

WOOD DENSITY AND HYDRAULIC PROPERTIES OF PONDEROSA PINE FROM THE WILLAMETTE VALLEY VS. THE CASCADE MOUNTAINS

*Laurent A. Bouffier*¹

Graduate Student
Institut National Agronomique Paris-Grignon
16 Rue Claude Bernard, 75231, Paris

Barbara L. Gartner†

Associate Professor

and

Jean-Christophe Domec†

Post-doctoral Associate
Department of Wood Science and Engineering
Oregon State University
Corvallis, OR 97331

(Received March 2002)

ABSTRACT

The Willamette Valley (WV) race of ponderosa pine (*Pinus ponderosa*) is being widely planted for timber in the Willamette Valley, western Oregon, because it grows in habitats that are either too wet or too dry for Douglas-fir (*Pseudotsuga menziesii*). Compared to the eastern Cascade Mountains (CM), the WV has 3 to 5 times the annual precipitation and warmer temperatures year around. This study characterized the wood quality of the WV race (4 sites) and the CM (4 sites), and also compared the behavior of their wood for water transport for the living trees (1 site in the WV and 1 site in the CM). The average tree ages at the sites ranged from 30 to 83 years at breast height. Between rings 27 and 31, compared to the CM, the WV had denser wood (0.48 vs. 0.40 g/cm³), denser earlywood (0.41 vs. 0.36 g/cm³), and denser latewood (0.62 vs. 0.50 g/cm³), with no significant differences in mean latewood proportion (about 0.35) or mean growth ring width (about 2.5 mm). The pith-to-bark trend in density differed between regions. In the WV, total wood density, earlywood density, and latewood density increased with growth ring from the pith. In the CM, total wood density and latewood density decreased slightly with growth ring width, and earlywood density remained unchanged. An additional sample of younger trees (23 years at breast height) from a genetic trial in the WV in which the seed source was the CM, had low density wood in the first few rings (like the CM trees) but had a steady increase in wood density with growth ring number (like the WV trees). Specific conductivity (k_s) of trunk wood was lower in the WV, consistent with its higher wood density and suggestive that the WV race is more drought-adapted than the CM populations. There was no decline in k_s from outer to inner sapwood in the WV trees, but a large decline in the CM trees. In water transport experiments, at an applied air pressure of 3.0 MPa, the WV and CM trees had lost 19% and 32% of their k_s , respectively, again suggesting that the WV trees are slightly more drought-adapted than are the CM trees. At the other applied air pressures tested (0.5, 2.0, 4.0, and 5.0 MPa), there were no significant differences in loss of conductivity between the two sites. Trunk wood from breast height had a 50% loss of k_s at 3.3–3.6 MPa. The loss of relative water content (100% – RWC) was about the same in both sites, except at 4.0 MPa, in which the CM trees had a larger loss of RWC than the WV trees. More work is needed on physiology to better understand the wood density/water transport relations. Ponderosa

¹ Formerly Student Intern at Oregon State University.

† Member of SWST.

pine may be more interesting to study than other species because the earlywood, which transports most of the water, shows substantial density differences between geographic regions.

Keywords: Wood density, vulnerability to embolism, earlywood density, specific conductivity, ponderosa pine, wood quality, ecological wood anatomy.

INTRODUCTION

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is one of the most widely distributed pines in the western United States (Oliver and Ryker 1990). Its many disjunct populations in a variety of habitats have led to high levels of geographic differentiation and genetic diversity (Squillace and Silen 1962; Conkle and Critchfield 1988; Linhart 1988). The trees in the Willamette Valley (WV) in western Oregon have the potential to be important locally for timber because they can thrive in sites that are too wet or too dry for the predominant timber species in the region, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). There is great interest in planting more of the Willamette Valley ponderosa pine (locally referred to as "valley pine"). The Willamette Valley Ponderosa Pine Conservation Association, formed in 1994, had 87 members in 2001, including commercial timberland enterprises, small woodland owners, small businesses, and other supporting groups and individuals. About 700,000 WV ponderosa pine seedlings were sold for the 2001 planting season, but there was demand for 1.0 to 1.2 million seedlings (Howard Dew, personal communication). With a habitat very different from that of the ponderosa pines of the dry mountain slopes 50–100 km to the east ("east side pine"), it is conceivable that the wood of the WV pine is physically and structurally different than the wood of the Cascade Mountains (CM). However, no research had addressed this issue. The CM wood of this hard pine is used for dimension lumber, boards for cut stock, moulding, mill work, cabinets, door and window manufacturing (Blatner and Govett 1988), and pulp. What are the qualities of this WV wood?

