (0.01 MPa m^{-1}) has been plotted for each parameter based on their 1-meter value (dotted lines). Error bars are standard errors.

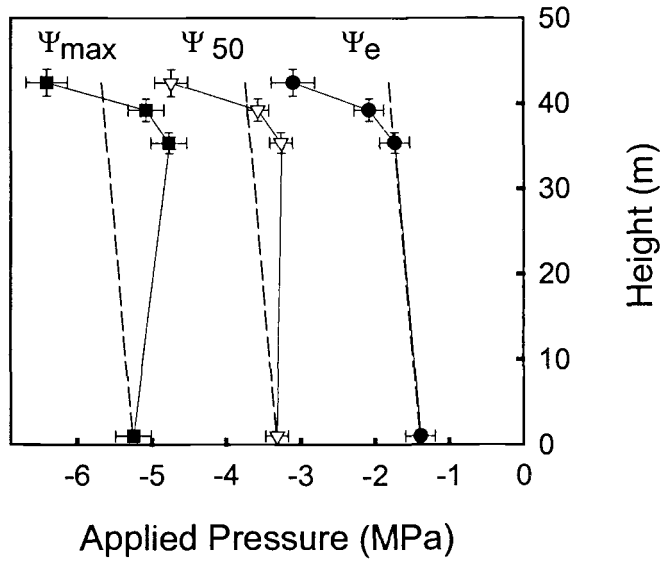


Table II.4. The first two columns represent the effect of radial and height position in the tree on the linear regression coefficients, slope (%RWC MPa^{-1}) and intercept (%RWC), of the relationship between RWC (%) and applied pressure (MPa). The slopes (r^2>0.97, P<0.01) represent the average capacitance over the total range of pressure applied. The next three columns represent the effect of radial and height positions in the tree on the RWC-based capacitances (%RWC MPa^{-1}) for the three phases $C_{0-0.5}$ (between 0 and 0.5 MPa), $C_{0.5-3}$ (between 0.5 and 3.0 MPa), and C_{3-5} (between 3.0 and 5.0 MPa). Values with different letters within a column are significantly different (P<0.05). LS means (±SE, n=6) were generated from the PROC MIXED procedure, and multiple comparisons among means were calculated using LSD.

Radial position	Height position	Regression parameters Slope	Intercept	$C_{0-0.5}$	$C_{0.5-3}$	C_{3-5}
Outer	Node 5	6.7 ± 0.4 b	99.4 ± 1.4	4.7 ± 1.9 a	5.0 ± 0.8 a	7.8 ± 1.3 a
sapwood	Node 15	8.6 ± 0.6 ac	100.5 ± 2.1	4.6 ± 1.9 a	6.1 ± 0.7 a	12.2 ± 1.2 b
	Node 35	8.9 ± 0.6 ac	100.6 ± 2.3	7.6 ± 1.8 a	5.7 ± 0.7 a	11.6 ± 1.2 b
	1 meter	7.4 ± 0.3 b	95.9 ± 1.0	12.6 ± 1.8 b	6.7 ± 0.7 a	13.1 ± 1.1 b
Inner	Node 15	8.8 ± 0.3 ac	98.9 ± 1.1	5.0 ± 1.9 a	9.3 ± 0.7 b	11.2 ± 1.2 b
sapwood	Node 35	10.1 ± 0.4a	98.3 ± 1.5	5.0 ± 1.8 a	11.2 ± 0.7 c	10.6 ± 1.2 b
	1 meter	8.2 ± 0.4ac	96.4 ± 1.5	15.9 ± 1.8 b	6.2 ± 0.7 a	10.9 ± 1.2 b

Table II.5. Effect of height position in the tree on the RWC-based capacitances (%RWC MPa^{-1}) for the three phases $C_{0-0.5}$ (between 0 and 0.5 MPa), $C_{0.5-3}$ (between 0.5 and 3.0 MPa), and C_{3-5} (between 3.0 and 5.0 MPa). Values with different letters within a column or/and a row are significantly different ($P<0.05$). LS means (±SE, n=6) were generated from the PROC MIXED procedure, and multiple comparisons among means were calculated using LSD.

Height position	$C_{0-0.5}$	$C_{0.5-3}$	C_{3-5}
Node 5	4.7 ± 1.7 a	5.0 ± 1.5 a	7.8 ± 1.2 a
Node 15	4.7 ± 1.7 a	7.3 ± 1.4 a	11.8 ± 1.4 b
Node 35	7.3 ± 1.6 a	8.0 ± 1.4 a	11.2 ± 1.4 b
1 meter	14.1 ± 1.6 b	6.5 ± 1.4 a	12.1 ± 1.4 b

Table II.6. Effect of height position in the tree on the volumetric capacitances (kg l^{-1} MPa^{-1}) for the three phases $C_{0-0.5}$ (between 0 and 0.5 MPa), $C_{0.5-3}$ (between 0.5 and 3.0 MPa), and C_{3-5} (between 3.0 and 5.0 MPa). Values with different letters within a column or/and a row are significantly different ($P<0.05$). LS means (±SE, n=6) were generated from the PROC MIXED procedure, and multiple comparisons among means were calculated using LSD. To convert these values to dry weight basis (kg MPa^{-1} kg^{-1}) multiply the table values by 0.46, 0.42, 0.41 and 0.51 kg l^{-1} respectively for node 5, node 15, node 35 and 1 meter. This change does not change the significance values except for C_{3-5} at 1 meter that becomes significantly different than C_{3-5} at node 5, and for $C_{0-0.5}$ at node 15 that becomes significantly different than $C_{0.5-3}$ and C_{3-5} at node 15.

Height position	$C_{0-0.5}$	$C_{0.5-3}$	C_{3-5}
Node 5	0.035 ± 0.012 a	0.036 ± 0.012 a	0.055 ± 0.012 a
Node 15	0.035 ± 0.012 a	0.053 ± 0.011 a	0.086 ± 0.011 b
Node 35	0.051 ± 0.011 a	0.057 ± 0.011 a	0.090 ± 0.011 b
1 meter	0.096 ± 0.011 b	0.046 ± 0.011 a	0.065 ± 0.011 a

significant differences between the three phases for the top of the tree only ($F_{2,74}<-1.69$, $P>0.09$, Tables II.5 and II.6). The mean water storage capacity did not change for the tip of the trunk. For $C_{0.5-3}$, and for both definitions for water storage capacity, we did not find any significant difference between the different locations in the trunk ($F_{2,74}<0.64$, $P>0.52$). On a RWC basis, the $C_{0-0.5}$ was significantly higher for the bottom of the tree and C_{3-5} lower for the tip than for the other locations (Table II.5). For the volume basis the C_{3-5} for the top of the tree behaved like the bottom ($F_{2,74}=0.62$, $P=0.54$, Table II.6). The overall RWC-based capacitance increased sharply with an increase in k_s (Fig. II.5b), from 5% RWC MPA^{-1} at node 5 to 10% RWC MPa^{-1} at the base.Using the total height and sapwood area at each position in the tree (Table II.2), we estimated a total water storage capacity between 0.5–3.0 MPa of 59 liters per unit change in water potential (that represents 7% of the total volume of water of the sapwood) and 78% of this total water storage capacity comes from the trunk below node 35, which itself averaged several nodes below the average base of the crown.

II.5 DISCUSSION

II.5.1 Methodological issues

Using the material from young trees, we found statistically inseparable results for samples prepared using the split segments and those prepared using roundwood for parameters of the vulnerability curves (Fig. II.3). This finding shows that damages to sample edges have no significant effect on sample conductivity or vulnerability to cavitation, validating the appropriateness of this technique for this type of study and plant material. The open edges of the samples did not affect the responses of the loss of hydraulic conductivity to an applied pressure. The hypothesis that too many openings in the sample could create more cavitation and underestimate the RWC is therefore not valid for trunk and roundwood of this species, so air-injection

techniques can be used to measure the vulnerability to cavitation on raw pieces of wood subsampled from xylem segments of very large size, and not only from excised branches.

There was no measured effect of storage duration on conductivity, capacitance, or vulnerability parameters. This result suggests that changing the water every day and storing samples in the dark are efficient in the preventing value-altering microbial growth. When western hemlock (*Thuja occidentalis* L.) wood samples were stored at room temperature, their specific conductivity decreased by 34% after two weeks (Lin et al. 1973). When our samples were stored at 5°C in clean water, their specific conductivity did not decrease statistically even after 21 days. This result agrees with Erickson's study (1960) of permeability of Douglas-fir and western hemlock sapwood. He showed that storage in water at 5°C started to produce a lower rate of k_s after one month, with markedly lower rates if stored in bags without water.

The way in which capacitance was calculated affected the conclusion one would draw at the low water potentials (Tables II.5 and II.6). The difference between the two methods of expression is of importance because of the changes in wood density by height and radial position. The use of the volumetric capacitances is confounded by trends of variation in the wood density, and can be used only to compare specimens with the same density. For example if a sample with low density wood (top of the tree) is compared with a denser one (bottom of the tree), the specimens may have the same volumetric capacitances but the denser wood will contain less water and in fact will have a higher storage capacity based on its total available water present in the lumen cells. This trend is more obvious for more negative water potentials because the amount of water present is already far from saturation.

The capacitances we found from 0–0.5 MPa xylem tension are lower than those estimated for the same species by Waring and Running (1978, Fig. 2) (130% RWC MPa^{-1} and 0.65 kg l^{-1} MPa^{-1}) and for Scots pine (*Pinus sylvestris* L.) by

Waring et al. (1979, Fig 1) (110% RWC MPa^{-1} and 0.50 kg l^{-1} MPa^{-1}), but are similar for higher values of water potential (6% RWC MPa^{-1} and 0.30 kg l^{-1} MPa^{-1}). They reported that samples lost around 60% of their water between xylem tensions of 0 and 0.5 MPa. First, the discrepancy in capacitances at high water potential can be explained by the fact that Waring and Running (1978) and Waring et al. (1979) used wood samples that were cut into small flat disks (18 mm diameter by 4 mm in the tree's axial direction). Their proportion of cut-open tracheids was too high to estimate capacitances correctly because the water inside a cut-open tracheid is only held by capillarity, rather than capillarity and the tension within the xylem stream (Tyree and Yang 1990) so those studies overestimated capacitance in this range of water potentials. Secondly, our estimates in the range of water potentials from 0 to 0.5 MPa were also inaccurate, underestimating the water held by capillarity but accurately estimating the water released by cavitations. Unlike Waring and Running (1978) and Waring et al. (1979), who produced negative pressure by using the method of equilibrium dehydration of wood samples over salt solutions, we used positive pressure from the pressure chamber. One cannot accurately estimate capillary water changes by using the pressure chamber because positive pressure cannot displace capillary water, or water that is held by surface tension at the air-water interface in either an embolized tracheid or between adjacent tracheids (Zimmermann 1983; Tyree and Yang 1990). The hypothesis of capillary water storage holds 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 would be released at a pressure potential close to zero, and would stop before –0.6 MPa (Holbrook 1995; Tyree and Yang 1990). The high capacitance due to changes in the amount of capillary water represented half the water capacitance in *Thuja*, *Tsuga* and *Acer* but this capillary water storage has been interpreted to have no adaptive implication because it occurs when the environmental conditions are still favorable (Tyree and Yang 1990).

The only data of which we are aware for xylem capacitances using a similar method on saturated stemwoods are from Edwards and Jarvis (1982). Their values (estimated from Fig. 5) are very similar to the values we estimated for the first two phases of water change. They showed capacitances, which also corresponded to water release by cavitation events only, at −0.5 MPa ranging from 10% RWC MPa^{-1} for *Pinus contorta* D. to 20% RWC MPa^{-1} for *Picea sitchensis* B. and at 0.5–3.0 MPa ranging from 14% RWC MPa^{-1} for *Pinus contorta* D. to 22 % RWC MPa^{-1} for *Picea sitchensis* B.

II.5.2 Trunk segmentation in relation to vulnerability to cavitation

As judged by the parameter Ψ_{50} (the water potential at which 50% of conductivity is lost), the overall outer sapwood is less vulnerable to cavitation than the overall inner sapwood. However, if we judge by Ψ_e (the air entry point), the overall inner sapwood is not significantly more vulnerable to cavitation than overall outer sapwood.

More intriguing is that at the base of the tree, Ψ_e and RWC do not differ significantly between inner and outer sapwood. The average inner sapwood values tend to be even more negative (Table II.2). These results suggest that refilling of embolisms has been completed during the 29-years difference in wood age between these radial positions (Table II.1). It would be interesting to test whether this pattern is conserved in a conifer with higher sapwood area such as *Pinus sylvestris* L., which here can be up to 80 years worth of sapwood (Mencuccini et al. 1997), or *Pinus ponderosa* L., which have up to 200 years (Ryan et al. 2000).

Although the resistance of water flow was higher in the top of the trunk (lower hydraulic specific conductivity), the tip of the trunk of Douglas-fir mature trees was less vulnerable to cavitation than the proximal (lower) parts. Wood higher up is modified (relative to basal wood) to be more resistant to cavitation than the wood at the base. Initial inspection of these data appears inconsistent with the segmentation hypothesis (Zimmerman 1983; Tyree et al. 1983), which suggests

that during severe drought, the loss of conductivity will develop primarily in the distal parts of the tree to protect the proximal part by stopping any water movement and thereby any water loss.

However, to assess the segmentation hypothesis relative to the tree's hydraulic architecture, one needs to know not only the parameters of the vulnerability curves throughout the trees, but also the most negative water potentials experienced. More research must be done to address this issue. The hydrostatic gradient causes water potentials to be lower at the top of the tree than at the base. However, the actual potential gradient will depend on the spatial and temporal patterns of conductivity, transpiration, and water storage. The lower Ψ_e at the top of the branched bole (node 35) parallels the hydrostatic gradient, suggesting that the air entry potential will be reached simultaneously in the base of the bole and in this intermediate position under static conditions of no transpiration. However, above node 35, the calculated water potential becomes more negative with height than one would predict based on the hydrostatic gradient alone (Fig. II.6).

II.5.3 Relative hydraulic failure occurring in the trunk sapwood by position

Using the midday gradient of 0.019 MPa m^{-1} (Bauerle et al. 1999), a water potential of −1.5 MPa at the base of the tree and tree height of 43 m, we calculate that a difference of 0.8 MPa or 8% loss of hydraulic conductivity between the top and the bottom of the tree will be required to maintain the water column. This difference corresponds to a 13% loss of conductivity at the bottom, and a 5% loss in hydraulic conductivity at the top of the tree. Thus, there is a higher loss of conductivity at the bottom than the top of the tree. If we develop our scenario for a severe drought with a water potential of −2.5 MPa at the base of the tree, and use the same mid-day gradient, the difference in loss of hydraulic conductivity becomes even greater, with a 30% loss of conductivity at the bottom and a 15% loss of conductivity at the top of the tree.

For conifers, the drop in water potential is mainly confined to the branch ramifications (Tyree et al. 1983; Tyree 1988). In old-growth Douglas-fir (>450 years), the potential gradient is about 0.0105 MPa m^{-1} at predawn (statistically indistinguishable from the hydrostatic gradient, 0.0100 MPa.m^{-1}) and nearly twice as high at noon during a sunny day (Bauerle et al. 1999). Those reported midday gradients were for foliage high in the tree on branches, not the leader, and the samples were not foil-covered, and therefore the 0.019 MPa m^{-1} used for our calculations overestimated the actual loss of conductivity that occurred in the trunk. The gross approximation made above for a loss of 5% in xylem hydraulic conductivity at the top of the tree follows Bond and Kavanagh's observations (1999) that leaf water potentials of upper branches of mature Douglas-fir typically generate < 5% loss of xylem conductivity.

In the first study presenting the extent of xylem cavitation in mature Scots pine trees, Jackson et al. (1995) showed that the loss of conductivity at the base of the trunk (measured by acoustic emissions) occurred for water potentials as high as −1.2 MPa. Our study confirms that the lower parts of the trunk of mature Douglas-fir trees (from base to node 35) may operate close to the edge of hydraulic safety. However, the calculated values presented here on loss of hydraulic conductivity suggest that the main stem of the top (node 5) of the tree does not operate near a critical value for cavitation even when the bottom of the tree does so. This former result is in contrast with model predictions that distal parts of tree species operate near the edge of dysfunction for water transport (Tyree and Sperry 1988).

II.5.4 Ecophysiological implications: trade-off between water storage capacity and vulnerability to cavitation

For the young trees, the low capacitance found for the range of potentials over which the plants usually operate (between 0.5–3.0 MPa) suggests that their water uptake is linearly related to the water loss by the leaves. Few cavitation events occur at water potentials less negative than −3.8 MPa (Fig. II.3a). Between the

young trees and the mature trees, at a water potential more negative than the air entry point (–1.3 to –3.1 MPa, depending on height and radial position for the mature trees), the cells cavitated across the same range of xylem tension (the slopes *s* of the responses to an increase in water potential were around 30% loss of k_s MPa^{-1}, Fig. II.3a and Table II.3). This parameter *s* is species-dependent and may be related to the tracheids that have the largest pores in their pit membranes (Pammenter and Vander Willigen 1998).

In this paper we show that within the tree at high water potential (>–0.5 MPa), the base has a higher water storage capacity (water release by cavitation) than the top and is more vulnerable to cavitation than the top. Stored water is more accessible to the bottom part of the trees than the top and it can represent an important fraction of the water-use in dry condition (Table II.5). However, using –0.4 MPa as the maximum water potential encountered at the tree base (during the winter, from Domec and Gartner personal communication), we can estimate that RWC at the base of the trunk will never rise above 92%. In fact, 92% is an overestimate (caused by the methodological problem of measuring capillary water storage with a pressure bomb, as discussed above). This estimate contrasts with Waring and Running's report (1978) that water content recovers fully in this species, but it is consistent with other studies that showed that, without generating positive pressure, xylem never fully rehydrates during the winter (Chalk and Bigg 1956; Jackson et al. 1995).

The similar values found for the biological range of water potential (between –0.5 and –3.0 MPa, Tables II.5 and II.6) indicate that every location of the trunk behaves the same in terms of water storage whereas the tree top is much more resistant to cavitation. For the top of the trees, the trade-off associated with low vulnerability to cavitation is at a cost of low hydraulic conductivity and water storage capacity (Stratton et al. 2000). Increasing the vulnerability to cavitation by a factor of 2.0 is at the cost of decreasing the capacitance by a factor of 2.6 (data not shown) and the specific conductivity by a factor of 4.5 (Fig. II.5a). The more

resistant higher part of the trunk, without compromising its capacitance, could have two adaptive functions: protection of the main meristem against severe drought, and provision of water at the beginning of the growing season to support the growth of the leader before new xylem has been produced.

Limited data show that in going from juvenile (top of the tree) to mature wood (lower parts of the trunk) in Douglas-fir, there are changes by a factor of 1.7 in wood density, 4.5 in stiffness (Senft et al. 1985), and 2.9 in tracheid length (Megraw 1985). Our study shows that there is a change by a factor of 2.0 in the water potential at which embolism occurs. With higher C_{3-5} values, the mature wood is more efficient in using the water released by cavitation events for the more negative water potential near the edge of 50% loss of conductivity (<–3.0 MPa). Assuming that the stomata are closed at these water potentials, this feature may help the tree to survive until the next rain falls to mitigate cuticular water loss (Tyree et al. 1991).

In conclusion, we have proposed a simple technique for analysis the vulnerability curves by determining coefficients that have a physiological significance and that can be compared easily among species, plants parts, and other studies. We also suggested a new technique for calculation of capacitances based on RWC adapted to the differences in the wood density of the samples. Our study shows that it is possible to study trunk water relations of mature trees and not solely branches by using the air injection method. Trunk xylem of Douglas-fir has a change of hydraulic properties from the inner to the outer sapwood as well as from the bottom to the top of the tree. We believe that these findings represent a new step in the understanding of tree-trunk water relations. We now have evidence that the main bole of mature Douglas-fir does play an adaptive role in preserving the whole tree from hydraulic failure. To better address the importance of the occurrence of cavitation and the seasonality of their repair, we are currently measuring the changes in trunk relative water content and water potential by height and depth into sapwood in the field. These data will help us better understand tree

adaptation to its environment as well as the functional trade-offs between production of wood for water transport and its production for mechanical support. These current results will also be of interest to tree breeders, who are interested in minimizing the amount of juvenile wood in trees: our results suggest that this juvenile wood may be important for the tree during times of drought.

II.6 ACKNOWLEDGMENTS

This project was supported by USDA CSREES 96-35103-3832 and 97-35103-5052, and a special USDA grant to Oregon State University for wood utilization research. We are grateful to R. Spicer for help in the setting up of the hydraulic conductivity apparatus, M. Pruyn for her sincere global help, Dr. K. L. Kavanagh for the early discussions on the vulnerability curves and two anonymous referees for their useful suggestions.

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Chapter III

Age- and Position-related Changes in Hydraulic vs. Mechanical Dysfunction of Xylem: Inferring the Design Criteria for Douglas-fir Wood Structure

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Domec, J.C. and B.L. Gartner. 2002. Age- and position-related changes in hydraulic vs. mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. Tree Physiology. 22, 91–104

III.1 SUMMARY

We do not know why trees produce a variety of wood characteristics as a function of cambial age. Part of the answer could lie in the tradeoff between hydraulic properties and mechanical support. In conifers, longitudinal tracheids represent 92% of the cells and are involved in both water transport and mechanical support functions. We used three hydraulic parameters to estimate the 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. 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).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), all Douglas-fir [*Pseudotsuga menziesii* (Mirb)].

For the natural range of Ψ, S_{H12} showed a linear decrease from the top of the tree to the base, with a minimum value of 0.95. The tips ("juvenile wood") of both young and mature trees had a hydraulic safety factor 1.4 and 1.6 higher, respectively, than the bases ("mature wood"). Modeling analyses suggested that if trees were made only of pure mature wood, this value would be reduced to 0.7.

The mechanical safety factor was 1.2 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 suggested that if trees were made only of mature wood, these values would increase to 1.7 and 2.3, respectively.

Hydraulic safety factors were at least two times lower than mechanical safety factors, suggesting that design criteria for Douglas-fir wood structure have evolved primarily in response to hydraulic rather than mechanical needs. The

results suggest that forest managers must consider the role of juvenile wood in tree physiology to avoid producing plantations vulnerable to drought.