The trees have been present in the WV since before European settlement (Hibbs et al.

2002), but there is contradictory evidence regarding whether they are of a different genetic race than those in the CM. Isozyme studies found no difference in estimates of population genetic parameters comparing WV provenances to those from eastern Oregon, southwestern Oregon, and Fort Lewis, Washington (Gooding 1998). In contrast, evidence from provenance tests (Silen 2002) and anecdotes from tree growers about their different insect resistance, growth, and survival, all suggest that the WV trees are a different race than are the CM trees. Much research shows that ponderosa pine is highly drought-adapted mainly because of its deep roots (Parker 1969), its water-conservative pattern of stomatal opening, its relatively low leaf area/sapwood area (Waring et al. 1982), and other morphological and physiological adaptations (reviewed in Bassman 1988), but not because of any special ability to transport water under drought stress (Stout and Sala 1999; Piñol and Sala 2000; Maherali and DeLucia 2000a).

Wood density is an important index to the properties of the wood (e.g., Forest Products Laboratory 1999), and therefore it is often used as a way to compare wood quality of species and populations. We have found few reports on the wood density in ponderosa pine. Burdon and Low (1991) found a decrease in density to about rings 6–10, then an increase in rings 11–15 in New Zealand. Domec and Gartner (2003) showed a decrease in density from the pith to about rings 60–70, then an increase until about ring 150, where it leveled off at about 0.45 g/cm³ for trees from the east side of the Oregon Cascade Mountains. Stamm (1970) showed for one log (geographic origin not reported) an increase in density from the pith to ring 8, then a decrease to about ring 55, then an increase to ring 90 where it leveled off at about 0.35 g/cm³. Thinning and fertilizing had no significant effects

on wood density in spite of large effects on ring width in trees from the Sierra Nevada in central California (Echols 1972), and thinning itself had no significant effect on wood density in the Black Hills, South Dakota (Myers 1960). The latter results imply that density in this species is relatively unresponsive to management activities that alter growth rate.

The primary roles of wood in living trees are mechanical support and water transport, so if wood density is altered, water transport is likely to change (Gartner 1995; Stratton et al. 2000). Ecophysiologicalists report specific conductivity (k_s , equivalent to permeability in the wood science literature), which is a measure of how much water will pass through a sample of a given cross-sectional area and length, with a given driving force, per unit time. Note that it indicates the potential flow, not the actual flow, because the driving force (which is related to transpiration rate, leaf area, water availability at the root surface, and root surface area) varies in time. Also note that it is usually measured in the axial direction. In conifers, factors influencing k_s are proportion of latewood (Domec and Gartner 2002b) and tracheid dimensions (Pothier et al. 1989; Maherali and DeLucia 2000a). Other factors that influence water transport include not only k_s and the driving force, but also sapwood area and path length. All things being equal, k_s is likely to be higher in low density than high density wood, assuming that the differences in density are related to earlywood tracheid diameters (rather than cell wall thickness, latewood characteristics, or latewood proportion).

The above discussion related to water transport when the plant is fully hydrated. A second hydraulic concept regards water transport when the xylem water is under tension, referred to as the vulnerability to embolism (e.g., Tyree et al. 1994). Specific conductivity is measured, then the sample is subjected to a simulation of tension in the water column (which causes air bubbles to be pulled into some of the tracheids), and k_s is re-measured. The sample is again subjected to a simulation of tension in the water column (this time with

a stronger tension), and so on (Sperry et al. 1988). One graphs the loss of conductivity vs. the simulated tension in the water column, and compares the form and position of the curves. Because it is hard experimentally to put tension on the water column, ecophysiologicalists put positive pressure on the outside of the sample, leaving the ends at atmospheric pressure, so the xylem experiences a negative of the water pressure difference from inside to outside the xylem. Experiments show that the same population of tracheids will embolize with either positive or negative pressures (Cochard et al. 1992). All things being equal, dense wood is less vulnerable to embolism than is less dense wood (Hacke et al. 2001). A typical curve for twigs, branches, and stems is sigmoidal, with a zone at which very little conductivity is lost with increasing tensions, followed by a zone of rapid loss of conductivity, and ending with a zone of slow loss as total loss approaches 100%. However, earlywood and latewood have very differently shaped curves in conifers: the earlywood curve drives the sample's curve almost entirely (Domec and Gartner 2002b). Latewood loses much of its conductivity with very little tension in the water column, but then it levels off, and does not lose much more of its conductivity. Note that vulnerability to embolism has been reported for the trunk wood of only two species: *Pseudotsuga menziesii* and *Pinus ponderosa* (Domec and Gartner 2001, 2003). All the other research in this field has been conducted on twigs, branches, and roots.

This study compared the radial patterns of wood density (total density, earlywood density, and latewood density) of native ponderosa pines from several sites in the WV and in the CM, and also the pattern at one site that had trees with a CM seed source growing in the WV. Secondly, this study compared k_s and vulnerability to embolism of wood from one site in the WV to literature values of trees from one site in the CM (Domec and Gartner 2003). The goals were to learn if the trees in the WV and CM differ in their radial patterns of wood density and in their ability to transport water.

MATERIALS AND METHODS

Sites and plant materials

The wood of ponderosa pine (*Pinus ponderosa* var. *ponderosa*) was studied from nine sites (Table 1). Five of the sites were in the Willamette Valley or its eastern foothills (WV), and four of the sites were on the eastern side of the Cascade Mountains (CM). The Monmouth site, a genetic trial of ponderosa pines from CM seed sources (from 1,200 m and 1,650 m elevation in central Oregon) growing in the WV (Sorensen and Miles 1982), was studied to infer whether the wood density patterns are environmentally or genetically determined. Climate data (Taylor and Hannan 1999) are shown for the meteorological station closest to the sites (Table 2). The WV sites were at lower elevation (Table 1), had 3–5 times more precipitation, and were warmer at all seasons than were the CM sites (Table 2). This study made use of previously collected data on water transport physiology of ponderosa pine trees from one CM site, Crescent (Domec and Gartner 2003). Therefore, we used Crescent as one of our CM sites to core for wood density determination.

All sites had about 500 to 750 trees/ha, were naturally seeded (except for the Monmouth site) and were on level to gently sloping terrain. However, they were under different ownership, had different ages (ranging from 30–83 years at breast height for site means), and had many different management regimes.

We cored at least 20 trees/site at sites 1–4, but found that variability in density values was low, so we cored fewer trees in the remaining sites. Some cores were later discarded because of pitch pockets, branch traces, or compression wood. We chose trees that were characteristic for the intermediate and dominant trees at the site, avoiding trees that were small, forked, or strongly leaning, or that had broken tops or obvious disease. At the Monmouth site, we chose trees regardless of genetic family. We took one breast height increment core (5.0 mm in diameter) from each tree, stored it in a paper straw, and then recorded the tree's

TABLE 1. Characteristics of sites and ponderosa pine trees sampled for wood density.

Site, nearest town	Lat. (N), long. (W), elevation (m)	Cores ¹ (n)	Age ² (y)	Dbh ³ (cm)	Height ⁴ (m)	Live crown ⁵ (m)	Active management
Willamette Valley (WV)							
1 Crawfordville	44°21', 122°51', 150	20	30 ± 1.0	28.8 ± 1.1	18	10–14	Thinned 1980
2 Albany	44°35', 123°09', 50	18	32 ± 1.4	37.8 ± 1.1	18–20	10	None
5 Molalla	44°38', 122°48', 150	13	46 ± 2.5	48.2 ± 2.0	20–25	15–18	Currently, cattle grazing
6 Sweet Home	44°22', 122°52', 200	10	83 ± 5.4	41.2 ± 3.5	22–30	12–21	None
Cascade Mountains (CM)							
3 Gilchrist	43°28', 121°40', 1400	21	38 ± 2.0	28.8 ± 0.6	18–20	4–6	Thinned 2001
4 Bend	44°06', 121°25', 1400	23	47 ± 0.6	29.9 ± 1.0	17–18	3–5	Thinned 1970s
7 La Pine	43°40', 121°36', 1400	12	56 ± 3.8	29.1 ± 1.3	13–16	4–6	Thinned about 1980
8 Crescent	43°32', 121°41', 1350	15	81 ± 5.6	26.0 ± 1.2	10–15	3–8	None
CM source planted in WV (CM/WV)							
9 Monmouth	44°49', 122°43', 100	16	23 ± 0.6	25.3 ± 0.9	12–14	6–7	Annual mowing for brush control, pruned for access

¹ Number of trees from which cores were X-rayed.