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

III.2 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).

III.3 INTRODUCTION

Is there a tradeoff between the mechanical and hydraulic functions of wood (Gartner 1996)? The answer depends on the scale of the observation. At the cellular level there is a tradeoff. Cells specialized for high conductivity usually have wide lumens, thus lower density and stiffness (modulus of elasticity, or MOE). At the structural level, tradeoffs are indicated by lower specific conductivity (k_s) and higher density and stiffness in lianas than in self-supporting plants or plant parts (Gartner 1991*a*,*b*, Chiu and Ewers 1992, Rowe and Speck 1996) and by lower conductivity in compression wood than in opposite wood (Spicer and Gartner 1998*a*). At the tissue level, however, the two functions 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 deZeeuw 1980, Pothier et al. 1989).

Wood produced near the pith is commonly called juvenile wood (JW), whereas wood produced beyond the 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 (reviewed in Megraw 1986). Among other features, the MW is more dense, has much longer cells (Megraw 1986), and has higher k_s than JW (Mencuccini et al. 1997, Pothier et al. 1989, Sellin 1991, Spicer and Gartner 2001). There are no reports comparing the vulnerability to cavitation of JW and MW.

We hypothesize that various parts of a tree (e.g., base, tip) have different needs for water transport and mechanical support, thus requiring wood of very different structure. We suggest that environmental pressures have led to the

evolution of large radial changes in anatomy from JW to MW for hydraulic reasons more than for mechanical reasons. The rationale is that small changes in wood structure from the pith outward might result in enormous changes in hydraulic performance, yet have only a small effect on mechanical performance. Even very small changes can cause an increase in k_s (which scales with conduit r^4) or vulnerability to cavitation. The pith-to-bark increase in structural stiffness is dominated by an increase in the second moment of area (I, m^4), not by changes in material properties. As a stem increases in diameter from 1 to 100 cm, its I increases by 10^8 (1,000,000%), but its MOE increases by only about 15%.

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 interpret the function with the lowest safety factor as the most important for the design of the tissue because it has the greatest risk. 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 safety factor rather than overestimating it. This paper represents a first attempt to combine hydraulic performance during water stress with mechanical performance to infer the design criteria for wood tissue.

III.4 MATERIALS AND METHODS

III.4.1 Plant material and experimental site

We examined three age classes of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] trees (Table III.1). We measured vulnerability to cavitation, relative water content (RWC), and xylem water potential (Ψ) on samples collected from 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°57N, 123°21W; 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, Oregon. By felling or climbing mature trees, we obtained a vertical profile describing variation in vulnerability to cavitation, water storage and *in situ* RWC and Ψ with increasing tree height.

III.4.2 Hydraulic specific conductivity, vulnerability, and relative water content curves

We measured specific conductivity (k_s) in water-soaked samples, then induced embolism at progressively higher applied air pressures, each time measuring both k_s and weight (for calculation of RWC). We sampled six 4-year-old seedlings harvested in April 1999 two nodes down from the top and used the entire stem cross-section (note that we conducted experiment made on the wood between the nodes, not at the node itself). We sampled six 10-year-old saplings harvested in March 1999 five nodes down from the top and used excised chunks, as described below. We also 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. We sampled the trunks of the six mature trees harvested in March 1998 (reported in Domec and Gartner 2001) 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). We sampled three branches from each of the three mature trees climbed (>5 cm from the branch/stem junction) 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 6:00 AM, immersed them in water, and transported them to the laboratory. We removed the bark for small-diameter samples (all seedling and branch measurements), and for the larger pieces

of wood we extracted samples with a chisel. We soaked samples under a vacuum for 48 hours 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 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. To make the measurements, we transferred the sample alternately between the membrane-lined pressure sleeve, needed to ensure fluid did not leak from the sides of samples (Spicer and Gartner 1998*b*), and the double-ended pressure chamber, used to cause embolism (Salleo et al. 1992, Sperry and Saliendra 1994). The pressure chamber was pressurized to 0.5 MPa, then increased by 1.0-MPa steps 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 the specific conductivity at a given pressure. We fitted hydraulic vulnerability curves by the least squares method based on a sigmoidal function:

$$PLC = \frac{100}{1 + exp[a(\Psi - b)]} \quad . \qquad (1)$$

Parameter 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 pit membranes are overcome within the conducting xylem and where cavitation and embolism begin (Sperry and Tyree 1988). Although this value is only a linear approximation of the true air entry point, which, as shown by the VCs, starts very close to $\Psi = 0$, it provides a useful value in comparisons among curves. Likewise, Ψ_{88} could be termed the full embolism point,

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

	Mean Height (m)	Age (year)	Mean diameter at breast height (cm)	Mean sapwood area at the base (cm^2)	Mean leaf area per tree (m^2)
Mature trees	44.7 ± 1.3	105 ± 5	64 ± 2	750 ± 98	302 ± 82
Saplings	5.6 ± 0.3	10 ± 1	3.5 ± 2.4	41 ± 7	17 ± 3
Seedlings	1.2 ± 0.1	4	0.96 ± 0.20	0.92 ± 0.06	0.20 ± 0.01

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 determined RWC for each sample used to construct a VC and from cores obtained from the trees in the field (to infer *in situ* cavitation). To get a rate of change in RWC associated with cavitation, we determined RWC initially and after each pressure by recording the water displacement by volume (V_f, cm^3) and the fresh mass (M_f, g) by weight and length. Following final pressurization, we recorded the dry mass (M_d, g) and using the length could back-calculate the dry mass and then calculate RWC assuming a cell-wall material density of 1.53 g cm^{-3} (Siau 1984):

$$RWC = \frac{M_f - M_d}{(V_f - M_d/1.53)} \qquad \text{(dimensionless)}, \qquad (2)$$

We made *in situ* vertical profiles of RWC for cores obtained in mid-September 1999 and mid-March 2000 one hour before sunrise and at mid-day between noon and 6:00 PM solar time.

III.4.3 Trunk and leaf water potential

We determined water potential (Ψ) for trees in the field in order to use the vulnerability curves (constructed in the laboratory) to estimate the PLC in the field. To estimate trunk Ψ at the base of the trees, we used temperature-corrected stem psychrometers (Dixon and Tyree 1984; PWS Instruments, Guelph, Ontario, Canada) installed at 1.8 m above the ground on the three mature trees. 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 Inc., Logan, Utah) to take measurements every half hour for 4 consecutive days

during summer (September 10–13, 1999) and 3 consecutive days during winter (March 15–17, 2000).

On the same three trees, we measured the leaf and trunk Ψ values within the crown at three heights, corresponding to nodes 5, 15, and 35, counting down from the top (determined from cores taken with an increment borer). We used a pressure chamber (PMS Instruments Co., Corvallis, Oregon) to measure three foliage-bearing branch cuttings per tree and per height every 15 min for 2 hours at predawn (Ψ_{pd}) and 3 hours at mid-day (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 used foliage-bearing branches and the pressure chamber to measure Ψ periodically. 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 ones used to develop the VCs. We also measured the seasonal change in Ψ_{pd} and Ψ_{mid} (taken at 1:00 PM 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 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.

III.4.4 Trunk relative water content

From the wood samples tested in the laboratory, we knew the relationship between the negative of the applied air pressure and RWC. Therefore, knowing the Ψ of standing trees, we could estimate the RWC, then compare it to the 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 up in the tree, but we split and weighed each core (M_f) within 10 min of harvest. Back at the laboratory, we determined V_f and M_d for the cores as described previously, then calculated RWC (Equation 2). We collected the cores at predawn (RWC_{pd}) and between 1:00 and 3:00 PM 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 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.

III.4.5 Wood density and the derived properties

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

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

where M_d is the oven dry weight (dried at 105°C), and V_f is the 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 correct from dry to green conditions (Bodig and Jayne 1982). Second, we used the standard equations from the Wood Handbook (Forest Products Laboratory 1987) relating mechanical properties of green wood to density (shown in italics):

$$\text{MOE} = (5.4 \times 10^3)\text{Density}, \qquad (4)$$
$$MOE = (6.7 \times 10^3)Density^{0.81},$$

$$\text{MOR} = 39.5\text{Density}, \qquad (5)$$
$$MOR = 44.4Density^{1.04},$$

$$\text{MCS} = 15.6\text{Density}, \qquad (6)$$
$$MCS = 21.1Density^{1.02}.$$

We used a transverse section made with a microtome and 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) with an image analysis system consisting of a compound microscope, a video camera, and the software package NIH Image (v. 1.60, Rasband 1996). We then calculated an average latewood proportion for each sample as the mean of the average latewood proportion of all the growth rings analyzed for that sample.

III.4.6 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 from the initial and final Ψ of catastrophic xylem dysfunction. Both Ψ_{12} and Ψ_{88} come from the VCs. 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 (in 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 (in MN).

We estimated P as the sum of the fresh mass of the branches, the trunk, and the leaves taken as green. We estimated the total leaf mass by weighing one quarter of the total leaf biomass of the 6 mature trees harvested for our previous study (Domec and Gartner 2001), the 6 saplings, and the 15 seedlings used to determine RWC and Ψ. To estimate the mass of the branches, we applied a linear relationship, determined in the laboratory on the branches used for the vulnerability curves, between the fresh weight of the leaves and the fresh weight of the branches (Table

III.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 by 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:

$$S_{Mh} = L_{cr}/L, \tag{10}$$

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 III.1a for details), and L is 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 (MCS × area) before collapse of the tree, which does not affect the conclusions, since 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 before failure that the branch can sustain (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} (Cannel 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 III.1b for details) and assuming that the branches were horizontal, we calculated the failure points to be at 13% ± 2% and 55% ± 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 MW (properties equal to the average sapwood at the base of the mature tree). We changed the JW properties of the seedlings and saplings by the properties of the MW found at the base of mature trees.

III.4.7 Statistical analysis

We used least squares methods to fit relationships between hydraulic parameters and applied pressure, as well as linear and non-linear 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 Inc., Cary, North Carolina).

Figure III.1. (a) Critical load (P_{cr}) and critical (L_{cr}) length in buckling for the trunk of mature trees and (b) critical distributed load (p_{cr}) of branches. The calculation of the load (P) was corrected from 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 $I = 0.25\pi r^4$.

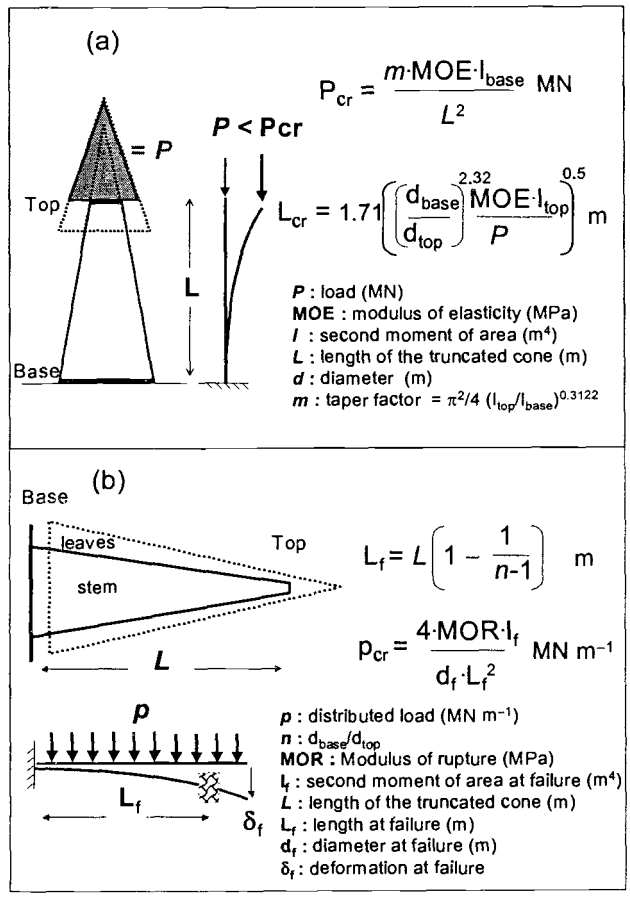


Table III.2. Parameters used to estimate the branch weights, the radius, and the density load at each height in the tree based on the six mature Douglas-fir trees sampled at four heights. Relationships used were polynomial, with either three (quadratic) or two (linear) parameters as: $ah^2 + bh + c$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

	a	*b*	*c*	r^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})	$2.18E^{-1}$	−10.91	$5.30E^{+2}$	0.99

III.5 RESULTS

III.5.1 Vulnerability and relative water content curves

Vulnerability to cavitation varied among organs and age classes. The trunks of the 10-year-old saplings were less vulnerable than the bases of mature trees from 0 to 2 MPa. They became more vulnerable, however, at more negative applied pressures, as indicated by the slope of the curve and the potential at which 50 PLC occurred (Figure III.2a, Table III.3). The trunks of the 10-year-old saplings and the mature trees were more vulnerable to cavitation than their branches. Branches from saplings were less vulnerable to cavitation than branches from mature trees (Table III.3). However, none of the parameters of vulnerability to cavitation for the three types of branches of the mature trees differed from one another significantly ($P > 0.1$). For all types of branches combined, the average Ψ_{12} (12 PLC) and Ψ_{88} (88 PLC) were -4.7 ± 0.1 MPa and -7.2 ± 0.2 MPa, respectively.

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

III.5.2 Field measurements and hydraulic safety factors

In mature trees, the trunk water potential (Ψ) decreased linearly from bottom to top at all four measuring points (Figure III.3a). For the winter predawn measurements, the slope of the curve of Ψ by 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 at those taken at mid-day ($P = 0.36$). In summer, the slopes for the predawn and mid-day values were 39% and 46% higher

Figure III.2. Relationship between (a) vulnerability curves for Douglas-fir trunk (Sapling trunk) and branches (Sapling branch) of 10-year-old saplings and branches of mature trees (Mature branch) at the three nodes considered showing the percentage loss of xylem hydraulic conductivity (PLC) and (b) the relative water content (RWC) vs. the negative of air pressure used in air injection experiments. Error bars are standard errors. 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).

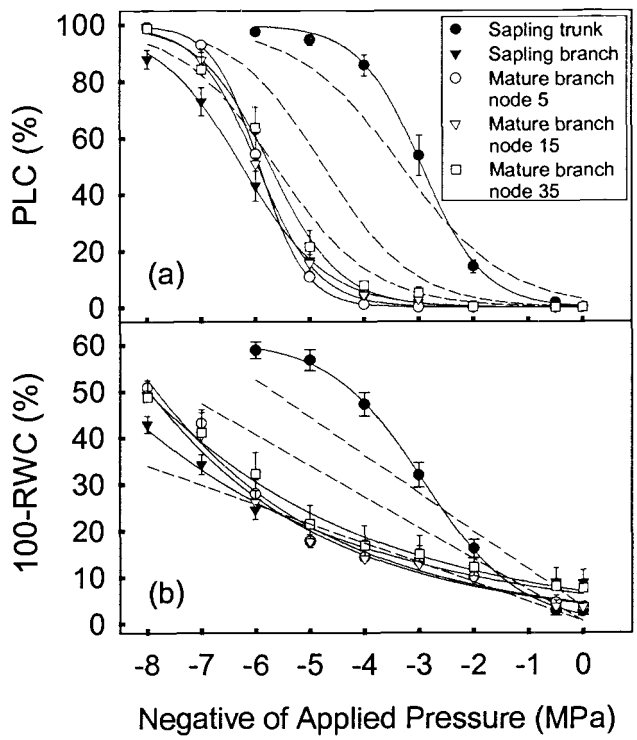


Table III.3. Mean parameters (± SE) describing the percent loss of conductivity (PLC), sapwood water deficit (100 ! %RWC), and function type used to fit the sapwood water deficit parameters in trunk and branches in three age classes of Douglas-fir. The vulnerability parameters were fit using the least 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 ($s = a \cdot 25$) and *b* 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
Trunks						
4-year-old seedlings[1]	2	29.7 ± 3.2 ab	−5.6 ± 0.2 a	-4.2 ± 0.3 a	14.7 ± 1.7	$\alpha\Psi + \beta$
10-year-old saplings	5	43.7 ± 4.7 cd	−2.9 ± 0.1 b	1.2 ± 0.1	−2.9 ± 0.1	$61/[1 + e^{\alpha(\psi-\beta)}]$
Mature trees[1]	5	30.4 ± 4.4 ab	−4.7 ± 0.2 c	−6.7 ± 0.3 b	0.6 ± 1.4	$\alpha\Psi + \beta$
Mature trees[1]	15	33.7 ± 3.9 ab	−3.6 ± 0.2 d	−8.7 ± 0.5 c	0.5 ± 1.8	$\alpha\Psi + \beta$
Mature trees[1]	35	33.0 ± 3.9 ab	−3.3 ± 0.2 d	−9.4 ± 0.6 c	0.3 ± 1.9	$\alpha\Psi + \beta$
Mature trees[1]	98 (base)	25.9 ± 3.9 a	−3.3 ± 0.2 bd	−7.8 ± 0.3 d	3.9 ± 1.3	$\alpha\Psi + \beta$
Branches (4-year-old)						
10-year-old saplings	5	31.8 ± 4.4 a	−6.3 ± 0.2 e	−2.3 ± 0.1 e	6.4 ± 0.5	$\beta e^{\alpha\Psi/10}$
Mature trees	5	57.9 ± 6.8 c	−5.9 ± 0.1 a	−3.1 ± 0.1 f	4.5 ± 0.7	$\beta e^{\alpha\Psi/10}$
Mature trees	15	41.8 ± 3.2 cd	−5.9 ± 0.1 a	−3.1 ± 0.2 f	4.3 ± 0.6	$\beta e^{\alpha\Psi/10}$
Mature trees	35	35.7 ± 3.0 bd	−5.8 ± 0.2 a	−2.5 ± 0.1 e	7.0 ± 0.5	$\beta e^{\alpha\Psi/10}$

[1] Parameters taken from Domec and Gartner (2001)

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

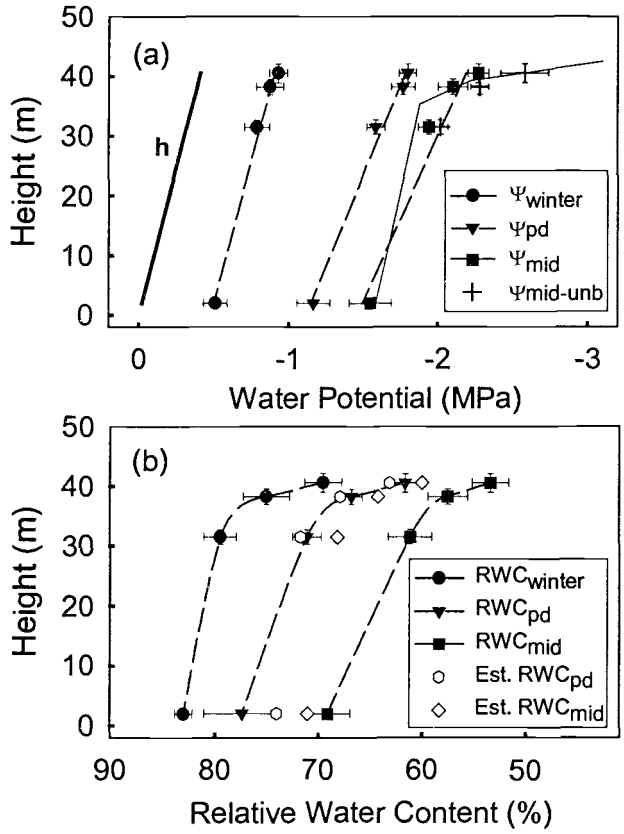


Table III.4. Mean (± SE) water potential (Ψ) and relative water content (RWC) in the trunks of the 4-year-old saplings, the 10-year-old seedlings, and the mature trees at breast height. Winter and summer values were measured in mid-March and mid-September, respectively.

	Winter[1]		Summer predawn		Summer mid-day	
	Ψ (MPa)	RWC (%)	Ψ (MPa)	RWC (%)	Ψ (MPa)	RWC (%)
4-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
10-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 mid-day winter values were not significantly different ($P < 0.05$), the mean of the two time points is given.

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 bottom to tree top, but unlike Ψ, this decrease was not linear (Figure III.3b). The average daily change in RWC (8.2% ± 0.4%) for the summer measurements was comparable to the total change (7.2% ± 0.5%) between the winter and summer predawn values (Table III.4). The estimated RWC (Figure III.3b), based on Ψ measurements and the relationships between PLC and RWC (Table III.3), fit well with the measured summer predawn water potential. For mid-day, the estimated values fit well only for the base of the trees. For the tops of the trees, the values underestimated the measured RWC by 11–12% for nodes 5, 15, and 35. For the saplings and seedling trees, the estimated RWC based on Ψ was within 5% of the measured RWC (data not shown).

The seasonal predawn water potentials (Ψ_{pd}) showed a 1.0 MPa change between the least negative values (winter) and the most negative values (after 2 months without rain) for both mature and young trees (Table III.4), measured at breast height. The minimum leaf water potential ($\Psi_{mid\text{-}unbagged}$) measured on young trees never fell below –2.2 MPa, and the difference with the estimated trunk water potential ($\Psi_{mid\text{-}bagged}$) remained constant at around –0.3 MPa (Figure III.4). Relative water content was always lower for the inner sapwood of the mature trees than for the outer sapwood ($P < 0.035$, Figure III.4). The sapwood water deficit (100 – %RWC) was related linearly to Ψ for all cases studied (Table III.5), which comprised 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 III.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_{H12}) 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 base (Figure III.5b, Table III.6) ($P < 0.05$). The S_{H12} was significantly higher in the branches than in the trunk ($P < 0.05$), but did not differ statistically between the branches of the mature trees and those of the 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 the sample's mean number of rings from pith (cambial age) for both inner and outer sapwood (Figure III.6a).