² Age at breast height (1.4 m, mean ± SE).

³ Diameter at breast height (mean ± SE).

⁴ Approximate height of trees sampled.

⁵ Approximate height from the ground to the base of the live crown.

TABLE 2. *Climate characteristics for 30-year period (1961–1990) for meteorological stations near the sampled sites in the Willamette Valley and the Cascade Mountains (Taylor and Hannan 1999).*

Site(s) ¹	Meteorological station (elev.)	Precipitation (mm)					Temperature (°C) ²				
		Ann.	Win.	Spr.	Sum.	Fall	Ann.	Win.	Spr.	Sum.	Fall
Willamette Valley											
1, 6	Cascadia (80 m)	1,595	561	310	126	598	10.2	5.3	11.8	16.6	6.9
2	Corvallis (70 m)	1,083	417	145	74	447	11.1	5.9	12.7	18.1	7.8
5	Silverton (125 m)	1,166	411	204	102	449	11.2	6.0	12.9	18.2	7.8
9	Salem (60 m)	997	370	143	74	410	11.2	5.9	12.8	18.2	7.7
Cascade Mountains											
4	Bend (1,120 m)	297	94	57	39	107	7.9	1.8	10.1	15.8	3.9
3, 7, 8	Fremont (1,350 m)	298	94	61	36	107	5.9	−0.5	8.6	14.0	1.4

¹ From Table 1.² Average mean of daily maximum and minimum temperatures.

diameter at breast height. For each stand we estimated the total height of the sampled trees and the height from the ground to the base of the trees' live crowns.

For hydraulics, we studied trees from the Sweet Home site in the WV. This site was chosen because it was a site with trees at least as old as the trees from Crescent in the CM (the site to which the numbers would be compared), and a site at which we could destructively harvest the trees.

Wood density and growth ring width

Cores were oven-dried in their straws at 40°C for at least 48 h. The bark was removed, and the cores were cut at the pith. Cores were then conditioned to the moisture content of the X-ray room for one day, to insure that they would not change moisture content as they were X-rayed. Extractives were not removed. Voorhies (1969) reported that extraction of ponderosa pine decreased the density (dry mass/green volume) from 0.42 to 0.37. Most of the trees we sampled had not yet produced heartwood at breast height, so heartwood extractives were rarely present.

Next, cores were line-scanned with a direct-scanning X-ray densitometer, producing one value every 100 μm along the 100- μm wide scan. Sample thickness was taken as 5.0 mm, which is the inner diameter of the borer; a subsample of the cores were measured in the field, and their diameter did not differ measurably

from 5.0 mm. Data were deconvoluted using standard methods following the Lambert-Beer law (e.g., Liu et al. 1988) to give a plot for each sample that was X vs. radial position along the sample, where X was a value that was proportional to density. We determined the constant of proportionality between X and density (dry mass/green volume) for each sample separately, as follows. Each sample's bulk density was estimated from its dry mass and volume (calculated from core length and diameter). We then scaled the plot of X vs. radial position for each core separately such that the plot's mean density equaled the sample's measured bulk density, and we used that scalar as the constant of proportionality.

DendroScan software (Varem-Sanders and Campbell 1996) was used to find the boundaries between growth rings (the steepest point between the maximum latewood density of one year and the minimum earlywood density of the next year) and between earlywood and latewood (the point within a growth ring that has the average density between minimum earlywood and maximum latewood densities). These boundaries were then verified by comparison of graphs to samples. Next, data were summarized for each growth ring in each core to give growth ring density (total, earlywood, latewood), growth ring width (total, earlywood, and latewood), and latewood proportion.

Hydraulic properties

The hydraulic properties of sapwood from the WV (Sweet Home site) were compared to those properties already measured from the CM (Crescent site, Domec and Gartner 2003). Note that the data in Domec and Gartner 2003 are a compilation of several sites, and the data used here are from that individual site. We took one breast height disk about 20 cm thick from six trees, following Domec and Gartner's methods closely (details in Domec and Gartner 2003). The major differences between the two studies were that the CM samples were taken in March 2000 and these samples were taken in February 2002 (both dates are within the dormant season in these sites), the CM samples were taken from a height of 1.6 m and these samples were taken at a height of 1.4 m (breast height), and the CM samples averaged 49 years and these samples averaged 86 years.

Disks were transported in wet plastic bags and stored at 5°C until samples were prepared, which occurred within 12 h of felling the trees. The disk was first reduced into quarters with a maul and a wedge, and then the samples were extracted with a hammer and chisel. We removed one piece of wood from the inner sapwood and one from the outer sapwood from two mutually perpendicular radii from each disk. Outer samples were made of the outermost sapwood (bark inward), and inner samples started about 3–4 growth rings exterior to the sapwood/heartwood border (to avoid the transition zone), and extended inward from there. Samples were about 10 mm in the tangential direction, 9 mm in the radial direction, and 90–130 mm in the axial direction. They were stored at 3°C in water that was changed daily, and they were tested within four days.

Samples were submerged in water under a vacuum for 48 h to refill some of the embolized tracheids. Initial specific conductivity ($k_{s(i)}$) was then measured on the sample as described below. Curves of vulnerability to embolism were constructed using the method de-

scribed by Domec and Gartner (2001). The method measures the percent loss of conductivity by moving the sample alternately between a membrane-lined pressure sleeve where k_s is measured (Spicer and Gartner 1998), and a double-ended pressure chamber where embolisms are induced by air injection (Sperry and Saliendra 1994). After each k_s measurement, we removed about 1 mm of wood from each end of the samples to have a new surface for each experiment.

Initial specific conductivity ($k_{s(i)}$) was measured using filtered (0.22 μm) water adjusted with HCl to pH 2 to prevent microbial growth, and with a hydraulic head of 0.0044 MPa. Efflux was collected in a 1-ml-graduated micropipette (0.01 ml graduation). We recorded the time required for the meniscus to cross ten consecutive graduation marks, and used only the values that were steady. Samples were subjected to several air pressures ranging from 0.5 to 5.0 MPa until more than 95% loss of conductivity was reached. The temperature of the solution, the fresh mass (M_f), and the length of each sample were recorded before and after each k_s measurement, and final fresh volume (final V_f , by water displacement) was measured after the last k_s measurement. We estimated sample volume for each k_s measurement from the relative length measurements.

Hydraulic vulnerability curves were fitted by the least squares method based on a sigmoidal function:

$$\text{loss of conductivity (\%)} = \frac{100}{(1 + e^{a_1(\Psi - b_1)})} \quad (1)$$

where loss of conductivity (%) is $(k_{s(i)} - k_{s(\Psi)})/k_{s(i)}$, the parameter a_1 is an indicator of the slope of the linear part of the vulnerability curve, Ψ is the water potential (usually a tension), and b_1 the water potential at which 50% loss of conductivity occurred (Ψ_{50}). We calculated the actual slope (slope = $a_1 \cdot 25$) of the linear part of the vulnerability curve and the pressures at 12% loss of conductivity ($\Psi_{12} = 2/a_1 + b_1$) and at 88% loss of conductivity ($\Psi_{88} = -2/a_1 + b_1$) (Domec and Gartner

2001). The value Ψ_{12} , termed the air entry point (Sparks and Black 1999), is an estimate of the xylem water potential at which the resistance to entry of air through the pit membranes is overcome and embolism begins (Sperry and Tyree 1988). Likewise, Ψ_{88} , termed the full embolism point, is interpreted as approximating the water potential of the xylem before it becomes nonconductive.