III.5.3 Mechanical safety factors

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

$$\text{Percent latewood} = 123.54\text{Density} - 32.46 \quad (r^2 = 0.95, P < 0.001). \qquad (12)$$

By combining all types of samples (mature trees, saplings, seedlings, and branches), the relationship was:

$$\text{Percent latewood} = 162.18\text{Density} - 47.9 \quad (r^2 = 0.93, P < 0.001). \qquad (13)$$

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

Figure III.4. Temporal change in water potential and RWC for (a) mature and (b) young Douglas-fir trees over 2 consecutive years at breast height. Filled circles and filled triangles are RWC for the outer and inner sapwood, respectively. The open circles, open squares, and open triangles are water potentials for predawn unbagged leaves (Ψ_{pd}), mid-day bagged leaves (Ψ_{mid}), and mid-day unbagged leaves, respectively. Histograms represent the monthly precipitations recorded 9 km from the study site. Error bars are standard errors.

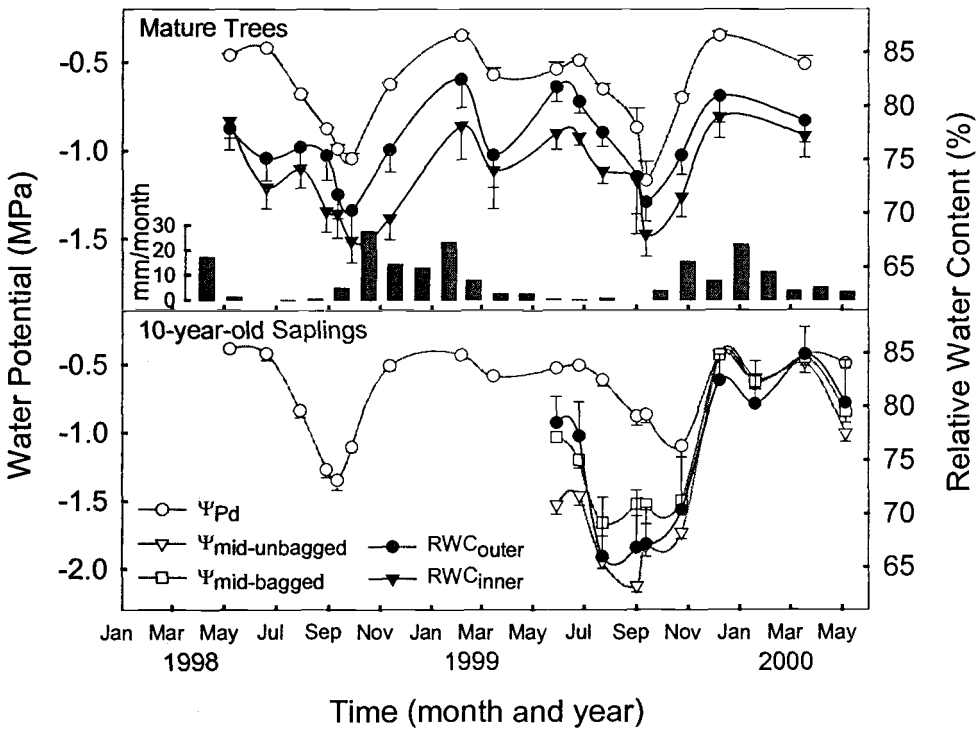


Table III.5. Slopes (a) and intercepts (b) of the linear regressions of the sapwood water deficit (100 – %RWC) vs. the water potential (Ψ) measured in the field for the mature trees, the 10-year-old saplings, and the 4-year-old seedlings ($100 - \%RWC = a\Psi + b$, $P < 0.001$ in every case).

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

Figure III.5. Height in mature Douglas-fir trees vs. (a) percent loss of conductivity (PLC), with symbols the same as in Figure 3, and (b) hydraulic safety factor for the 12 PLC (S_{H12}). Filled and open symbols are for the main trunks and the branches, respectively. The vertical line represents $S_{H12} = 1$. The numbers 4 and 10 are for the 4-year-old seedlings and the 10-year-old saplings, respectively.

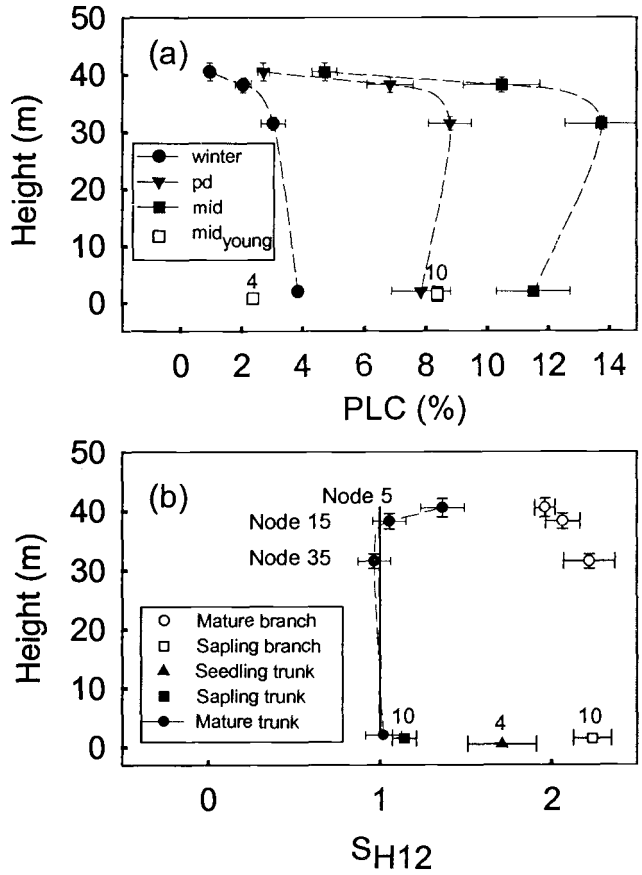
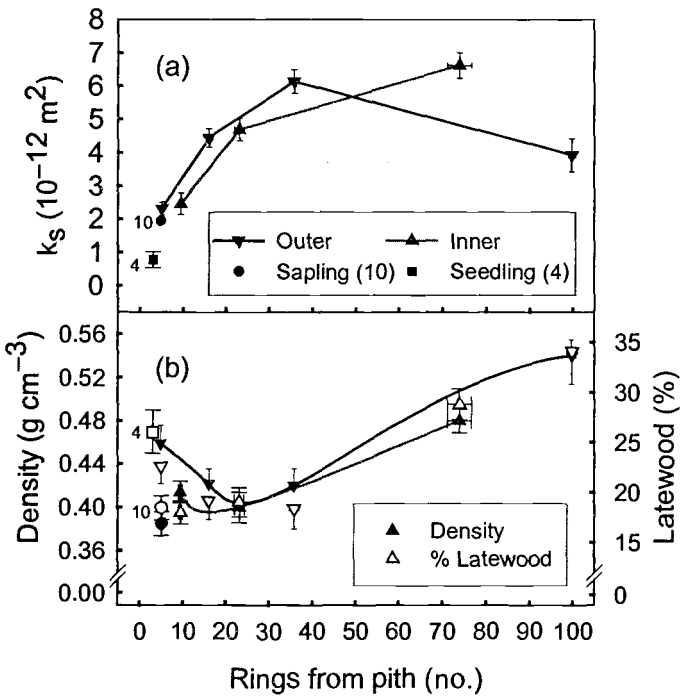


Figure III.6. (a) Hydraulic specific conductivity (k_s) measured at full water saturation vs. the number of rings from pith (no.) in the trunks of mature Douglas-fir for the outer samples (Outer) and the inner samples (Inner) and in the trunks of 10-year-old saplings and 4-year-old seedlings. (b) Wood density and percent latewood vs. the number of rings from pith (no.) in Douglas-fir trees. The numbers 4 and 10 are for the 4-year-old seedlings and the 10-year-old saplings, respectively. Error bars are standard errors and, for clarity only, one side of the bars has been shown in (b).



density, along with the actual taper and load distribution with height, was associated with a 19% decrease in the minimum S_{Mh} (the mechanical safety factor for height) calculated along the trunk (Figure III.7). Minimum S_{Mh} ranged from about 1.5 in mature trees to 5.0 in 10-year-old saplings (Table III.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_{Mbra} (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 the mature trees, the lowest values of S_{Mh} and S_{Mb} were found between heights of 29 m and 31 m for both cases (71% of tree height; Figure III.7).

III.5.4 Tradeoffs between juvenile wood and mature wood

All types of samples (trunks and branches from 4-year-old seedlings, 10-year old saplings, and mature trees) showed an inverse relationship between low values of k_s ($< 4 \times 10^{-12}$ m^2), which represent branches and JW, and S_{H12} (Figure III.8). At higher values of k_s, S_{H12} was constant at about 1, meaning that the parts of the plant with high k_s, or MW, operate just at the point where embolisms could occur.

A change from JW to MW at the top of the tree would decrease S_{H12} by 49% and result in values lower than the unity (Table III.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 not very sensitive to whether wood in the tree was juvenile or mature. The minimum values of S_{Mh} and S_{Mb} for pure MW were 10% and 16% higher, respectively, than for JW (Table III.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 III.6 and III.7). By looking at one type of wood, we

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

		PLC (%)	Ψ_{12} (MPa)	$S_{H12} = \Psi_{12}/\Psi$	$S_{H88} = \Psi_{88}/\Psi$
Mature trees					
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**
10-year-old saplings					
Pure juvenile wood		**8.37**	**–1.80**	**1.14**	**2.59**
Pure mature wood		12.88	–1.57	0.99	3.21
4-year-old seedlings					
Pure juvenile wood		**2.68**	**–3.93**	**1.71**	**3.17**
Pure mature wood		30.72	–1.57	0.68	2.21

Figure III.7. Mechanical safety factors by height for the critical height (triangles) and for the critical buckling load (circles) 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 open and closed symbols.

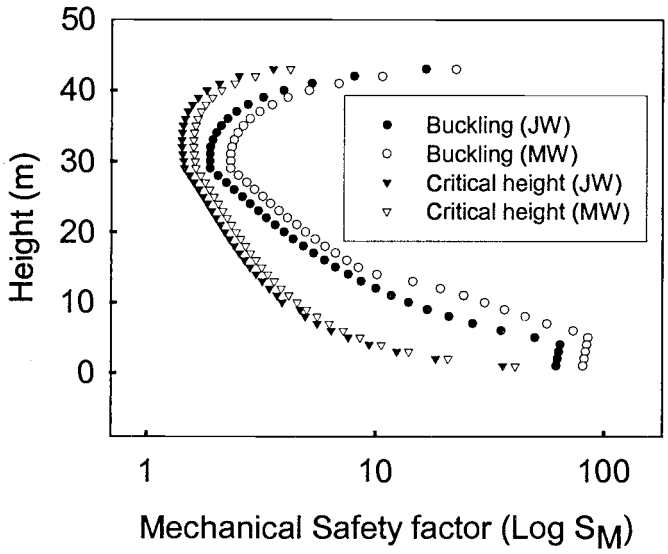


Table III.7. Wood density (g cm^{-3}) and minimum safety factors on a height basis (S_{Mh}), on a buckling basis (S_{Mb}) for the trunks and for the branches on a bending basis (S_{Mbra}) under static loading. For the trunks, values are listed considering the wood as pure juvenile wood or pure mature wood, and bold font represents actual values found in natural conditions; all other values are modeled.

Type of wood modeled	Density (g cm^{-3})	S_{Mh}[1]	S_{Mb}[1]	S_{Mbra}[2]
Mature trees				
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)	
10-year-old saplings				
Normal	**0.39 ± 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)	
4-year-old seedlings				
Normal	**0.47 ± 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)	
Branches				
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)
10 year-old saplings node 5	0.55 ± 0.02			3.23 (2.02)

[1]Values are the most risky (lowest) values resulting from calculations using Equations 4–6; Values in parenthesis are calculated using the equations from Forest Products laboratory (1987).
[2]Values in parenthesis are for branches carrying ice load.

determined strong relationships between wood density and hydraulic parameters (Table III.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.

III.6 DISCUSSION

III.6.1 Tradeoffs between hydraulic and mechanical properties of wood

The results of this research suggest that trees have evolved large radial changes in anatomy for hydraulic more than for mechanical function. We base this conclusion properties showed larger changes in hydraulic than in mechanical safety factors; S_{H12} would be < 1 at the tree top if it were MW (Tables III.6 and III.7). For mature trees, then, the hydraulic loss in favor of gained mechanical properties would involve producing the highest wood or JW (leaders) able to buffer water deficits. On the other hand, the tradeoff for MW would be to best serve the plant with high conductivity (k_s) (Gartner 1995) while maintaining S_{H12} just on the edge of the critical point by stomatal restriction of transpiration (Figure III.8).

Why don't trees produce JW throughout their trunks? The inverse relationship between hydraulic safety and k_s shows that hydraulically safer wood (JW) has lower k_s (Figure III.8). If trees had JW, they would need a larger sapwood area to have the same water flux, which would increase the number of parenchyma cells (Gartner et al. 2001) and therefore the respiratory demands (Pruyn et al. 1999).

Why don't trees produce MW throughout? Mature trees would fail hydraulically at the tip if they did so (Table III.6). Mature wood, located at the tip of a tree, would experience a Ψ too negative to avoid embolism (Figure III.3a). However, this high negative Ψ apparently does not result either 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 III.6a). The high negative Ψ in the wood at the top of the tree therefore must result from the dynamics of water flow. The rate of delivery of water under high transpiration cannot always keep up with demand at the top of the tree (Phillips et al. 2001).

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, but also with high S_{H12} and S_{H88} (Table 8), meaning that JW can be very safe hydraulically and mechanically at the same time. In theory, high values in k_s and stiffness could result simultaneously from changes in the latewood percentage (De Kort 1993) and the tracheid diameter in earlywood (Calkin et al. 1986). At the JW level only, therefore, if there is a tradeoff, it might not be found in maintenance of high k_s. In the field and during a drought, young seedlings and leaders of mature trees must react rapidly to water change conditions, so the ability to buffer the environment with low vulnerability to embolism would be adaptive. If JW allows a tree to resist low water potentials, then tree breeders could make trees more vulnerable to drought by trying to reduce the ratio of JW to MW. Skipping the JW formation by over-watering in a nursery setting or by creating MW too rapidly could produce increased mortality in the field and result in high economic and environmental costs.

III.6.2 Water storage capacity of the trunk

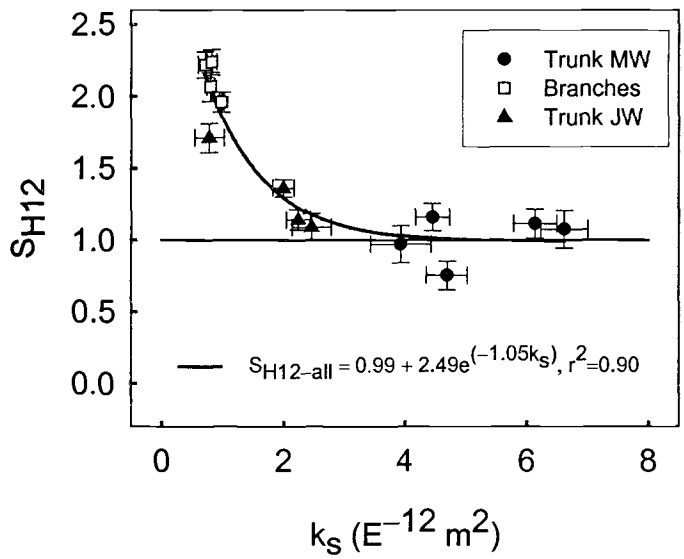
The slope of the water potential (Ψ) with height in the trunks of the mature trees followed the hydrostatic gradient (Scholander et al. 1965, Zimmermann 1983) during the winter (at predawn and mid-day) when there was no transpiration. The slope was steeper than the hydrostatic gradient during the summer at predawn and mid-day, when there was transpiration. This result contrasts with observations made in Douglas-fir trees at Wind River, Washington, in which the Ψs returned to

Table III.8: Slopes and intercepts (in parenthesis) of the linear regressions of the hydraulic conductivity (k_s), the hydraulic safety factors for 12 PLC (S_{H12}) and the hydraulic safety factors for 88 PLC (S_{H88}) vs. the wood density. Based on their respective mean ring from pith (or cambial age), data has been separated into juvenile wood (JW or samples ≤ 20 rings from the pith including branches), mature wood (MW or samples with ≥ 35 rings), or all types of wood combined (All = MW + JW).

	Density JW ($g\ cm^{-3}$)		Density MW ($g\ cm^{-3}$)		Density All ($g\ cm^{-3}$)	
k_s ($E^{-12}\ m^2$)	−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 ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$).

Figure III.8. Hydraulic safety factor for the air entry point (S_{H12}) vs. the hydraulic specific conductivity (k_s) for all types and for the three age classes of trees sampled (branches, 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 in the box. The horizontal line represents $S_{H12} = 1$.



values predicted from the hydrostatic gradient by the predawn measurements (Bauerle et al. 1999). Those trees were older (average age > 450 years old) that Those we studied and, above all, the site was much wetter than our site (2000 vs. 1000 mm per year). At our site, cuticular water loss and water movement in the trunk could have occurred at night.

The water potential at the top of the trunk was 0.25 MPa (predawn) and 0.34 MPa (mid-day) more negative (representing the friction) than the hydrostatic gradient alone (Figure III.3a). Considering the 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 around 0.01 MPa m^{-1}, comparable with data from other studies described in Hellkvist et al. *(1974)*. The steeper predawn slope compared to the hydrostatic slope could explain why the estimated Ψ based on RWC did not coincide with the Ψ measured at on three pieces of evidence. First, hydraulic safety factors for 12 PLC (S_{H12}), which represents the point of air entry described by Sparks and Black (1999), were lower than mechanical safety factors. Second, the hydraulic safety factor was close to unity, indicating that it is important. Third, reciprocal modeling of JW and MW predawn for the bases of the mature trees and during the day for the tops of the mature trees, whereas these values fit well for the small trees (Figure III.3b). A nightly recharge of the trunk would indeed cause RWC to drop below the value expected for the top of the tree during the day and above the value expected for the base during the night (Waring and Running 1978). Such an overnight gradient could help recharge the upper branches and the trunk. The predawn Ψ at the base of the mature tree was 0.30 MPa lower than that within the 10-year-old saplings (Table III.4), indicating that some water movement took place at the base of the trunk (assuming that the young trees were in equilibrium with Ψ of the soil). The daily change in RWC of the trunk also indicates that studies measuring water storage and 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 trees and young saplings, comparable with findings by Waring et al. (1979), but only half the value reported by most studies on the same species from wetter sites (Chalk and Bigg 1956, Waring and Running 1978). The outer sapwood of mature trees averaged higher RWC than the inner sapwood at most dates. We cannot determine with our data whether RWC is lower in inner sapwood because inner sapwood has existed longer (Clark and Gibbs 1957) or because growth rings closer to the pith have lower RWC. This latter possibility suggests that the lower the cambial age of the sapwood, the harder it is to refill, which agrees with the steeper slopes found between Ψ and RWC for the lower parts of the trunks (base and node 35) compared to the young trees and the tops of the mature trees (coefficients α in Table III.3). A structural basis for that hypothesis could be related either to tracheid morphology or to the lower wood density in JW than in MW (Abdel-Gadir and Krahmer 1993).

III.6.3 Patterns and structural basis for differences in hydraulics among plant parts

Our study showed that JW in young trees had the same k_s as same-aged tips of mature trees (Figure III.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 ($P < 0.001$). This pattern has been reported in 28-year-old radiata pine (Booker and Kininmonth 1978) and in 34-year old Douglas-fir (Spicer and Gartner 2001). The same pattern also was suggested, but not measured, in studies comparing k_s at the same height in the trunk for different age classes (Pothier et al. 1989, Mencuccini et al. 1997).

Following the same pattern as k_s, S_{H12} and S_{H88} in the JW in young trees was the same as in same-aged tips of mature trees (Table III.6). Again, we know of no other research investigating this question. 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 are strongly correlated with higher k_s (Figure III.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 close to where cavitation begins (Tyree and Sperry 1988, Sperry and Pockman 1993). We hypothesize that S_{H12} is determined by factors related to the size of earlywood tracheids, in which the smaller the tracheid, the higher the value of S_{H12}, because smaller earlywood cells are harder to embolize. Within individual trees, S_{H88} followed the trend of wood density, which was high at both the tip and the base (Table III.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). The higher the latewood proportion, the harder it is to fully embolize the sample. It is well-known in wood science literature that latewood pits are less apt to aspirate than earlywood pits (Meyer 1971) because latewood pit membranes are less flexible (Petty 1972).

For branches, our data showed an average value of –5.9 MPa difference in the water potential at which 50 PLC occurs (Table III.3). This value is in the same order of magnitude as –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 PLC (Figure III.2) and with never more than 5 PLC (Figure III.5), which is a common measurement for branches in field condition (Bond and Kavanagh 1999). If we define hydraulic function as the

ability to resist cavitation, therefore, rather than the ability to transport water, it means that trees evolve higher hydraulic functions in the branches and near the pith, with the reverse farther out. Part of the explanation could lie within the anatomical structure of these samples (short tracheid length and small tracheid diameter in the earlywood), which might allow some water loss without any PLC (segmentation and redundancy of the hydraulic pathway at the cell level). The drop in RWC with no 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, because a pressure chamber cannot generate the negative pressure necessary to displace capillary water held by surface tension (Zimmermann 1983, Domec and Gartner 2001). In the current study, applied air pressure vs. xylem water deficit in the laboratory gave slopes (Figure III.2) comparable with field data (Table III.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 1.2 value shown in Table III.3).

The k_s of a sample was not a direct result of its RWC, even though the two factors are related (i.e., Jackson et al. 1995, Phillips et al. 1996). In the current study, PLC and RWC changed differently with respect 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 the current experiment was the 10-year-old sapling trunks, which showed a linear decrease in k_s with decreasing RWC. This trend is in contrast to the trend in the tips of the trees, which are positioned on the capacitor of the entire stem. These results suggest that the non-linear response seen in the bases as well as in the tips of mature specimens at low Ψ is related to a water storage capability that the saplings do not have. During a drought, the trunk works as a resistor-capacitor system at low Ψ, making it more efficient to use stored water (McDowell et al. personal communication). The non-

linear decrease could also result from the wider range and distribution in lumen volume between single tracheids found at the base of the tree (Panshin and de Zeeuw 1980), which would increase the deviation from a linear pattern.

III.6.4 Mechanical safety factors

The mechanical safety factors were quite insensitive to whether the wood was JW or MW, because the term that changed in JW vs. MW (MOE or MOR, depending on the safety factor) was small relative to another term in the equation. The key quotient is MOE · I or MOR · I. MOE and MOR increased from JW to MW by about 18%. However, the second moment of area, I, increases as a function of stem radius to the fourth power, which almost entirely swamps the contributions of MOE and MOR.

We did not intend the indices of mechanical safety used in the study to be realistic. We meant them to be conservative estimates (erring on the side of too low a safety factor) correlated with actual mechanical safety. Even though the models we used were under static load conditions, the values found for S_{Mh}, S_{Mb}, and S_{Mbra} are consistent with values reported in other studies (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 wood structures are mechanically reliable (Niklas 1998). Minimum mechanical safety factors in branches were higher, because of higher wood density and thus strength (Table III.7). With respect to mechanical performance, we assumed that critical buckling load governs tree mechanical behavior. This may be true if we compared trees to vines (Gartner 1991b), or as we did, one value of wood density to another in a single tree. The problem with using buckling loads as the mechanically controlled feature is that buckling is led by stiffness, not strength, and further, by definition, the ratio of $P_{cr}/P > 1$ or 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 Cannel 1987, Kerzenmacher and Gardiner 1998). Without doubt, the issue is tied to root structure and foundation strength of the ground (Coutts 1986, Niklas and Spatz 2000). The use of real values for the MOE 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 would not be likely, however to change the magnitude of the values found, because we used the lower relationships available from the literature between density and MOE (Niklas 1992).

III.7 CONCLUSION

For mature trees and among three tree age classes, we have given hydraulic coefficients that have a physiological significance and that can be used easily in other studies. This paper shows that the trunk of a mature tree functions on the edge of its critical point relative to hydraulic function in field conditions, whereas the trunk of a young tree behaves in a hydraulically safer manner. Trees appear to produce juvenile wood higher up for hydraulic, not mechanical function. One implication of this research regards forest products. Because juvenile wood is inferior to mature wood for use in many structural applications, there is an incentive to produce less of it. If tree breeders alter the amount of juvenile wood in trees, however, they may inadvertently produce stock susceptible to drought. Our research raises many questions related to the amount of sapwood trees have and the hydraulic function of that sapwood. More research is needed in other tree species with wider sapwood, and in other age classes to increase our understanding of the patterns of xylem heterogeneity and the apparent cause for the evolution of these patterns.

III.8 ACKNOWLEDGMENTS

This work was supported by: USDA CSREES 97-35103-5052. Deep thanks to Jeff Langlois and Dr. R. Leichti for aid on the mechanical part, Andre Melliott, Nathan Poage and Michele Pruyn for assistance in tree-climbing, and Owen Burney for providing the seedlings. This manuscript was improved by comments from Dr. B.J. Bond, Dr. K.L. Kavanagh and Dr. R. Leichti and three anonymous reviewers. This is paper #3499 of the Forest Research laboratory, Oregon State University, Corvallis, Oregon.

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Chapter IV

Relationship Between Growth Rates and Xylem Hydraulic Characteristics in a Chronosequence of Ponderosa Pine Trees.

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IV.1 ABSTRACT

Our first objective was to quantify effects of tree age and stem position on specific conductivity (k_s), vulnerability to embolism and water storage capacity (capacitance). Our second objective was to determine relationships between hydraulic characteristics and radial and height growth rates. We measured xylem k_s, and the vulnerability of xylem to embolism in trunks of young, mature and old-growth trees in a chronosequence of ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.) growing in a mixed-stand. The air injection method was used to measure the radial and spatial patterns of xylem embolism in trunks. Within sapwood at all heights and in all ages of trees, outer sapwood had 25–60% higher k_s than inner sapwood ($P<0.05$). Water potential at which embolism starts (the air entry point) was 1.3 MPa lower in inner sapwood than outer sapwood within the mature trees, but no different radially for either the old growth or young trees. However, wood at the base (mature wood) and treetop (juvenile wood) of old growth trees were significantly more resistant to embolism than the intermediate parts of the trunk ($P<0.05$). There was no significant difference in water storage capacity between the top of the old growth trees, the mature trees and the young trees ($P>0.2$). Water storage capacities increased sharply with an increase in k_s and vulnerability to embolism. Radial growth rate of juvenile wood was 53% higher than mature wood ($P=0.02$). There was no difference in radial growth rate for the last 200 years of growth within the mature trees, with an average value of 1.5 mm year^{-1} ($\pm$ 0.1). Height growth rates were significantly higher in the mature trees than in the other trees ($P<0.002$) with a peak at 75 years. In the mature trees the rates stayed constant through the life span of the trees with an average value of 2.2 mm year^{-1} ($\pm$ 0.2). Our results suggested that increase in height growth in ponderosa pine is associated with 1) high vulnerability to water-stress induced embolism 2) low sapwood k_s 3) high sapwood water storage capacity.

Key words: embolism – height growth rate – juvenile wood – mature wood – *Pinus ponderosa* (Dougl. ex Laws.) – trunk vulnerability curve – water storage capacity

IV.2 INTRODUCTION

Nearly all of our understanding of vulnerability to embolism in trees comes from the study of branches or young trees. In most studies, vulnerability curves (VCs) have been produced using either excised branches (Sperry & Tyree 1988; Cochard 1992) or from small tree seedlings grown in pots or in nursery beds (Tyree, Alexander & Machado 1992; Kavanagh *et al.* 1999). Recently, VCs were reported from the trunks of mature Douglas-fir trees, a conifer species with narrow sapwood area (Domec & Gartner 2001). However, there is a crucial lack of information on the hydraulic functioning of the whole trunk for conifer species, especially those with wide sapwood area, and for trees of different ages. Within the same natural conditions, are old-growth trees more vulnerable to embolism-induced by water-stress than mature and young trees? Although it has been shown that stem segments from seedlings and saplings exhibited more resistance to embolism than those from adult trees (Sperry & Saliendra 1994; Matzner, Rice & Richards 2001), no studies have investigated vulnerability to embolism in the main trunk of trees of different age growing in the same condition.

Vulnerability to embolism is influenced by the structure of the xylem and the ability of different parts of a tree to prevent embolism (Hacke *et al.* 2002; Domec & Gartner 2002). Piñol & Sala (2000) showed that pine species maintain a large amount of sapwood and a high leaf specific conductivity at the cost of being more vulnerable to embolism than the other conifers studied. Trees have a wide range of wood properties that change non-uniformly with distance from the pith. Low-density wood produced near the pith is commonly called juvenile wood (JW),

whereas high-density wood produced beyond the JW is called mature wood (MW). The first 10–30 rings wide from ground level to the treetop in tree are made of JW that are subsequently covered with MW. Throughout its life a tree produces JW at the tip and MW near the bottom. Have these differences in wood property from pith to bark evolved to maintain the hydraulic capacity of the tree, as in Douglas-fir (Domec & Gartner 2002), or are they neutral characters? Lower specific conductivity (k_s) in JW than in MW has been shown within conifer species with wide sapwood by studies comparing hydraulic properties at the same height of trees of different age (Pothier *et al.* 1989; Mencuccini, Grace & Fioranvanti 1997). There are no reports comparing the vulnerability to embolism of JW and MW in species with wide sapwood and crucial details needed to understand trunk vulnerability to embolism are still lacking. It is logical to hypothesize that the top and the bottom of a tree and the inner and outer sapwood of species with wide sapwood would be characterized by wood of very different hydraulic properties.

Water stress is a major factor limiting plant growth (Tyree and Jarvis 1982; Pyrke & Kirkpatrick 1994). At the whole-plant level, limited soil water supply has a strong effect on plant growth and metabolism (see reviews by Hsiao 1973; Schulze 1986; Jones 1992). Drought avoidance or tolerance is critical for survival and growth in water-limited environments (Tyree and Ewers 1991; Zhang et al. 1997). Growing periods with little water can lead to decreased diameter and height growths (Zhang, Marshall & Fins 1996; Marshall, Rehfelt & Monserud 2001), poor resistance to other stresses, disruption of food production and distribution, and changes in timing and rate of physiological processes (Wright 1976). In conifers, plant height growth over the age of a tree is generally sigmoidal: during the maturation processes, growth peaks decline and nearly stop after 150 years (Monson et Grant 1989; Larcher 1995; O'Hara 1996). The hydraulic limitation hypothesis proposed for this age-related decline in height growth (Ryan & Yoder 1997; Bond & Ryan 2001), states that hydraulic resistance increases as trees grow and age and that this increased resistance results in lower rates of photosynthesis

and transpiration (per unit leaf area) in older trees and reduced productivity in older stands. Should the changes in hydraulic parameters of sapwood reflect the changes in radial and vertical growth rates? If yes, then what leads to such changes: is it more related to changes in k_s, vulnerability to embolism or water storage capacity?

In this study, we explored the above questions by investigating the hydraulic properties of trunks in a chronosequence of old-growth (> 200 years), mature and young individuals of a conifer species with wide sapwood. Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is generally intolerant of shade but often grows in pure multi-aged stands at low density (Barrett 1979; Smith 1986), which allowed us to study several cohorts of age classes growing in the same conditions. We analyzed the relationship of radial and height growth rate to k_s, vulnerability to embolism and water storage capacity to infer which, if any, of the wood hydraulic factors appears to control growth rate. Our hypotheses were: (1) for a given stand, old-growth ponderosa pine trees are more vulnerable to water-stress induced embolism than mature and young trees; (2) small changes in wood structure from the pith outward strongly affect hydraulic performance; and (3) growth rates and sapwood hydraulic characteristic are correlated positively.

IV.3 MATERIALS AND METHODS

IV.3.1 Plant material and sample preparation

The study site is a mixed-age ponderosa pine stand located on the eastern side of the Oregon Cascade Range (43°32'N; 121°41W) on a private forestland (Crown Pacific Co.). The mean annual precipitation is 645 mm (www.orst.edu/Dept/IPPC) and the elevation is 1355 m with deep volcanic ash derived soils. The stand is a mix of ponderosa pine and lodgepole pine (*Pinus contorta*) ranging from 15 to 400 years old, and with approximately 250 trees per hectare. Trees sampled were the same as used by Pruyn, Gartner and Harmon (2002). Six old-growth trees (>260-

year-old) in March 1999, six mature trees (>70-year-old) and six young trees (>20-year-old) in March 2000 were selected based on their cambial age at breast height, their heights and their health (free of broken tops, stem deformities or disease) (Table IV.1). After felling the trees, four heights of the old-growth trees were sampled, at 1-meter height (node 220), at node 65 (lower third part of the crown), and at nodes 50 and 15 counting down from the treetop. For the mature trees, only nodes 50 and 15 were sampled, and for the young trees, only node 15. The height to each of these sampled nodes was recorded (Table IV.2). At each height, and from each tree, disks with an approximate thickness of 20 cm were cut, immediately transported to the laboratory three hours away in wet plastic bags, and stored at 5°C until blocks were prepared. From each cross-section disk, four blocks were cut: two from the inner sapwood and two from the outer sapwood within three days of felling the trees. Preparation of these specimens made from the blocks followed the procedures outlined by Domec and Gartner (2001). The specimens (about 10 mm radial direction, 10 mm tangential direction, and 130-170 mm axial direction) were split along the grain first with a maul and wedge, and then with a chisel, then stored at 3°C in clean water changed every day until they were used within three weeks.

IV.3.2 Hydraulic specific conductivity, vulnerability and relative water content curves

Samples were submerged under a vacuum for 48 hours to refill some of the embolized tracheids. Initial specific conductivity ($k_{s(i)}$) was then measured on 130–170 mm segment as described below. We expressed $k_{s(i)}$ as length square (m2), which is the direct consequence of separating the viscosity from water in terms of pressure difference (Darcy's law). Vulnerability curves (VCs) of the samples were constructed using the method described by Domec and Gartner (2001). The method measures the percent loss of conductivity (PLC) on segments taken directly from the trunk by moving the sample alternately between the membrane-lined pressure sleeve to measure k_s (Spicer and Gartner 1998) and the double-ended pressure chamber for causing embolism using air injection (Sperry

Table IV.1. Mean values (± SE, n=6) for morphological characteristics of young, mature and old-growth ponderosa pine sampled coming from the same site.

	Mean Height (m)	Age at the base (year)	Mean diameter at breast height (cm)	Mean sapwood area at the base (cm^2)	Mean leaf area per tree (m^2)
Old-growth trees	33.3 ± 0.4	225 ± 27	62.1 ± 1.9	2390 ± 114	540 ± 35
Mature trees	12.4 ± 0.9	72 ± 5	26.8 ± 1.8	375 ± 71	71.7 ± 16.1
Young trees	2.9 ± 0.1	31 ± 3	7.7 ± 0.6	55.7 ± 6.2	10.8 ± 1.9

Table IV.2. Mean values (± SE, n=6) for morphological characteristics of mature ponderosa pine trees by height position (node) counting down from the top of the tree, at 1 m from the ground, and at the base (about 30 cm). The base of the live crown was located a few nodes below node 65 at a mean height of 29 ± 1 m. The whole sapwood width has been divided in two parts to determine the outer sapwood shell (comprised between the outer part of the sapwood and the middle of the sapwood width) and the inner sapwood shell (comprised between the middle of the sapwood width and the heartwood-sapwood boundary). The proportion of outer sapwood (%) has been calculated in dividing the outer sapwood shell by the total sapwood area.

Sample type	Nodes from top	Mean height (m)	Diameter (cm)	Sapwood area (cm^2)	Heartwood area (cm^2)	Proportion of outer sapwood (%)	Number of sapwood rings (no.)
Young trees	Node 15	1.1 ± 0.2	7.7 ± 0.6	35.2 ± 5.9	0.12 ± 0.04	100	15 ± 1
	Base	0.3	10.1 ± 0.5	55.7 ± 4.4	0.14 ± 0.07	70 ± 1	29 ± 3
Mature trees	Node 15	8.6 ± 0.8	9.48 ± 0.5	55.5 ± 7.4	0.64 ± 0.12	100	16 ± 1
	Node 50	1.6 ± 0.2	19.2 ± 0.8	192 ± 28	9.5 ± 2.9	67 ± 1	41 ± 2
	Base	0.3	25.9 ± 1.6	375 ± 71	4.4 ± 2.2	71 ± 1	54 ± 3
Old growth trees	Node 15	31.0 ± 0.3	6.92 ± 0.2	24.1 ± 3.1	2.6 ± 0.3	100	14 ± 1
	Node 50	25.5 ± 1.2	22.1 ± 1.1	322 ± 61	17.7 ± 3.5	66 ± 1	41 ± 3
	Node 65	21.4 ± 1.2	31.8 ± 0.8	624 ± 43	53.4 ± 8.3	65 ± 1	52 ± 1
	Base	0.4 ± 0.1	62.3 ± 1.8	2387 ± 114	213 ± 41	64 ± 1	116 ± 5

and Saliendra 1994). Samples were soaked in water, then $k_{s(i)}$ was measured using filtered (0.22μm) water adjusted with HCl to pH 2 in order to prevent microbial growth, and hydraulic head of pressure of 0.0045 MPa. Efflux was collected in a 1-ml-graduated micropipette (0.01 ml graduation). We recorded the time required for the meniscus to cross five consecutive graduation marks, and only used the values that were steady. Samples were subjected to several air pressures ranging from 0.5 to 5.0–6.0 MPa until more than 95 PLC was reached. The temperature of the solution (to calculate water viscosity), the fresh mass (M_f), the volume (V_f) and the length of each sample were recorded before and after each hydraulic conductivity measurement (see below). After each k_s measurement we removed about 1 mm of wood from each end of the stems to have a new surface for each experiment. Hydraulic vulnerability curves were fitted by the least squares method based on a sigmoidal function:

$$PLC = \frac{100}{\left(1 + e^{a_1(\Psi - b_1)}\right)} \qquad (1)$$

where PLC is the percent loss of conductivity ($(k_{s(i)} - k_{s(\Psi)})/k_{s(i)}$), the parameter a_1 is an indicator of the slope of the linear part of the vulnerability curve and b_1 the potential at which 50 PLC occurred. The actual slope ($s = a_1 \cdot 25$) of the linear part of the vulnerability curve and the pressures at 12 PLC ($\Psi_{12} = 2/a_1 + b_1$) and at 88 PLC ($\Psi_{88} = -2/a_1 + b_1$) were determined from the fitted curves (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). 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.

To estimate the rate of change in relative water content (RWC) associated with embolism, we determined RWC initially and after each applied pressure by recording the volume by water displacement (V_f; cm^3) and the fresh mass (M_f; g) by mass 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 density of cell wall material of 1.53 g cm^{-3} (Siau 1984):

$$\mathrm{RWC} = \frac{M_f - M_d}{V_f - M_d/1.53} \qquad (2)$$

The loss of RWC (100 – %RWC) over the range of applied pressure were fit using the following sigmoidal function:

$$100 - \%\mathrm{RWC} = \frac{\mathrm{Max}}{\left(1 + e^{a_2(\Psi - b_2)}\right)} \qquad (3)$$

where Max is the maximum loss of RWC possible, a_2 is a indicator of the slopes of the linear part of the curves and, and b_2 the potential at which Max/2 loss of RWC occurred ($\Psi_{max/2}$).

Water storage capacity can be defined as the amount of water withdrawn from the stem at a given water potential relative to zero water potential (Holbrook 1995). We expressed water storage capacity as the change in RWC per unit Ψ, which allows us to compare differences in storage capacities that are not only related to a difference in total water volume but also to tissue density (Domec & Gartner 2001). One cannot accurately estimate capillary water changes by using the pressure chamber because positive pressure cannot displace capillary water

(Zimmermann 1983; Tyree & Yang 1990). The hypothesis of capillary water storage stipulates 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 were correct, then maximum capillary water storage would be released at a pressure potential close to zero, and would stop before –0.5 MPa (Holbrook 1995; Tyree & Yang 1990). Therefore, to avoid underestimating capillary water at low applied pressure, volumetric RWC-based capacitance, defined as $C_{RWC}=d_{RWC}/d\Psi$ (Edwards and Jarvis 1982) was computed for a phase in each dehydration curve from 0.5 to 2.0 MPa ($C_{0.5-2}$). This range corresponds to the natural range of water potential encountered by these trees (Hubbard, Bond & Ryan 1999; Ryan *et al.* 2000; authors' personal observation).

We analyzed these data further by looking at the values from the derivative of Equation 3. These values are the slope of each tangential line at an applied pressure, Ψ, which by definition corresponds to the instantaneous water storage capacitance. The derivative of Equation 3 is:

$$\frac{d(\%Loss\_(1-RWC))}{d\Psi} = \frac{-a_2 \cdot \left(e^{a_2(\Psi - b_2)}\right) \cdot Max}{\left(1 + e^{a_2(\Psi - b_2)}\right)^2} \qquad (4)$$

We computed an instantaneous RWC-based capacitance at Ψ equal Ψ_{12}, which corresponds to the water storage capacity at the air entry point. We also computed another one at a phase corresponding to the maximum water storage capacity possible within the entire range of applied pressure (C_{max}). Using the procedure outlined by Domec & Gartner (2001), it can be shown that C_{max} occurs when $\Psi = b_2$ (Domec and Gartner 2001) and therefore also corresponds to the slope of the linear part of the sigmoidal curve:

$$C_{max} = a_2 \cdot \text{Max}/4 \quad (5)$$

IV.3.3 Wood density and latewood proportion

We determined wood density values (g cm^{-3}) for each sample that was tested hydraulically:

$$\text{Density} = M_d/V_f, \quad (6)$$

where M_d is the oven dry mass (dried at 105°C), and V_f is the fresh volume. We used a transverse section made with a microtome and 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) with an image analysis system consisting of a compound microscope, a video camera, and the software NIH Image (v. 1.60, Rasband 1996). We then calculated the mean latewood proportion for each sample as the mean of the latewood proportions of all growth rings analyzed for that sample.

IV.3.4 Tree growth rates

We measured tree height (m) and trunk diameter (cm) at breast height (DBH) and at each node sampled. Mean annual growth rate in height (cm $year^{-1}$) for the corresponding number of sapwood rings was estimated by dividing the mean height of bole above each disk by the cambial age (Table IV.2). At node 15, we divided directly the height to the top of the tree by the number of rings. For node 65, the number of rings in sapwood corresponded to the height growth above the next disk (between node 50 and treetop). For the base and node 50, the number of rings in sapwood corresponded to a growth located between nodes 110–230 and nodes 15–50 respectively, so we took a weighed average (by year) between the total annual growth height between these two disks.

Number of rings in heartwood and sapwood as well as heartwood and sapwood areas were determined on a fresh sub-sample disk from each height for each tree. We drew two perpendicular diameters, counted the rings, measured heartwood and heartwood widths, and then averaged values for the two diameters. Sapwood area was taken as the area of whole disk (excluding bark and cambium) minus the area of heartwood. The annual radial growth rate (cm $year^{-1}$) for each sample (outer and inner sapwood) was calculated by dividing the number of growth rings in each sample by the sample width. Using the growth rate of the outer samples, percent yearly increment (% $year^{-1}$) of sapwood was calculated by dividing the difference between the sapwood areas of the last two rings to the total amount of sapwood.

IV.3.5 Statistical analysis

We used least squares methods to fit relationships between hydraulic parameters and applied pressure, and linear and non-linear relationships among hydraulic parameters. Each sample was used as a single replicate that gave a single value of each hydraulic parameter, which were compared among locations (radial tissues and height positions) by carrying out an analysis of variance (ANOVA) and covariance (ANCOVA) using a strip-plot randomized complete block design (trees as block) with radial tissue and height position being the strip plots factors. The experiment was designed to assess values at both inner and outer sapwood, but for height position we were interested in an estimate of the entire sapwood. Therefore, the effect of height position on the hydraulic properties was made by weighting the values by the proportion of the total sapwood area occupied by the outer and inner sapwood shells (Table IV.2). The inner shell represented the area from the third growth ring exterior to the heartwood/sapwood boundary to the middle of the sapwood zone, and the outer shell represented the area from the middle of the sapwood zone to the cambium.

All statistical procedures were conducted with Statistical Analysis Systems software (SAS 1997). Least square (LS) means were generated from a PROC MIXED procedure, and multiple comparisons among means were calculated using least square differences (LSD).

IV.4 RESULTS

IV.4.1 Hydraulic conductivity and vulnerability to embolism parameters

Hydraulic conductivity (k_s) for the lower disk (below the living branches) increased with tree age from $1.4 \pm 0.4 \times 10^{-12}$ m^2 in the young trees (node 15) to about $5.1 \pm 0.4 \times 10^{-12}$ m^2 in the mature trees (node 50) and $8.0 \pm 0.4 \times 10^{-12}$ m^2 in the old-growth trees (node 65; Table IV.3). At the top of the trees (node 15), k_s was 73% and 40% higher in the mature trees than in the young and old-growth trees, respectively. Outer sapwood had significantly higher k_s than outer sapwood for all samples ($P<0.05$). The larger differences occurred at nodes 50 with a 59% and a 49% increased between inner and outer sapwood in the mature and old-growth trees, respectively.

For the top (node 15) of the young, mature and old growth trees, the vulnerability to embolism parameters of the mature trees were significantly different than those in the old-growth and young trees (Fig. IV.1; Table IV.3; $P < 0.002$ for comparisons of Ψ_{12}, Ψ_{50} and Ψ_{88}). There were no significant differences in any of these parameters between the old-growth trees and the young trees ($P > 0.16$). The slope s of the vulnerability curves for the top of the trees were not significantly different ($P > 0.15$), with a mean value for all three age classes combined of 60.5 ± 5.5 PLC MPa^{-1}.

For the base of the trees (node 15, node 50 and 1-meter for the young, mature and old-growth trees respectively), the hydraulic parameters of the mature trees were significantly different than young trees for Ψ_{12}, Ψ_{50} and Ψ_{88} ($P < 0.007$),

significantly different than the old-growth and for Ψ_{12} and Ψ_{50} ($P < 0.01$) but marginally different for Ψ_{88} ($P = 0.07$). There was no difference for all three hydraulic parameters between the base of the old growth and the base of the young trees ($P > 0.09$; Table 3). The slopes s of the vulnerability curves at the base of the three different age-classes were not significantly different ($P>0.26$), with a mean value for all the three age-classes combined of 56.4 ± 6.2 PLC MPa^{-1}.

Within the old-growth trees, considering height and radial position as fixed effects for the lower three heights, the ANOVA showed there was no significant difference between the overall inner and outer sapwood for either Ψ_{12} ($F_{1,5}$=1.40, P=0.29), Ψ_{50} ($F_{1,5}$=0.90, P=0.39 or Ψ_{88} ($F_{1,5}$=0.08, P=0.79). Within the mature trees, inner sapwood at node 50 was 1.2 MPa less resistant to embolism than outer sapwood for the parameter Ψ_{12} (P=0.04) (Table IV.3). Using the weighted values from each disk and comparing the three age classes, we showed that k_s was strongly correlated (P<0.05) with the slope s and Ψ_{88} but not with Ψ_{12} and Ψ_{50} (Fig. IV.2). However, when comparing k_s with the other vulnerability parameters within the old-growth trees only, we found strong and significant relationships (see filled triangles in Fig. IV.2).

IV.4.2 Trunk water storage capacity

The changes in RWC versus the applied pressure showed a sigmoidal change, with significantly steeper slopes (represented by C_{max}) from the base to node 50 of the old-growth trees (P<0.05, Table IV.4, Fig. IV.1). There was no significant difference between the top of the old-growth trees, the mature trees and the young trees (P>0.2; Table IV.4).

Figure IV.1. Percent loss in conductivity (PLC) and percent water deficit (100–relative water content) vs. the opposite of applied air pressure in six old-growth (triangles) mature (squares) and young (circle) ponderosa pine trees. Curves represent the top (node 15, outer sapwood) and the base of the trunk (outer and inner sapwood). Filled symbols/full lines are for the outer sapwood and open symbols/dash lines are for the inner sapwood. The top of the mature trees had a higher water storage capacity and was more vulnerable to embolism than the young and old-growth trees (see Tables IV.3 and IV. 4 for the sigmoidal regression coefficients and statistical comparisons among position and heights). Error bars are standard errors.

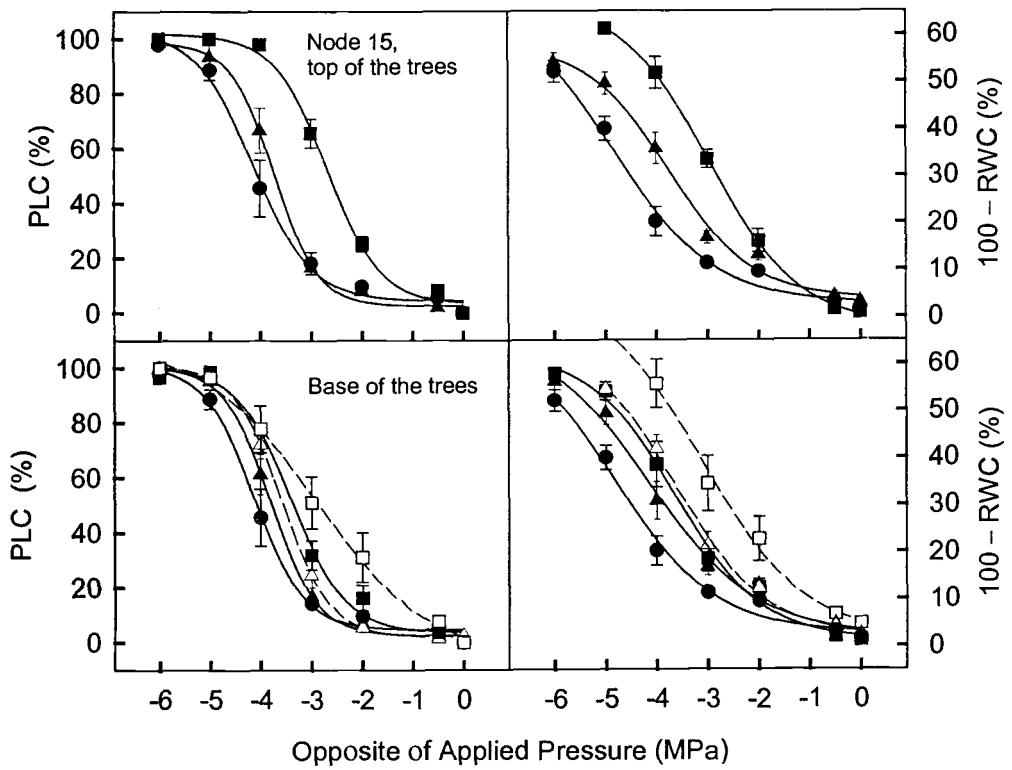
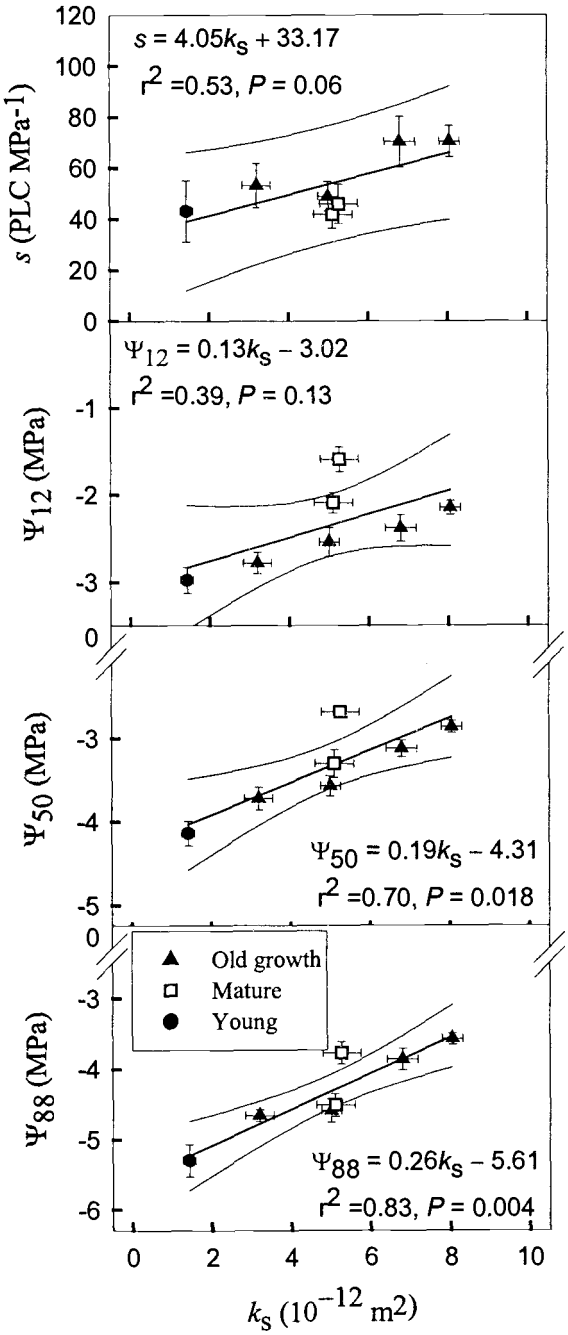


Table IV.3. Effect of position and tissue in the tree on the specific hydraulic conductivity (k_s), the slope of the linear portion of the vulnerability curve (s), the potential (b_1) at which 50% loss of k_s is reached, the air entry point (Ψ_{12}) and the full embolism point (Ψ_{88}). Each value is the mean (±SE) of 6 trees. Values with different letters within a column are significantly different ($P<0.05$). Multiple comparisons were calculated according to the mixed procedure.

Tree types	Tissue	Position	k_s (10^{-12} m^2)	$s_1 = 25 \cdot a$ (%Loss k_s MPa^{-1})	Ψ_{12} (MPa)	$b_1 = \Psi_{50}$ (MPa)	Ψ_{88} (MPa)
Young	Outer sapwood	Node 15	1.4 ± 0.4 a	43.1 ± 7.3 a	−3.0 ± 0.1 a	−4.1 ± 0.1 a	−5.0 ± 0.2 a
Mature	Outer sapwood	Node 15	5.3 ± 0.4 b	46.0 ± 7.3 ab	−1.4 ± 0.1 b	−2.5 ± 0.1 b	−3.3 ± 0.2 b
		Node 50	5.7 ± 0.4 b	43.9 ± 7.3 a	−2.2 ± 0.1 c	−3.3 ± 0.1 cd	−4.4 ± 0.2 ac
	Inner sapwood	Node 50	2.9 ± 0.4 c	29.1 ± 7.3 a	−0.9 ± 0.1 d	−2.5 ± 0.1 b	−4.0 ± 0.2 c
Old growth	Outer sapwood	Node 15	3.2 ± 0.4 cg	53.2 ± 7.3 ab	−2.9 ± 0.1 a	−3.7 ± 0.1 ad	−4.6 ± 0.2 a
		Node 50	8.4 ± 0.4 d	78.1 ± 7.3 c	−2.5 ± 0.1 c	−3.1 ± 0.1 c	−3.7 ± 0.2 bc
		Node 65	9.7 ± 0.4 e	67.6 ± 7.3 bc	−2.2 ± 0.1 c	−2.9 ± 0.1 bc	−3.6 ± 0.2 bc
		1 meter	5.5 ± 0.4 b	47.3 ± 7.3 ab	−2.9 ± 0.1 a	−3.8 ± 0.1 a	−4.6 ± 0.2 a
	Inner sapwood	Node 50	3.4 ± 0.4 cg	54.3 ± 7.3 ab	−2.3 ± 0.1 c	−3.1 ± 0.1 c	−4.0 ± 0.2 c
		Node 65	4.9 ± 0.4 bf	75.8 ± 7.3 c	−2.2 ± 0.1 c	−2.8 ± 0.1 bc	−3.4 ± 0.2 b
		1 meter	4.2 ± 0.4 fg	51.7 ± 7.3 ab	−2.7 ± 0.1 a	−3.5 ± 0.1 d	−4.4 ± 0.2 ac

Figure IV.2. Trunk xylem safety vs. xylem efficiency of ponderosa pine trees. Trunk xylem safety is represented by the slope of the linear part of the sigmoidal curve (s), the mean air entry tension (Ψ_{12}), mean embolism tension (Ψ_{50}) and maximum embolism tension (Ψ_{88}). Xylem efficiency is represented by the mean specific conductivity (k_s). Error bars are standard errors.



Inside the old-growth trees, there was a significant difference only between outer and inner sapwood for $C_{\Psi 12}$ and C_{max} at node 50 ($P < 0.05$; Table IV.4). In an ANOVA with height and radial position as fixed effects, there was no significant difference between the overall inner and outer sapwood for either $C_{0.5-2}$ ($F_{1,5}$=0.11, P=0.75) or $C_{\Psi 12}$ ($F_{1,5}$=2.60, P=0.17). There was, however, a significant difference in C_{max} between the overall inner and outer sapwood ($F_{1,5}$=8.46, P=0.033). For the first three disks, this effect is due to the significant difference between the outer and inner samples at node 50 (Table IV.4).

For every sample, $C_{\Psi 12}$ and $C_{0.5-2}$ were significantly different (P<0.01) for the old growth trees and young trees but not for the mature trees (P=0.43). C_{max} and $C_{\Psi 12}$ increased sharply with an increase in k_s and Ψ_{12}, respectively (Fig. IV.3), from approximately 16% RWC MPA^{-1} at node 15 to 26% RWC MPa^{-1} at node 65 for the former.

IV.4.3 Tradeoff between hydraulic parameters, growth rates and wood density

Wood density increased by 2% from the inner to the outer sapwood growth rings at the base of the old growth trees and by 6% at the base of the mature trees. Between the bottom and the top, wood density of the outer sample (same year of growth) decreased by 20% and 19% for the old growth and mature trees, respectively (Fig. IV.4a). There was a strong linear relationship between the percent latewood and wood density for the pooled data from the trunk of old growth, mature and young trees:

$$\text{Percent latewood} = 130.6 \cdot \text{Density} - 30.5 \quad (r^2 = 0.80,\ P < 0.001). \qquad (7)$$

There were strong relationships between wood density, percent latewood and hydraulic parameters within JW and MW for k_s, and Ψ_{88} (Table IV.5). Density and percent latewood of MW was better correlated with the vulnerability parameters

than density of JW. Percent latewood of JW was correlated with the three kinds of capacitances whereas MW was not (Table IV.5). There were very few correlations when all the data were pooled together, and these correlations where always lower than when we examined just one type of wood.

Radial growth rate of JW was 53% significantly higher than MW (P=0.02). There was no difference in radial growth rate for the last 200 years of growth within the mature trees (Fig. IV.4b), with an average value of 0.15 (± 0.01) cm year^{-1}. Each new ring at node 15 increased the sapwood area by 11%, 9% and 16% within the old-growth, mature and young trees, respectively. At the base of the old-growth and mature trees, the yearly increment of sapwood was 2% and 4%, respectively. Height growth rates of ponderosa pine were significantly higher in the mature trees than in the other trees (P<0.002) with a peak at 75 years (Fig. IV.5a). In the mature trees the rates stayed constant through the life span of the trees with an average value of 0.22 (± 0.02) cm year^{-1}. For the top of the trees (node 15), height growth rates of old growth and young trees were not significantly different (P>0.16), with an average value of 13 (± 1) cm year^{-1}. We could not fit the usual height growth curves (Barrett 1978) because the predicted curve underestimated the height of the trees after 150 years (Fig. IV.5b).

Using the weighed values (by areas represented by outer and inner sapwood, Table IV.2) from each disk with the three age classes, we asked if there was a relationship between the height, diameter growth rates and yearly increment of sapwood and the hydraulic parameters. For all type of samples, Ψ_{12} was positively strongly correlated ($P < 0.001$) with the height growth rate (Fig. IV.6a). Within the old growth trees only, height growth rate was strongly correlated ($P < 0.05$) with k_s (Fig. IV.6b). For all type of samples, Ψ_{12} and k_s were correlated ($P < 0.05$) with the yearly percent increment sapwood (Fig. IV.7). There was, however, no correlation between any of the hydraulics parameters and the diameter growth rate (data not shown).

Table IV.4. Effect of position and tissue in the tree on the maximum water deficit (100 – RWC) reached (Max), the potential (b_2) at 50% loss of RWC, the maximum water storage capacity (C_{max}), which corresponds also to the slope of the linear portion of 100–RWC curve, the capacitance at the air entry point ($C_{\Psi 12}$), and between 0.5 and 2.0 MPa ($C_{0.5-2}$). Each value is the mean (±SE) of six trees. Values with different letters within a column are significantly different ($P<0.05$). Multiple comparisons were calculated according to the mixed procedure.

Tree types	Tissue	Position	Max (%RWC)	$b_2 = \Psi_{Max/2}$ (MPa)	$C_{max} = Max \cdot a_2/4$ (%RWC MPa^{-1})	$C_{\Psi 12}$ (%RWC MPa^{-1})	$C_{0.5-2}$ (%RWC MPa^{-1})
Young	Outer sapwood	Node 15	65.2 ± 5.4 a	–4.8 ± 0.2 a	16.5 ± 2.1 a	7.7 ± 1.5 a	4.3 ± 1.4 a
Mature	Outer sapwood	Node 15	69.1 ± 2.1 a	–2.9 ± 0.2 b	19.9 ± 2.1 a	9.9 ± 1.5 a	9.7 ± 1.4 b
		Node 50	61.2 ± 2.1 a	–3.6 ± 0.2 c	18.2 ± 2.1 a	9.5 ± 1.5 a	6.9 ± 1.4 a
	Inner sapwood	Node 50	73.7 ± 2.1 b	–3.1± 0.2 b	18.8 ± 2.1 a	6.5 ± 1.5 a	10.6 ± 1.4 b
Old growth	Outer sapwood	Node 15	53.9 ± 2.1 c	–3.7 ± 0.2 c	17.0 ± 2.1 a	13.1 ± 1.5 b	5.5 ± 1.4 a
		Node 50	57.2 ± 2.1 ac	–3.2 ± 0.2 bc	28.0 ± 2.1 b	18.1 ± 1.5 c	5.2 ± 1.4 a
		Node 65	60.3 ± 2.1 a	–3.0 ± 0.2 b	25.1 ± 2.1 bc	17.6 ± 1.5 c	6.1 ± 1.4 a
		1 meter	64.2 ± 2.1 a	–4.1 ± 0.2 c	15.4 ± 2.1 a	11.1 ± 1.5 ab	5.5 ± 1.4 a
	Inner sapwood	Node 50	58.2 ± 2.1 a	–3.2 ± 0.2 b	21.7 ± 2.1 c	13.6 ± 1.5 b	4.8 ± 1.4 a
		Node 65	57.7 ± 2.1 ac	–2.8 ± 0.2 b	24.9 ± 2.1 bc	19.1 ± 1.5 c	6.0 ± 1.4 a
		1 meter	63.4 ± 2.1 a	–3.6 ± 0.2 c	18.27 ± 2.1 a	13.9 ± 1.5 b	5.4 ± 1.4 a

Figure IV.3. (a) Mean air entry tension (Ψ_{12}) vs. the capacitance between 0.5 and 2.0 MPa of ponderosa pine trees. (b) Specific conductivity (k_s) vs. maximum capacitance (C_{max}, which corresponds also to the slope of the linear portion of the change in relative water content vs. the applied pressure). Error bars are standard errors.

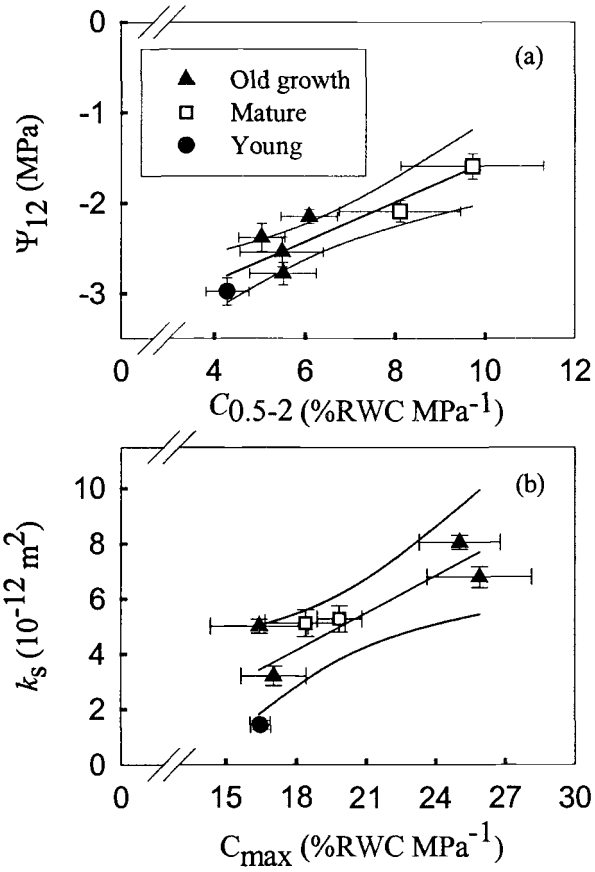


Figure IV.4. (a) Wood density and (b) radial growth rate as a function of cambial age (ring from pith) within the old-growth trees and the mature trees (insert). Error bars are standard errors.

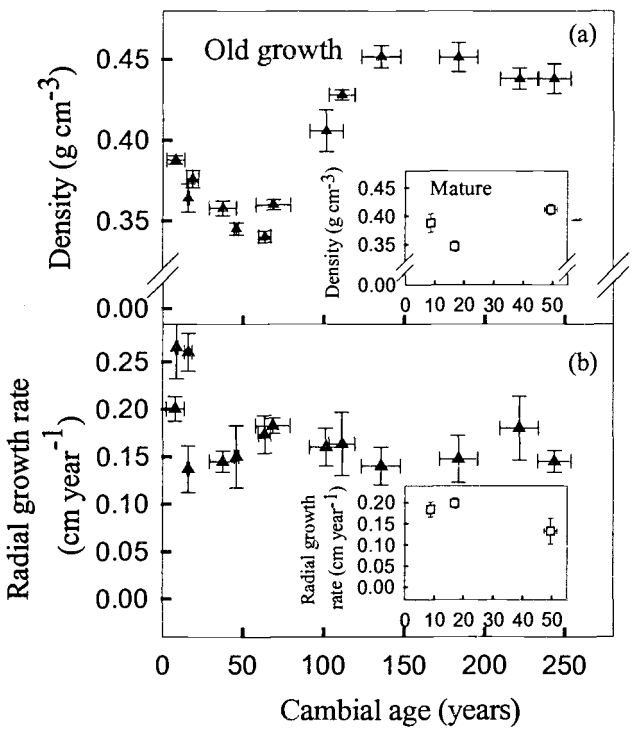


Figure IV.5. (a) Height growth rate (b) tree height as a function of cambial age (ring from pith) within the old-growth trees and the mature trees (insert). Error bars are standard errors. The solid line represents the usual curves of height growth with tree age for ponderosa pine and for a site index of 28 (Barrett 1978).

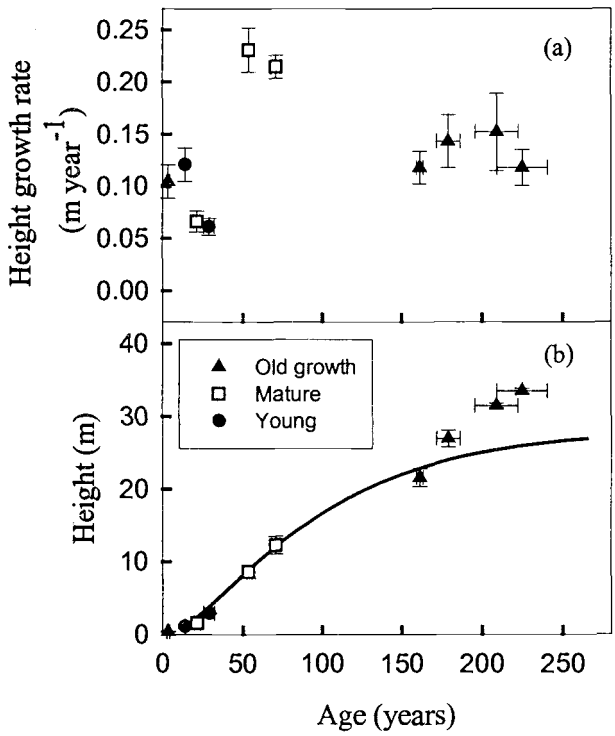


Table IV.5. Slopes and intercepts (in parenthesis) of the linear regressions of the hydraulic conductivity (k_s), the air entry point (Ψ_{12}), the potential at which 50% loss of RWC is reached (b_1=Ψ_{50}), the full embolism point (Ψ_{88}), the slope of the linear portion of the vulnerability curve (s), the capacitance between 0.5 and 2 MPa ($C_{0.5-2}$), the capacitance at the air entry point ($C_{\Psi 12}$) and the maximum water storage capacity (C_{max}) vs. the wood density and percent latewood. Based on their respective mean ring from pith (or cambial age), data has been separated into juvenile wood (JW or samples ≤ 25 rings from the pith, n = 36), mature wood (MW or samples with ≥ 50 rings, n = 24), or all types of wood combined (All = MW + JW, n = 66). Values in boldface represent values with a significance level < 0.001. [1] Significance levels refer to the slope of the regression; ns = not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$.

Table IV.5

	Density (g cm^{-3})			Percent latewood		
	JW	MW	All	JW	MW	All
k_s (10^{-12} m^2)	**–27.3 (13.6)**	**–42.3 (23.7)**	–21.6 (13.2)	**–0.16 (6.12)**	**–0.25 (12.64)**	–0.03 (5.61)
	r^2 = 0.56**[1] a	r^2 = 0.78** b	r^2 = 0.16*	r^2 = 0.35** a	r^2 = 0.46** a	r^2 = 0.01 ns
Ψ_{12} (MPa)	–4.7 (0.5)	–5.4 (–0.3)	–5.0 (–0.5)	–0.04 (–1.55)	–0.04 (–1.33)	–0.04 (–1.72)
	r^2 = 0.06 ns	r^2 = 0.23*a	r^2 = 0.11*	r^2 = 0.09 ns	r^2 = 0.29*	r^2 = 0.13*
Ψ_{50} (MPa)	–9.4 (0.3)	**–7.7 (–0.2)**	**–7.8 (–0.3)**	–0.06 (–2.17)	**–0.05 (–2.09)**	–0.04 (–2.42)
	r^2 = 0.30** a	r^2 = 0.65, **[a]	r^2 = 0.35, **	r^2 = 0.25** a	r^2 = 0.47** a	r^2 = 0.23 **
Ψ_{88} (MPa)	**–14.1 (1.1)**	**–9.7 (–0.2)**	**–10.7 (–0.1)**	**–0.08 (–2.79)**	**–0.05 (–2.85)**	–0.05 (–3.17)
	r^2 = 0.52** a	r^2 = 0.81** a	r^2 = 0.50**	r^2 = 0.32** a	r^2 = 0.41** a	r^2 = 0.24**
s (PLC MPa^{-1})	–325 (183)	–153 (126)	–220 (150)	–1.35 (85.50)	–0.27 (71.05)	–0.62 (78.12)
	r^2 = 0.25** a	r^2 = 0.21* b	r^2 = 0.16**	r^2 = 0.08 ns	r^2 = 0.01 ns	r^2 = 0.03 ns
$C_{0.5-2}$ (RWC MPa^{-1})	–2.7 (7.8)	–18.2 (13.0)	–13.3 (11.4)	–0.37 (29.31)	–0.27 (18.96)	–0.04 (23.25)
	r^2 = 0.01 ns	r^2 = 0.14*	r^2 = 0.02 ns	r^2 = 0.17*	r^2 = 0.06 ns	r^2 = 0.01 ns
$C_{\Psi 12}$ (RWC MPa^{-1})	–57.4 (34.3)	–15.0 (21.3)	–34.2 (26.8)	–0.46 (20.69)	–0.02 (14.34)	–0.11 (15.80)
	r^2 = 0.21*	r^2 = 0.04 ns	r^2 = 0.09*	r^2 = 0.29**	r^2 = 0.01, ns	r^2 = 0.02 ns
Cmax (RWC MPa^{-1})	–40.7 (38.2)	–21.2 (16.7)	–7.3 (26.8)	–0.37 (29.30)	0.44 (14.44)	0.04 (23.25)
	r^2 = 0.11 ns	r^2 = 0.02 ns	r^2 = 0.01 ns	r^2 = 0.18*	r^2 = 0.06 ns	r^2 = 0.01 ns

Figure IV.6. Height growth rate (GR_H) vs. (a) the Mean air entry tension (Ψ_{12}) and (b) the specific conductivity (k_s). The regression line in (b) was fitted through the young and old-growth trees only. Error bars are standard errors.

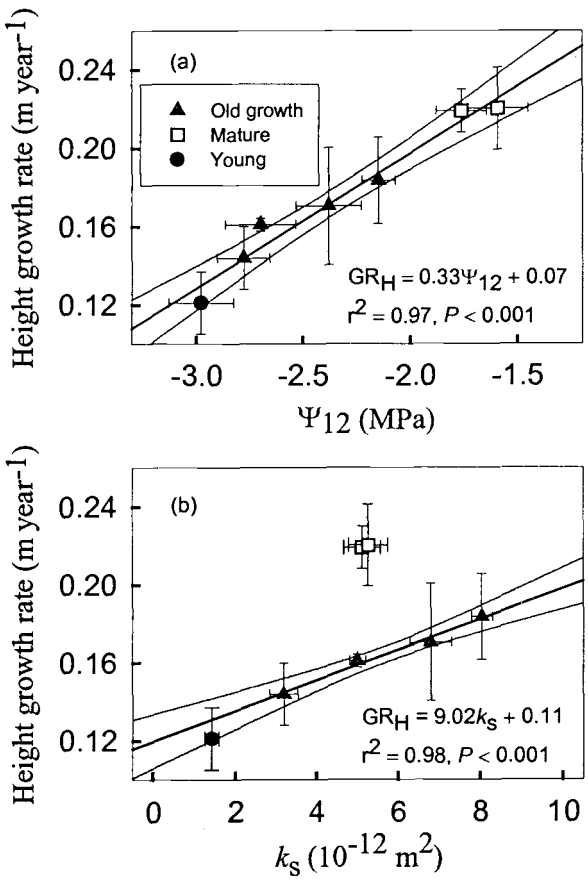
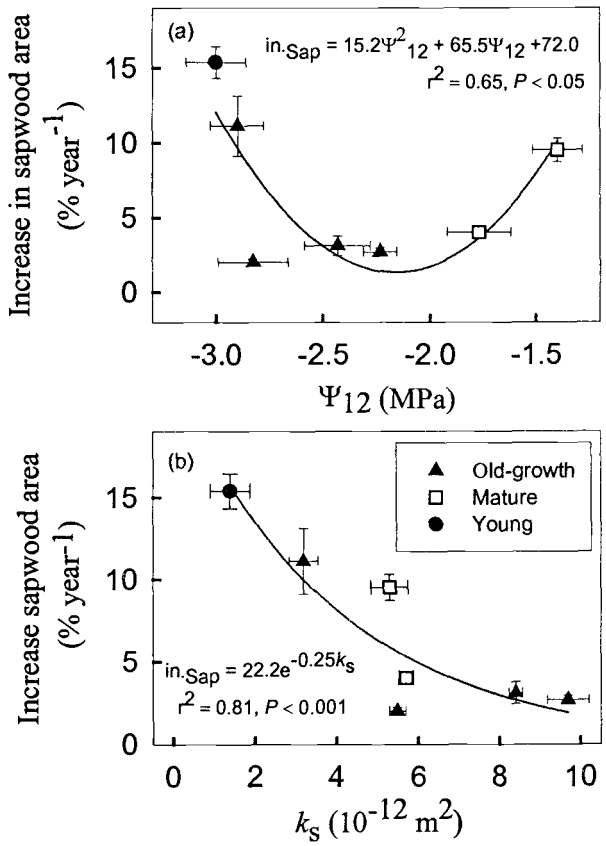


Figure IV.7. Yearly increase in percent sapwood area (in.$_{Sap}$) vs. (a) the mean air entry tension (Ψ_{12}) and (b) the specific conductivity (k_s). Error bars are standard errors.



IV.5 DISCUSSION

IV.5.1 Tradeoffs between hydraulic and wood properties

The tradeoffs between hydraulic and mechanical properties of wood indicate that in both MW and JW, high wood density was associated with low k_s (Table IV.5). This result implies that MW and JW cannot be both hydraulically efficient and mechanically resistant at the same time. This result may also explain why we found a decrease in wood density up to the age of 50 years old (that could be considered as the boundary between JW and MW) and also why we observed that the wood density appeared to decline with cambial age (Fig. IV.4). At the cellular level, if there is a tradeoff between wood density and wood hydraulic efficiency, it might be found in maintenance of high k_s. Developmental changes that increase tracheid length and proportion of earlywood will increase sapwood conductivity, and in the same time decrease wood density. Tracheid length and diameter increase rapidly with cambial age in conifers (Panshin & DeZeeuw, 1980) and the proportion of earlywood decreases (Megraw, 1986). We found two distinct slopes of k_s between MW and JW, as if these two types of wood behaved independently from one another with regard to wood density. The steeper slope found within MW suggests that k_s in MW is more sensitive than JW to any change in wood density. Within MW, wood density was also strongly correlated with low Ψ_{12} but not within JW. It appears that MW could adjust its resistance to embolism just by increasing its wood density but at a cost of reducing k_s. On the other hand, an increase in hydraulic wood efficiency in JW due to decreasing wood density would have no effect on its hydraulic safety. We propose that distinct differences between JW and MW evolved in conifers for hydraulic reasons, as shown within mature Douglas-fir (Domec & Gartner 2002). Any change in wood density from pith to bark reflects more the need of a change in hydraulic efficiency rather that the need in higher mechanical resistance as trees grow.

IV.5.2 Hydraulic trends within trees

Ponderosa pine trunks exhibited greater vulnerability to embolism than those of Douglas-fir (Domec & Gartner 2001). Contrary to one of our initial hypotheses, vulnerability to embolism at the top of the old growth trees (JW), for any of the hydraulic parameters, was not lower than at the bottom (MW; Fig. IV.1, Table IV.3). In the main trunk of ponderosa pine, we found that the base and the top (node 15) of the old growth trees were less vulnerable to embolism than were the intermediate parts of the trunk (node 65 and node 50). This result was unexpected given the sensitivity of sapwood embolism with height in old Douglas-fir trees (Domec & Gartner 2001). Within the mature trees the pattern was reversed with higher vulnerability to embolism at the treetop than at the base. For Ψ_{12}, our results also indicated that inner sapwood was only more vulnerable to embolism than outer sapwood in the mature trees, but not within the old growth trees, which supported what we found in Douglas-fir (Domec & Gartner 2001). After more than 110 years, inner (old) sapwood is still as efficient and safe as outer (young) sapwood. Subject to lower (less negative) water potentials, the base of the old growth would be at lower risk of embolism than the other parts of the trunk, with the node 65 (lower third of the live crown) being the least safe of all.

There appears to be a tradeoff between k_s and resistance to embolism. The vulnerability parameters by height position were negatively correlated with k_s within the old growth trees (still true by including the young trees but not the mature trees for Ψ_{12}, Fig. IV.2). Increasing the vulnerability to embolism by a factor of two was at the cost of decreasing the specific conductivity by a factor of eight (Fig. IV.2). The strong relationships between k_s and the vulnerability parameters by height position found within the old growth trees was consistent with Douglas-fir pattern (Domec & Gartner 2001). There was a steeper slope s in ponderosa pine than in Douglas-fir, which indicates a more conservative evolved strategy of the xylem because of a smaller margin of safety between Ψ_{12} and Ψ_{88} (Sperry 1995), and because of a twofold difference in C_{max}. At the branch level, Linton, Sperry &

Williams (1998), and Piñol & Sala (2000) reported that among conifer species (including ponderosa pine), the xylem with the highest hydraulic conductivity tended to be the most vulnerable.

We suggest that for an individual, Ψ_{12} is determined by factors related to size of bordered pits in the earlywood tracheids. Typically within a conifer, earlywood tracheid size decreases from the bottom to the top of the tree (Panshin & De Zeeuw 1980), which would lead to smaller bordered pits, harder to embolize because of smaller pores and lower flexibility of the membrane (Petty 1972, Sperry & Tyree 1990; Domec & Gartner, unpublished data). We also suggest Ψ_{88} is determined directly by the proportion of latewood and not by the wood density as suggested by Hacke *et al.* (2000). Latewood proportion in conifers is highly correlated with wood density (Equation 7; De Kort 1993). The higher the latewood proportion, the harder it is to fully embolize the sample, and the lower the k_s because of a lower proportion of wide tracheids.

For the young and old growth trees, the low storage capacity found for the functioning range of water potentials (between 0.5 and 2.0 MPa) suggests that their water uptake would be in phase in time with the water lost by the leaves. The advantage of maintaining this steady state flow is underscored by the fact that few embolism events occur at water potential less negative than –2.5 MPa (Fig. IV.1). For the old-growth trees, contrary to what has been found within the trunk of mature Douglas-fir (Domec & Gartner 2001), water storage capacities for the natural range of Ψ were not significantly lower for the tip of tree than for any other locations. This result might be a consequence of higher sapwood volume in ponderosa pine, which compensates for lower values of capacitance at the base of the trees. The high water storage capacities associated with the air entry points ($C_{\Psi 12}$) may benefit the old growth trees during soil drought by isolating the branches and meristems from the roots. We hypothesize that the wide sapwood structure of ponderosa pine trees versus the small one in Douglas-fir is an adaptation to drier environment to help the tree to better resist to more negative

water potentials without changing its ability to transport water. To examine the effect on whole trunk water relations, future work should include measurement of water potential gradients and sap flows along the trunk and shoots.

IV.5.3 Trends between trees

Contrary to our expectations, no general trend can be applied regarding tree age vs. vulnerability to embolism. Vulnerability to embolism in the old growth trees was not higher than in the young trees (Fig. IV.1). In contrast, mature trees were less resistant to embolism than the older and younger age classes. Mature trees had a 12 PLC at −1.6 and −1.9 MPa for nodes 15 and 50 respectively, which are water potentials likely to occur in such dry sites (Hubbard, Bond & Ryan 1999; Ryan *et al.* 2000; authors' field observations). In the mature trees, high vulnerability to trunk embolism was not compensated by high water storage capacity compared to young and old growth trees Table IV.3). At node 15, mature trees had higher conductivity than young and old-growth trees, which suggests that the degree of embolism experienced by these trees would affect the supply of water to the leaves.

Embolized tracheids would be replaced faster in small diameter section of the trunk or within younger trees whereas at the base of old trees, new rings would have a minor effect. This faster replacement in young trees was at the cost of lower k_s (Fig. IV.7b), suggesting that the more efficient for water transport that the sapwood becomes, the less dependent the old sapwood is on the newly sapwood. The specific conductivity of the sapwood depends in part on the fraction of tracheids that are not embolized and thus are functional for conduction. Many studies have shown a clear relationship between the occurrence of embolisms in conducting cells and a reduction in specific conductivity of the xylem (Tyree *et al.* 1991; Zwieniecki & Holbrook 1998). The effects of embolism and possible refilling of tracheids will be highly significant for the conductivity of the sapwood. Although still poorly understood (Tyree *et al.*, 1999), the refilling process is

important to compensate for factors such as a low increase in sapwood area from one year to another in old trees.

Until recently (Domec & Gartner 2001), all vulnerability curves made on tree trunks in general and on ponderosa pine in particular were on small seedlings or branches from the upper parts of the trees (Maherali & De Lucia 2000; Piñol & Sala 2000). In ponderosa pine branches, 50PLC occurred at mean water potential of –2.6 MPa (Maherali & De Lucia 2000), which approximates the value reported in the trunk for mature trees but is higher than the trunk values of old-growth trees (Table IV.3).

IV.5.4 Correlations between hydraulic parameters and growth in height

The hydraulic differences between the three age classes were correlated with the growth rate in height. The best correlation we found was with Ψ_{12} for all three age classes (Fig. IV.6), which suggests that in ponderosa pine trees, the primary meristem has a control over the hydraulic properties of the wood developed from the secondary meristem. A higher height growth rate means higher carbon allocation and water need for the terminal shoot. For old-growth trees (and still true by including the young trees), to meet such higher water need, the cambium developed wood with higher k_s but at the cost of lower resistance to embolism for Ψ_{12} (Fig. IV.6). For a given cambial age, we know of no other data to compare with these cambium functionalities. However, the lack of correlation between the same hydraulic parameter and the growth in diameter suggests that there is no direct control of the secondary cambium over the ability of wood to resist to embolism. A previous study showed that when trees start making MW when they culminate their height growth (Kucera 1994).

We hypothesize that the factors determining bud burst and primary growth have more impact on the hydraulic parameters than on the secondary growth rate. The earlywood indicates the conditions of both the spring and the previous year, whereas the width of the annual ring is more a function of the dry matter

production and depends on the supply of water and nutrients of the current year (Fritts 1976; Krause & Morin 1995*a*; 1995*b*). The time of the year when height growth units are initiated and when they elongate is important. Future studies could examine the hydraulic parameters at the beginning of the growing season (mid-May) such as the seasonality of RWC, and the pattern in water potential drops to see if there is a cambium control of these parameters through stomatal regulation (Nardini & Salleo 2000).

Seasonal changes in allocation may decrease wood and height growth through increased respiration of woody biomass (Ryan, Binkley & Fownes 1997) and/or increased root costs because of decreased nutrition (Grulke & Retzlaff 2001). It is possible that the release of water through embolism in mature trees would decrease wood respiration. A concurrent study on the same trees as those used here reported that sapwood at the treetop released 50% more CO_2 than at the bases, and that sapwood of the mature trees had lower rates of respiration than the old-growth and young trees under control conditions (Pruyn, Gartner & Harmon 2002). More detailed measurements of trunk respiration in response to water potential and embolism is necessary to link definitely an increase in height growth rate to a decrease in respiration due to an increase in water release by embolism.

Height growth of ponderosa pine ceases by age 200 (O'Hara 1996; Ishii *et al.* 2000). Height growth at our study site (Fig. IV.5b) did not fit the growth curves found in the literature (Barrett 1978). A cohort in a multi-aged stand typically shows higher growth rates when it is the oldest cohort in the dominant canopy position (Milnore 1979; O'Hara 1996). Older trees in mixed stands grow rapidly because they receive plentiful resources and are competing with fewer adjacent trees in older cohorts (Oliver & Larson 1991). McTague & Stanfield (1991) reported constant diameter increment over all diameter size classes in uneven-aged ponderosa pine in western Montana and that at a age greater than 100 years, the predicted dominant height based on site index and the actual height measured diverged because of the lack of site-quality and elevation variables in the height

equations. Daubenmire (1961) and Stansfield & McTague (1991) showed that the shape of the dominant-height curve and site index equations differed between habitat type and moreover as in our study, they showed more rapid growth rates between the ages of 25 and 70 years, contrasting with the classical site index curves developed for the same species but mainly dealing with managed, even-aged stands expected to be harvested when younger than 120 years (Meyer 1961; Barrett 1978; Oliver & Powers 1978; Hann & Scrivani, 1987).

Water supply is determined by the water potential gradient from soil to leaf, and the resistance and capacitance of the hydraulic pathway. In this study, conductivities and water storage capacities have been shown to be higher in the old growth trees than in the mature and small trees. Recently, Ryan & Yoder (1997) proposed that transpiration and net CO_2 uptake, and therefore growth, are limited by increasing axial hydraulic resistance as trees become older and taller. They proposed that there would be a negative feedback between tree height and the hydraulic conductance. To maintain flow rates over longer distances, West, Brown & Enquist (1999) hypothesized that larger trees compensate by widening tracheids or vessels (which increases specific conductivity). In this study, we indeed found an increase in k_s with cambial age at any given height within the old growth trees (Table IV.3), but also a positive correlation between growth rate and k_s (Fig. IV.6b). Therefore at the cell level, hydraulic limitation to tree height was not confirmed by this study. If trees had to compensate hydraulically for their height with a more efficient xylem, then the growth rate would have been lower. On the other hand the strong negative relationship between xylem safety and growth rate in height support the hydraulic limitation hypothesis (Fig. IV.6a). Trees were able to compensate for their lower growth rate by the production of a safer xylem. These findings should be confirmed by studying the tradeoffs between hydraulic parameters and growth efficiency expressed as trunk volume increment per unit leaf area (Waring 1983). Vander-Willigen and Pammenter (1998) concluded that based on growth efficiency, hydraulic conductivity was more sensitive to

environmental conditions than genotype whereas the opposite was true regarding vulnerability to embolism.

Although no data on gas exchange rates are available to support this idea, in previous studies of conifer species, Zhang *et al.* (1996, 1997) reported that some populations of Douglas-fir, ponderosa pine, and western larch used water and accumulated biomass quickly when water was available, but closed their stomata when water stress was imposed. Consistent with these observations, we found that the relative height growth rate of the ponderosa pine was highest for the trees most vulnerable to embolism, but was intermediate for trees that were less vulnerable. The plastic response of the mature trees would be advantageous in dealing with environmental stresses because it would confer a competitive advantage by optimizing carbon gain under favorable conditions and minimizing water loss when water is limiting (Scheiner 1993; Irvine *et al.* 2002). However, this compensation did come at the cost of increased vulnerability to embolism as suggested by Tyree & Ewers (1991). Partial trunk embolism would reduce transpiration rates and stomatal conductance through a reduction in hydraulic conductance (Meinzer & Grantz 1990; Hubbard *et al.* 2001). Stomata close to maintain leaf water potential above a critical level that would cause irreversible embolism (Cochard, Bréda & Granier 1996; Salleo *et al.* 2000). Maintaining a high rate of growth in height was at the cost of having partial trunk embolism, but was compensated by higher $C_{0.5-2}$ (Fig. IV.3a) that could buffer an increased in hydraulic resistance (Stratton, Goldstein & Meinzer 2000; Phillips *et al.* 2002).

IV.6 ACKNOWLEDGMENTS

This project was supported by USDA CSREES 96-35103-3832 grant to Oregon State University for wood utilization research. The authors acknowledge the assistance with tree felling provided by Roy Anderson, Michele Pruyn, Jennifer

Swenson and Andre Meliott. We thank Crown Pacific Limited partnership, Gilchrist Forestry Division, OR for providing the trees, Dr. Randy Johnson for field assistance, and Dr. B.J Bond, Dr. M. Unsworth, Dr. G. Howe and R. Leichti for corrections on the manuscript.

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Chapter V

How Do Water Transport and Water Storage Differ in Coniferous Earlywood and Latewood?

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Manuscript submitted to Journal of Experimental Botany.

V.1 ABSTRACT

The goal of this research project was to determine the water transport behavior of earlywood vs. latewood in the trunk of 26-year-old Douglas-fir (*Pseudostuga mensiesii* (Mirb.) Franco) trees. Specific conductivity (k_s) and vulnerability of xylem to embolism (air-injection method) were measured on a single growth ring and in a subset of earlywood and latewood samples within the same ring excised from breast-height disks of five fast growing trees. Earlywood/latewood ratio, field water potential (Ψ) and relative water content (RWC) were then used to predict differences in conductivities and vulnerability to embolism. In hydrated excised segments, earlywood has about 10 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 of the whole wood, with 50% loss of conductivity at –2.2 MPa. Latewood was more vulnerable to embolism than was earlywood at high Ψ but as Ψ decreased, the latewood showed very little further embolism with 50% loss of conductivity at < –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 15% and 42% loss of conductivity, respectively and that latewood resistance to water flow accounted for more than 70% of whole-ring resistance. Higher vulnerability to embolism in latewood than earlywood at field Ψ was associated with higher water storage capacity (21.8 %RWC MPa^{-1} vs. 4.1 %RWC MPa^{-1}, latewood and earlywood, respectively). The shape of the vulnerability curves suggested that air seeding through latewood may occur directly through pores of the strands and seal off at lower pressure than earlywood pores.

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

V.2 INTRODUCTION

The two distinct zones of growth within a tree ring are earlywood and latewood. The early season growth in a tree, which produces earlywood (periclinal growth), accounts for 60-80% of a ring's width growth for a year. As the growth rate slows and stops during fall the cells laid down are smaller, denser and mechanically stronger (and therefore appear darker).

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

Although the significance of the outermost ring to the hydraulic conductivity of the whole stem has been quantified in a ring porous tree (*Ulmus Americana*; Ellmore and Ewers, 1986), 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 vulnerability to embolism within a single ring and within its components. It is logical to infer that earlywood and latewood would have very different hydraulic properties. Differences in hydraulic conductivity and vulnerability to embolism between earlywood and latewood is 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 diameter than latewood tracheid (Panshin and deZeuuw, 1980; Ewers *et al.,* 1997). The tradeoff, however, is that conduits with high conductivity may be more vulnerable to embolism (Schulte and Gibson, 1987; 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 the plant-water status is favorable, but may limit plant water use during drought. In hardwoods, the small-diameter latewood vessels and the small-diameter 'vasicentric tracheids' that are 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 became air-filled, or does it not?

Embolism due to drought is thought to be caused by air seeding at inter conduits pit membranes (Zimmermann, 1983; Crombie *et al.,* 1985). Sperry and Tyree (1990) suggested that in conifers air seeding occurs through inter-tracheid pit membrane when the torus becomes displaced form its normal sealing position. They found that non-sealing of bordered pits of latewood in conifers may account for 20% of the total hydraulic conductivity after earlywood had sealed off at low water potential (Ψ). The shape of the vulnerability curves vary among and within species and it is thought that they reflect the water stress environment under which the plants grew (Tyree and Sperry, 1998; Tyree *et al.* 1994; Matzner *et al.*, 2001). Much less is known concerning the responses to embolism between earlywood and latewood, and how much embolism occurs in these two zones of a growth ring at field Ψ. The proportion and the xylem anatomy of earlywood versus latewood within a ring may be an adaptive hydraulic trait and not simply a consequence of water balance in the field. Earlywood and latewood may regulate water transport under stress based on their influence on hydraulic conductivity, cavitation

vulnerability, and internal storage capacity. Because of their bordered pit structure, earlywood tracheids are expected to be both more efficient and safer from embolism than latewood. If, as expected, cavitation resistance is higher within earlywood, then this would indicate that 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 (*Pseudostuga mensiesii* (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 our laboratory results and to describe earlywood and latewood water transport and storage when water is under tension.

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

V.3 METHODS

V.3.1 Plant material and sample preparation

The study was carried out in an even-aged (21-year-old) Douglas-fir stand (elevation 277 m, 44°43N, 123°20W) 15 km northwest of Corvallis, Oregon, growing on an inceptisol soil. We chose to study Douglas-fir because of its potential fast growth giving wide rings with distinct of latewood. The mean annual temperature and annual rainfall (1961–1996) are 12.4 °C and 1800 mm, respectively (Table V.1; www.orst.edu/Dept/IPPC/wea/). In mid June 2001 (before

Table V.1: Tree and sample 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
Percent earlywood	66.6 ± 2.3	59.7 ± 1.9	74.5 ± 1.9

the start of the summer drought) five trees were selected randomly and felled. A 20-cm thick disk was cut at breast height from each tree, and was immediately transported in a wet plastic bag to the laboratory where blocks were prepared. From each cross-section

disk, six blocks, taken at around 60° intervals around the circumference, were cut within the same single ring following the procedures outlined in Domec and Gartner (2001). Briefly, the samples were chiseled out of the wood with the long axis parallel to the grain then submerged in water and put under vacuum for 48 hours 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 through F. All hydraulic measurements on samples A were done on the entire sample, meaning both the earlywood and the latewood were left intact. Before the final measurement on each sample, samples B through F were sawn in half to 75 mm in the axial direction, and one half was designated B1 through F1, whereas the other half was designated B2 through F2. We removed the earlywood from samples B1 through F1 leaving just latewood, and we removed the latewood from samples B2 through F2 leaving just earlywood (see below and Fig. V.1).

V.3.2 Specific and hydraulic conductivities

Specific conductivity (k_s), is a measure of the hydraulic efficiency of the xylem in relation to the cross sectional area of wood and was calculated according to Darcy's law (Edwards and Jarvis, 1982):

$$k_s = \frac{V.L.\eta}{t.A.\Delta P} \qquad \text{in } m^2 \qquad (1)$$

where V is the volume of water that went through the sample (m^3), L is the sample length (m), η is the viscosity of water at the temperature at which the experiments

were conducted (N s m^{-2}), t is the time (s), A the cross section area (m^2) of the sample and ΔP is the pressure gradient (Pa).

Initial specific conductivity ($k_{s(i)}$) was measured on each 130–150 mm segment (intact segments A through 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, 1998*a*). Samples were soaked in water, then $k_{s(i)}$ was measured using filtered (0.22μm) water adjusted with HCl to pH 2 to prevent microbial growth, and a hydraulic head of 0.0028 MPa. Efflux was collected in a 1-ml-graduated micropipette (0.01 ml graduation). We recorded the time required for the meniscus to cross six consecutive graduation marks, and only used the values that were steady.

Hydraulic conductivity, k_h, which expresses the volume flow-pressure relationship but not on an area basis, is defined as

$$k_h = \frac{V.L.\eta}{t.\Delta P} \qquad \text{or} \qquad (k_h = A \times k_s) \qquad \text{in } m^4. \qquad (2)$$

All terms are defined as in equation 1.

V.3.3 Vulnerability curves

Vulnerability curves (VCs) of the wood samples were constructed using 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 principle of the method was to measure the percent 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 airtight 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 minute. After each air-injection k_s was re-measured and percent loss of conductivity (PLC) was calculated from:

$$PLC = \left(1 - \frac{k_{s(\Psi)}}{k_{s(i)}}\right) 100 \qquad (3)$$

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 because both ends of each sample were re-cut between measurements to have a new surface. VCs were determined by plotting PLC vs. Ψ, where Ψ is predicted as the negative of the applied air pressure (Pockman and Sperry, 2000).

After measuring the initial specific conductivity on intact samples A through F, we constructed vulnerability curves in two manners. The first one was to use sample A to construct an entire vulnerability curve, subjecting it to air pressures ranging from 0.5 to 5.0 MPa. The second one was to use different samples (B through F) for different air pressures to construct one curve, as follows (Fig. V.2). After we determined k_s for samples B and C (used as replicates for initial k_s), we sawed them in half, prepared samples B1 and C1 (only latewood) and B2 and C2 (only earlywood), and measured k_s again. After we determined k_s for sample D, we pressurized it to 0.5 MPa, re-measured its k_s, then sawed it in half, prepared samples D1 and D2, and measured their k_s.

Figure V.1: Sample preparation: six samples within ring 3–7 were removed from the tree disk 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 (B_1, B_2...F_1, F_2). For clarity only sample B is shown.

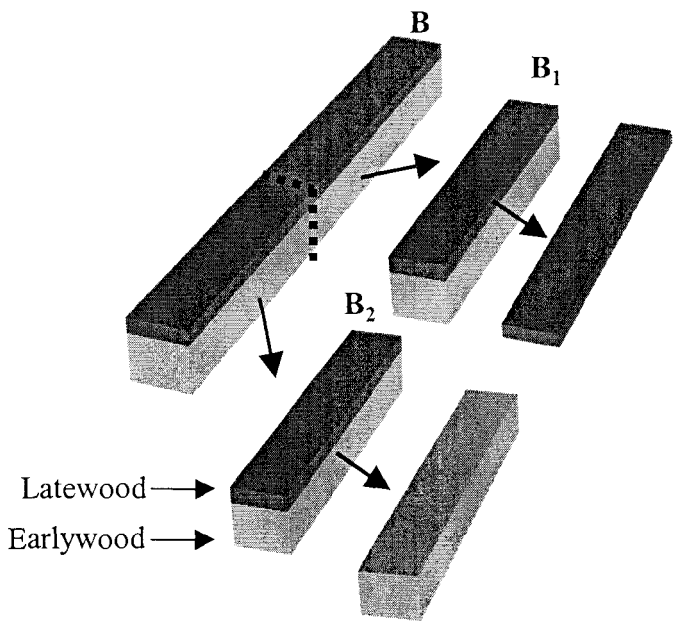
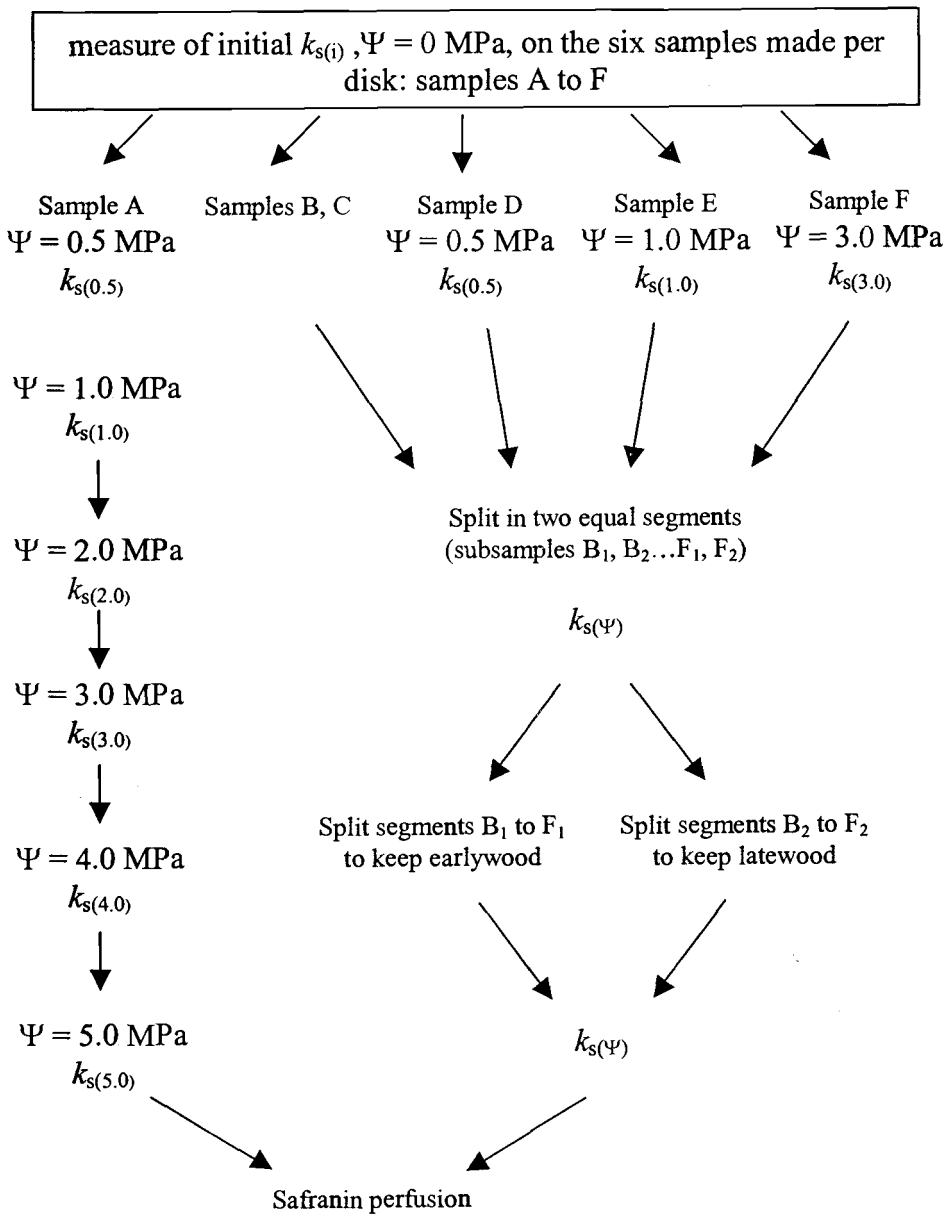


Figure V.2: Summary of procedures used to assay the specific conductivity (k_s) and the vulnerability curves within on single ring or whole sample (A) and earlywood and latewood samples (B–F).



Likewise, after we determined k_s for samples E and F, we pressurized them to 1.0 or 3.0 MPa (E and F, respectively), re-measured their k_s, then sawed them in half, prepared samples E1, F1, E2, and F2, and measured their k_s. For earlywood and latewood samples, PLC was determined by using the paired segments methods which compared $k_{s(\Psi)}$ of samples D1, D2, E1, E2, F1 and F2 to the average $k_{s(i)}$ of samples B1, B2, C1and C2 from the same disk (Fig. V.2). To test for difference between the paired segment method and the regular method (consisting of measuring PLC within the same samples at different Ψ), comparison was made at each Ψ between samples A and intact samples B–F.

V.3.4 Embolized area estimated by the staining method

Following each final conductivity measurement, the all samples were perfused with filtered (0.22μm) safranin-O (0.2% aqueous solution) under 0.015 MPa pressure head for 20 minutes while still enclosed in the pressure sleeve apparatus. For the initial measurements, the samples always stained completely, giving no evidence of embolism. Percentage of unstained wood area of each sample used for the VCs was analyzed with an image analysis system consisting of a compound microscope, video camera, computer and the software NIH Image (v. 1.60, Rasband, 1996).

V.3.5 Earlywood and latewood proportion

Total width and 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 using 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 0.01mm precision. Average earlywood proportion for each sample was then calculated.

V.3.6 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 ovendry wood (M_d):

$$MC(\%) = \left(\frac{M_f}{M_d} - 1\right) 100 \quad \text{(dimensionless)} \quad (4)$$

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 (cm^3) and M_f (g). Following final pressurization, M_d (g) was also recorded after drying at 104°C. Using length, the volume of cell wall material (V_s, cm^3) and M_d (g) were back-calculated at each given pressure, we then calculated RWC:

$$RWC = \frac{M_f - M_d}{(V_f - V_s) D_{H2O}} \quad \text{(dimensionless)} \quad (5)$$

where D_{H2O} is the density of water (g cm^{-3}). We calculated V_s from M_d assuming that dry cell-wall material has a density of 1.53 g cm^{-3} (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 allows us to compare differences in storage capacities that are not only related to a difference 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):

$$C_{RWC} = \frac{dRWC}{d\Psi} \qquad \text{in RWC MPa}^{-1} \qquad (6)$$

One cannot accurately estimate capillary water changes 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 were correct, then maximum capillary water storage would be released at a pressure potential close to zero, and would stop 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 to 0.5 MPa ($C_{0-0.5}$), a phase from 0.5 to 1.0 MPa ($C_{0.5-1}$) and a phase from 1.0 to 3.0 MPa (C_{1-3}).

V.3.7 Wood density and volume occupied by cell wall material, by water and by gas

Wood density values were determined for each sample tested hydraulically:

$$\text{Density} = M_d/V_f . \qquad \text{in} \quad (\text{g cm}^{-3}) \qquad (7)$$

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

$$V_{h2o}\ (\%) = \frac{(M_f - M_d)}{V_f} 100 \quad (8)$$

$$V_{cell\ wall}\ (\%) = \frac{M_f}{1.53 V_f} 100 \quad (9)$$

$$V_{gas}\ (\%) = (1 - V_{cellwall} + V_{h2o}) 100 \quad (10)$$

V.3.8 Field measurements

To examine the RWC in earlywood and latewood, 12 dominant trees were cored with a 12–mm increment borer on September 30, 2001, before the rain started. Cores were wrapped in plastic wrap immediately after removal and placed in a cooler. Cores were returned to the lab the same day and processed. The last growth ring was removed and the next two growth rings were divided into earlywood and latewood. We measured V_f, M_f and M_d and calculated RWC as described previously. We estimated trunk Ψ at breast height on leaves bagged in aluminum foil to prevent transpiration. We used a pressure chamber (PMS Instrument, Corvallis, OR) to measure three foliage-bearing branches per tree on the same trees used for RWC.

From samples tested in laboratory, we determined the relationship between the negative of the applied pressure and RWC and PLC. Then based on the measured Ψ of standing trees, we estimated RWC and compared to RWC in the field. We also estimated PLC in the field from Ψ and from RWC measured in the field.

V.3.9 Statistical analysis

Relationships between the hydraulic parameters and the applied pressure as well as the linear and non-linear relationships between hydraulic parameters were fit using the least-squares methods. Differences in hydraulic parameters between the entire samples and the subset of samples with tree as a blocking factor were determined using analyses of variance (ANOVA). Paired *t*-tests were specifically used to test

the difference in hydraulic parameters between earlywood and latewood. All statistical procedures were conducted with Statistical Analysis Systems software (1997; SAS Inc., Cary, NC).

V.4 RESULTS

V.4.1 Sample shape, staining tests

The average latewood made up 33% of the ring (± 2%, ranged from 26% to 40%) (Table V.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. V.3a). The slope of the regression line was not significantly different than one (P=0.26). Neither the hydraulic parameters, nor the estimated capacitances differed between the whole samples (B to F) and sub-samples pieces (B_1, B_2 to F_1, F_2) $P>0.62$, paired t-test, data not shown). Whole long samples (A) and small sub-samples pieces (D to F) had similar PLC at 0.5, 1.0 and 3.0 MPa (Fig. V.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. V.4). The slope of the regression line was however significantly lower than one (P=0.04).

V.4.2 Hydraulic parameters within earlywood and latewood

Specific conductivity (k_s) was significantly higher in earlywood than latewood ($P<0.001$, Table V.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 V.2).

Vulnerability to embolism varied among wood type samples. Latewood samples were more vulnerable to embolism than earlywood samples at 0.5 MPa

Figure V.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 than one (P=0.25). (b) Comparison of the percent loss of conductivity (PLC) at the three applied pressures between the small and whole samples.

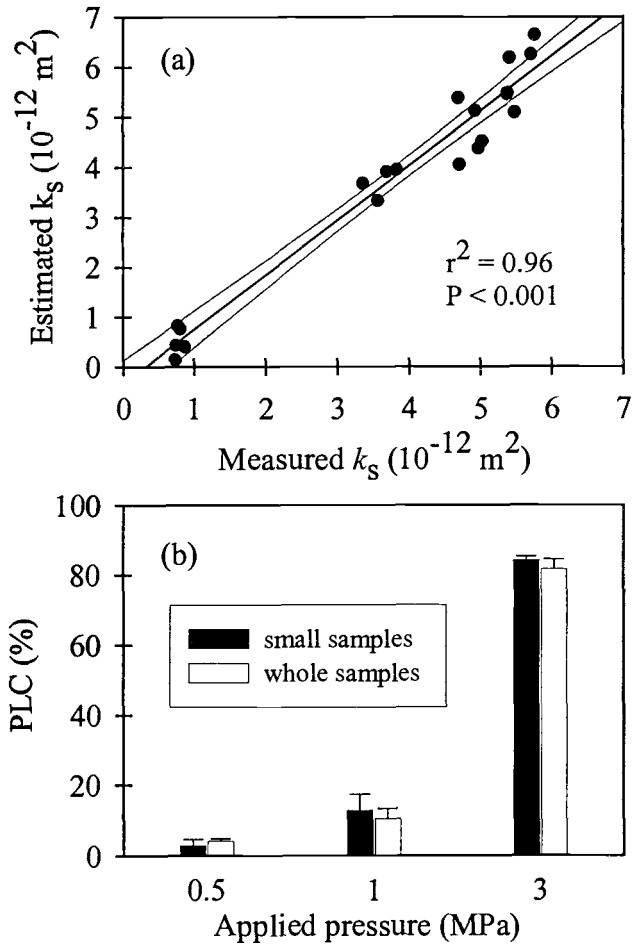
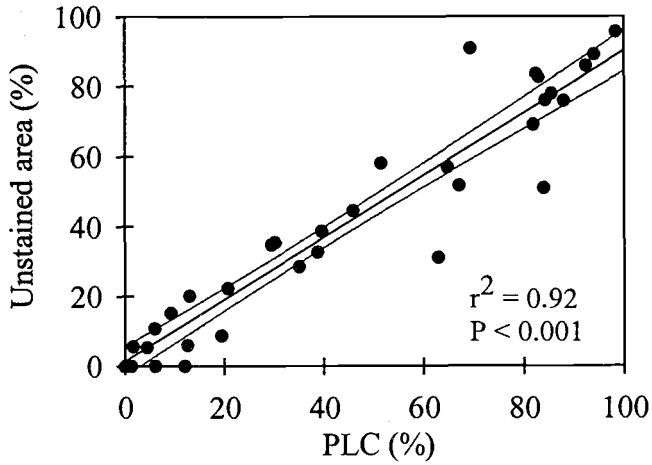


Figure V.4: Embolized tracheids measured by the percent loss of conductivity (PLC, equation 3) in the whole sample and in earlywood and latewood sub-samples versus the embolized area estimated by the staining method (% unstained area). The Regression line and the 95% confidence intervals are represented (n=80). The slope of the regression line was significantly different than one (P=0.04).



and 1.0MPa, but not a 3.0 MPa (Table V.2, Fig. V.5a). Earlywood samples were not significantly different than the whole wood sample ($P > 0.21$), and followed the same trend. The value Ψ_{50} (50 PLC) for the entire VC and earlywood were -2.3 ± 0.1 and 2.1 ± 0.2 MPa, respectively (Fig. V.5 a). At any applied pressure, whole wood samples and earlywood samples were significantly different than latewood samples ($P<0.04$).

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

Latewood had a much higher water storage capacity than earlywood between 0.5 and 1.0 MPa (22 vs. 4 %RWC MPa^{-1}, latewood and earlywood, respectively). This trend was reversed between 1.0 and 3.0 MPa (5 vs. 23 %RWC MPa^{-1}, latewood and earlywood, respectively; Table V.3). There was no significant difference between earlywood and latewood for $C_{0-0.5}$ (Table V.3). There was no significant difference between whole sample and latewood for $C_{0.5-1}$, but there was a significant difference between the whole sample and earlywood or latewood for $C_{0-0.5}$ and C_{1-3} ($P<0.05$). Within the earlywood samples, there was a significant difference in water storage capacity between $C_{0-0.5}$, $C_{0.5-1}$ and C_{1-3} ($P<0.006$). 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 ($P=0.7$)

Table V.2. Specific conductivity (k_s), hydraulic conductivity (k_h) and percent loss of conductivity at three negative of applied pressures in whole-wood, earlywood and latewood samples. Mean ± 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 ± 1.7 a	12.8 ± 4.5 a	84.1 ± 1.1 a
Earlywood	$7.3 \pm 0.5 \times 10^{-12}$ b	$3.4 \pm 0.1 \times 10^{-16}$ a	2.1 ± 1.9 a	10.3 ± 6.4 a	90.2 ± 2.8 a
Latewood	$6.4 \pm 0.9 \times 10^{-13}$ c	$2.0 \pm 0.5 \times 10^{-17}$ a	26.5 ± 9.1 b	32.1 ± 8.3 b	56.8 ± 8.9 b

Figure V.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. The error bars are standard errors (n=5).

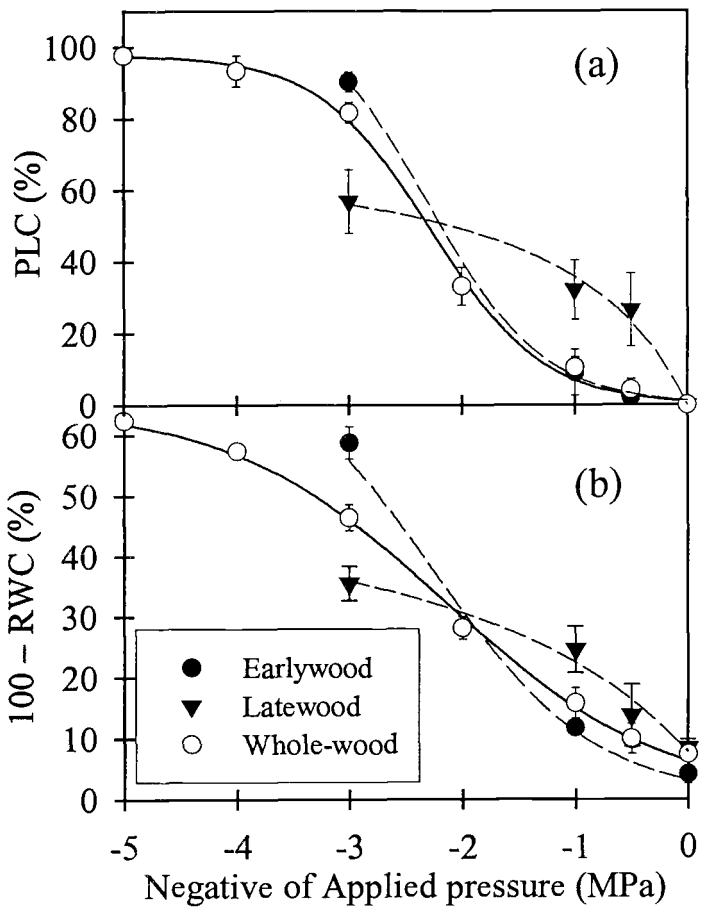


Table V.3: Effect of wood type on RWC-based capacitances (water storage capacity, % MPa^{-1} for the three phases $C_{0-0.5}$ (between 0 and 0.5 MPa), $C_{0.5-1}$ (between 0.5 and 1.0 MPa), and C_{1-3} (between 1.0 and 3.0 MPa). Means (± SE) are shown (n=5). Values within a column sharing the same letter are not significantly different at P=0.05.

	$C_{0-0.5}$	$C_{0.5-1}$	C_{1-3}
Whole wood	5.1 ± 1.2 a	11.3 ± 0.1 a	15.3 ± 0.2 a
Earlywood	11.3 ± 4.3 a	4.1 ± 2.5 b	23.5 ± 1.1 a
Latewood	10.5 ± 8.3 a	21.8 ± 7.1 a	5.5 ± 1.4 b

V.4.3 Latewood and earlywood composition

Percentages of gas 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 V.4). The latewood had higher percentages of wood and a lower percentage of water. At 3.0 MPA, latewood had lower percentage of air but had the same percentage of water. Latewood had more than twice the density of earlywood (0.26 g cm^{-3} vs. 0.60 g cm^{-3}).

V.4.4 Comparisons between field measurements and laboratory estimates

Minimum trunk Ψ measured at the end of the summer never dropped below -1.5 ± 0.2 MPa, for calculated minimum RWC of 72% ± 3 % for the whole ring. There was no significant difference between RWC in earlywood and in latewood, but the estimated RWC of earlywood from measured Ψ was significantly higher than of latewood (Table V.5). There was close agreement between the estimated PLCs from the measured Ψ and RWC for latewood but not for earlywood.

V.5 DISCUSSION

V.5.1 Earlywood/latewood segmentation to conductivity and vulnerability to cavitation

As expected, latewood had much lower specific conductivity (k_s) than earlywood. The very low k_s found in latewood can be explained by the cell's small tracheid diameter compared to earlywood. Hangen-Poiseille's law predicts that the large earlywood tracheids are responsible for most of the water flow within a single ring (Zimmerman, 1983). We found about 11-fold higher k_s in earlywood than latewood, which would correspond to a 1.8-fold increase in tracheid diameter

Table V.4: Wood density (dry mass/green volume), moisture content (MC), volume occupied by cell wall material ($V_{cellwall}$), volume occupied by water (V_{H2O}), volume occupied by gas (V_{gas}), and relative water content (RWC) at full saturation (after 48 hours under vacuum) in whole-wood, earlywood and latewood samples. Means (± 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_{H2O} (%)	V_{gas} (%)	RWC (%)
Whole-wood	0.39 ± 0.02 a	182 ± 12 a	25.3 ± 1.2 a	69.3 ± 2.1 a	5.4 ± 1.4 a	93 ± 2 a
Earlywood	0.26 ± 0.02 b	316 ± 18 b	16.7 ± 1.0 b	79.9 ± 1.0 b	3.4 ± 1.3 a	96 ± 2 a
Latewood	0.60 ± 0.01 c	92 ± 3 c	39.6 ± 0.7 c	55.4 ± 1.1 c	5.1 ± 1.0 a	92 ± 2 a

Table V.5: Estimated (est.) earlywood and latewood relative water content (RWC) and percent loss of conductivity (PLC) from measured field RWC and trunk water potential (Ψ_{trunk}) taken at midday. Field values of predawn, midday bagged, midday unbagged water potentials were 1.0 ± 0.1, -1.4 ± 0.1 and -1.7 ± 0.1 MPa, respectively ($n = 6$).

	Meas. RWC	Est. RWC from $\Psi_{trunk} = -1.4$MPa	Est.Ψ_{trunk} from meas. RWC	Est. PLC from meas. RWC	Est. PLC from meas. Ψ_{trunk}
Earlywood	75 ± 4	82 ± 1	-1.8 ± 0.2	27 ± 8	15 ± 2
Latewood	71 ± 2	73 ± 3	-1.8 ± 0.2	47 ± 3	42 ± 2

(Hangen-Poiseuille 's law), all other factors being equal. This result corresponds to ratio of tracheid diameters found in the literature for conifers (McMillan 1968; Cown 1975).

Results supported the hypothesis that earlywood is both more efficient to transport water and less vulnerable to embolism than latewood at water potential occurring in field under normal conditions (Tables V.2 and V.5). Thus, within a growth ring, there was a positive relationship between k_s and safety, and then, no tradeoff 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. Our study confirmed that wood from the trunk base of Douglas-fir trees may operate close to the edge of hydraulic safety due to high vulnerability to embolism of earlywood below –2.0 MPa (Domec and Gartner, 2002*a*).

Embolism formation is thought to be unrelated to conduit size but rather to the 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 (Bolton and Petty, 1978; Domec and Gartner, 2002*b*). The small and thick torus and strands of the bordered pits found in latewood may not allow the margo to act as a valve and to prevent air bubbles from spreading from one embolized tracheid to another. Gregory and Petty (1973) found that latewood membranes were more rigid than earlywood ones and that they could not seal-off completely at field water potentials in *Pinus sylvestris* (L.). Pores between the strands of the membrane in latewood are smaller than in earlywood (Petty and Puritch, 1970; Fengel, 1972) suggesting that air seeding occurs directly through these pores. 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. V.5b) may reflect the pore size distribution within the strands of the membrane in latewood. We

hypothesized that all the membranes were completely deflected at Ψ <–1.0 MPa and that the sealed torus created a closed system protecting the tracheids responsible for the remaining 40% of conductivity. Regarding the earlywood, Sperry and Tyree (1990) found that the porosity of the membrane that holds the torus is too large to prevent the air meniscus passage at water potentials lower than –0.1 MPa, but it is elastic enough to be completely deflected and to seal off the torus. They showed that the slippage of the torus from its sealed position created gaps big enough to developed cavitation in adjacent tracheids. This result may explain why there was a complete loss of conductivity for lower applied pressure in earlywood but not in the latewood (Fig. V.5a). The thicker torus of latewood would prevent it from slipping off from its sealed position (Domec and Gartner, 2002*b*).

By back-calculating the part of latewood in the remaining k_s at 3.0 MPa (Fig. V.5a), non-sealing of late-wood bordered pits in Douglas-fir appeared to account for 30% of the total hydraulic conductivity that remained. However, with its very low specific conductivity and proportion (33%) in a ring, a fully conductive latewood can only account for 5% of the initial conductivity at full saturation, but 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 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 needs to represent 90% of the whole ring area at full saturation, and 75% at 3.0 MPa. This high proportion of latewood within a growth ring is unlikely to be found in normal conifer wood, but can often occur in compression wood, which forms on the lower sides of branches or in leaning trunk (Westing, 1968; Timell, 1986)).

Compression wood of stems has wide annual rings and is much denser than normal wood due to an elevated proportion of latewood (Park, 1984; Yoshizawa *et*

al., 1987). Spicer and Gartner (1998*b*; 2002) found that compression wood in branches and seedlings of Douglas-fir had significantly lower k_s than normal wood. It can be hypothesized that compression wood in trunks would be more vulnerable to embolism than normal wood at high Ψ, but on the other hand may better resist to severe drought due to the higher latewood resistance to embolism at low Ψ. Old growth trees have also 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. This hypothesis could be a strategy for species like Douglas-fir growing in wet condition during the spring time and dry condition during summer time. It could also explain why vulnerability to embolism of mature Douglas-fir trees was higher at the base of the trunk than at the top of the trunk (under the crown), whereas its specific conductivity was lower (Domec and Gartner, 2001). The base of the coniferous trunk has higher latewood percentage than the top (Larson, 1962; Domec and Gartner, 2002*a*), which in the light of this paper explains the difference found.

V.5.2 Differences in water storage capacities between earlywood and latewood

The high water storage capacity observed at low 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 capacitances were not explained between 0 and 0.5 MPa, the other two estimated capacitances (Ψ= 0.5 to 1.0, and 1.0 to 3.0 MPa) were suitable.

This paper showed that within a growth ring, latewood had a higher water storage capacity than earlywood (Fig V.5b) 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 linearly related to the water loss by the leaves (Table V.3, Fig. V.5b). 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. V.5a). Therefore for earlywood, the trade-off associated with low vulnerability to embolism and high hydraulic conductivity is at a cost of low water storage capacity (Goldstein *et al.*, 1998; Stratton *et al.,* 2000). These characteristics may be important in old trees with higher latewood percent, and we could hypothesized that for the natural range of Ψ, earlywood will 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 condition (<–2.0 MPa), earlywood would be more likely than latewood to use water storage that can represent an important fraction, but then latewood would keep a minimum level of k_s by better resisting to embolism. This hypothesis could explain why trees with higher wood density and percent latewood are related to arid area (Polge, 1973; Megraw, 1985; Barajas-Morales, 1985) and are more resistant to cavitation (Alder *et al.,* 1996; Hacke *et al.,* 2001).

V.5.3 Tradeoff between hydraulic and mechanical properties of latewood and earlywood

Latewood had a density 2.3 times higher than earlywood (Table V.4) similar to other findings in the same species (Lutz, 1964; Tajima, 1967). The over-stated 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 its growth (Waring and Running, 1998). Gilmore *et al.* (1966) stated that the change from earlywood to latewood in *Pinus contorta* is almost due to the availability of soil moisture because a high moisture stress decreased auxin production. The regulation of cell diameter is hormonal and mediated by an auxin originating in the buds of growing shoots and 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 two and for just one year, would enhance the overall wood density by 34%, which will give also an increase in Young's modulus (E or wood stiffness) on the same range (Biblis, 1969) because wood density and E are correlated by a factor close to one (Bodig and Jayne, 1982). Mechanical performances (as judged by structural stiffness) increase 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·I (structural stiffness) and a change in latewood/earlywood ratio to 0.5 would increase E·I by only 26% (by using 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 also means a narrower growth ring. On the other hand, k_s would be reduced by 46% but the overall sapwood $C_{0.5-1}$ would be increased by 55%. Therefore, changing the proportion of latewood/earlywood for only one year would have more impact on hydraulic parameters than on mechanical resistance of the sapwood. The tradeoff and the advantage would be that more stored water would then be available for the trees due to an increase in capacitance as discussed above.

V.6 ACKNOWLEDGEMENTS

This project was supported by USDA CSREES 96-35103-3832 and 97-35103-5052, and a special USDA grant to Oregon State University for wood utilization research. The authors acknowledge the assistance with tree felling at Oregon State University McDonald Forest provided by Richard Symons, Andrew Chang and Duncan Wilson. We thank Marcel Merk, Jennifer Swenson, Laurent Bouffier and

Dr. Randy Johnson for field assistance, and Dr. B.J Bond, Dr. M. Unsworth, Dr. G. Howe and R. Leichti for corrections on the manuscript.

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Chapter VI

Conclusion

This work should help us better understand the adaptation of trees to their environments, through both methodological and interpretational advances. This research made several methodological contributions. I demonstrated a simple mathematical analysis of vulnerability curves for determining coefficients with a physiological significance and that easily can be compared among other studies. I presented a new way to calculate capacitance based on relative water content, rather than total water content, to put water storage into the context of how much space is available. I also determined hydraulic parameters within a single ring, opening the door for understanding the gross pattern of earlywood and latewood within a tree from the water transport perspective. My study introduces methodology for exploration of trunk water relations of mature trees and not solely branches by using the air injection method. I believe that these findings represent important steps in the understanding of tree-trunk and whole-plant water relations.

The research also contributed to fundamental understanding of tree physiology and growth. To the question "Is there a tradeoff between mechanical and hydraulic function of wood", this research has begun to provide answers. By defining hydraulic function as the ability to resist embolism rather than the ability to transport water, this research has shown that trees have evolved lower mechanical and higher hydraulic functions near the pith with the reverse near the bark. In other words, small changes that occur in wood properties from pith to bark

have a greater influence on tree hydraulics than on tree mechanics. When comparing vulnerability parameters with ring wood density or percent latewood, these results led us to believe that the structural basis for differences when embolism begins (Ψ_{12}) is determined by factors related to size of bordered pits in the earlywood tracheids. Typically within a conifer, earlywood tracheid size decreases from the bottom to the top of the tree, which would lead to smaller bordered pits, harder to embolize because of smaller pores and lower flexibility of the membrane. This research has shown that the full embolism point (Ψ_{88}), is determined directly by the proportion of latewood. The higher the latewood proportion, the harder it is to fully embolize, but the lower the specific conductivity is. Clearly, more anatomical study is needed to explore this hypothesis.

We now have evidence that the main bole of conifer species does play an adaptive role in preserving the whole tree from hydraulic failure. In determining the cavitation of stem wood and the maximum negative water potential as a function of radial and vertical position in the tree, wood near the pith has higher hydraulic function than near the bark in Douglas-fir, a species with narrow sapwood. In ponderosa pine (species with wide sapwood) there was no obvious trend in hydraulic function across the radius. The low "hydraulic plasticity" of wood for ponderosa pine was however, at the cost of low values of capacitance. I suggest that the wide sapwood of ponderosa pine trees is an adaptation to drier environments and helps the tree to better resist more negative water potentials without changing its ability to transport water.

My work has shown that hydraulic properties of trunk xylems of Douglas-fir and ponderosa pine change from the inner to the outer sapwood as well as from the bottom to the top of the tree and between earlywood and latewood. In term of water efficiency, this demonstrated lower conductivity in inner sapwood than in outer sapwood. In terms of water safety, however, inner and outer sapwood had similar vulnerability to embolism. This result suggested that refilling of embolisms

has been completed during the several years of difference in wood age between these radial positions.

To examine the effect on whole trunk water relations on hydraulic failure and to discern whether outer and inner sapwood at a given height in a tree experience different water potentials, future work should include measurement of water potential gradients as well as and sap flows along the trunk and shoots. Moreover, these findings should be confirmed by studying the tradeoff between hydraulic failure and hydraulic recovery in field conditions. The effects of cavitation and possible refilling of tracheids is then highly significant for the conductivity of the sapwood. Although still poorly understood, it appears that the refilling process plays an important role to compensate for factors such as a low increase in sapwood area from one year to another in old trees. Understanding refilling processes in conifers with wide and narrow sapwood areas is the next key in the study of tree trunk water relations.

Finally, to interpret the ecophysiology of an organism in an adaptive context, it is essential to study the features on which the selective pressures were relatively large. This research questions whether it is a rational goal of tree management and breeding to alter the existing quantity and structure of juvenile wood. The juvenile-mature wood quality issue is especially important as rotation ages decrease to 45-70 years, given that trees do not produce highest quality mature wood until after about 30 years. Juvenile wood (and to some extent latewood proportion) produced by a tree allows it to survive low water potentials, therefore any tree-breeding programs altering juvenile wood proportion or juvenile wood properties will produce drought vulnerable plants. In over watering in the nursery for example, trees could develop a lower resistant wood to dry conditions being unable to become mature in a dry stand. In other words, jumping the juvenile wood formation or creating mature wood too fast in nurseries would make the trees unable to survive in natural conditions. Furthermore, the growth responses due to irrigation are similar to those brought about by fertilization. That is, the response

depends on the time of year in which water is artificially applied. Consequently, early-season irrigation will favor crown development, which promotes earlywood formation, whereas late-season irrigation will prolong seasonal cambial activity, which promotes latewood formation. In most irrigation studies, water is supplied throughout the growing season resulting in greater growth and wider growth rings. Because both earlywood and latewood formation are promoted under this irrigation schedule, the effect on wood density is usually negligible. Because the hydraulic functions of juvenile wood and earlywood compared to mechanical are important, then programs that proceed to select or manage wood of desirable quality for users could result in high economic and environmental costs.

This research was concerned with conifers in the Pacific Northwest. Many questions remain on hardwoods, on the importance of different organs within trees, on other growth forms (e.g., vines, non-woody plant, herbaceous perennial), and in different ecosystems. The tools developed here will make some studies possible, and it is hoped that this dissertation contributes, albeit in a modest way, to our understanding of tree hydraulic functioning, and to further investigations.

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