To estimate the rate of change in relative water content (RWC) associated with embolism, we calculated RWC initially and after each applied pressure from V_f and M_f . Following final pressurization, we recorded the oven-dry mass (M_d ; in grams) after 48 h at 104°C and by using the length, estimated the M_d for each applied pressure. We then calculated RWC assuming a cell-wall material density of 1.53 g/cm³ (Siau 1984):

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

The loss of RWC (=100 - %RWC) over the range of applied pressure was fit using a sigmoidal function as follows:

$$100 - \% \text{RWC} = \frac{\text{Max}}{(1 + e^{a_2(\Psi - b_2)})} \quad (3)$$

where Max is the maximum loss of RWC possible, a_2 is a variable that is linearly proportional to the slope of the linear part of the curve, and b_2 is the water potential at which [(Max/2)·loss of RWC] occurred ($\Psi_{\text{max}/2}$). We calculated the actual slope ($C_{\text{max}} = a_2 \cdot \text{Max}/4$) of the linear part of the loss of RWC curves, which is an estimate of the maximum water storage capacity (see Domec and Gartner 2002a).

Density (dry mass/green volume) was calculated for each of the hydraulics samples. Through a dissecting microscope, we measured one end of each sample for the radial earlywood and latewood widths. We then calculated mean growth ring width and latewood % for each sample.

Data analysis

For each site, we calculated the mean value of each of the following properties for each growth ring number: wood density (total, earlywood, and latewood), growth ring width (total, earlywood, latewood), and latewood proportion. Because cores differed in number of growth rings, the sample size decreased from the pith outward. We included only rings for which sample size was at least six. We plotted values for visual comparison of all nine sites.

A linear regression model was used to test whether the ring density patterns for rings 10 to 40 differed by region using the PROC GLM procedure. All statistical procedures were conducted with Statistical Analysis Systems software (SAS 1997). The statistical model was

$$Y = a + b_1 \text{ring} + \text{region}_i + \text{site}_{ji} \\ + b_2(\text{ring} \times \text{region}_i) \\ + b_3(\text{ring} \times \text{site}_{ji})$$

where Y is the wood property of interest, a is the intercept, ring is the growth ring number from the pith, region_i is the effect of the i th region (either WV or CM), and tests whether intercepts differ between the two regions, site_{ji} is the effect of the j th site within the i th region, $(\text{ring} \times \text{region}_i)$ is the interaction of region and ring, and tests whether the slope of the wood property and ring number differ between regions, $(\text{ring} \times \text{site}_{ji})$ is the interaction of the j th site within the i th region and ring, and b 's are regression coefficients that are to be estimated. The study was a nested design. Therefore the error term for region_i is site_{ji} . Likewise, the error term for $(\text{ring} \times \text{region}_i)$ is $(\text{ring} \times \text{site}_{ji})$.

To compare the wood properties in the WV and the CM, we calculated means for the five-year period from ring 27–31. That range was chosen because it was the oldest rings we could choose given the ages of the cores of the eight sites in those two regions (Table 1). Because the cores in the trees from the CM/WV were younger than in the other sites, we chose rings 22–26 for comparison of WV, CM,

and CM/WV. Only the 12 CM/WV cores that went all the way to 26 years were included in the calculations. The slope of the plot of wood density vs. growth ring number excluded growth rings 1–10 because the pattern was variable from tree to tree, and there are more errors in data collection and interpretation in the growth rings nearest the pith.

Values of the hydraulics samples (density, growth ring width, and latewood proportion) for the two sites were compared using each tree as a single replicate with a separate ANOVA for outer sapwood and for inner sapwood. Specific conductivity (k_s) was compared in the same way, with a separate ANOVA for outer sapwood, inner sapwood, and total sapwood, where total sapwood weighted the values of inner and outer sapwood by their cross-sectional proportion of the sapwood. Values of the characteristics for the trees sampled for hydraulics (tree height, inside-bark diameter of the disk, age where sampled, number of sapwood rings, sapwood area, heartwood area, and proportion of the total sapwood that is outer sapwood) for the two sites were compared with ANOVA.

The data on loss of conductivity and loss of relative water content with applied air pressure were analyzed in two ways. The first was an ANOVA comparison of the parameters Ψ_{12} , Ψ_{50} , Ψ_{88} and the slope, all derived from the sigmoidal curves (fitted with the least square method). The second was a direct comparison of the data, not the fitted curves: we compared the values of loss of conductivity or loss of RWC at each of the pressures at which they were measured. We used a strip-plot randomized block design (tree as block) with the PROC MIXED procedure with pressure as the repeated measure factor because the value at one pressure depended on the value at the previous pressure.

RESULTS

Wood density and growth ring width

The wood from the Willamette Valley (WV) was denser than the wood from the Cascade

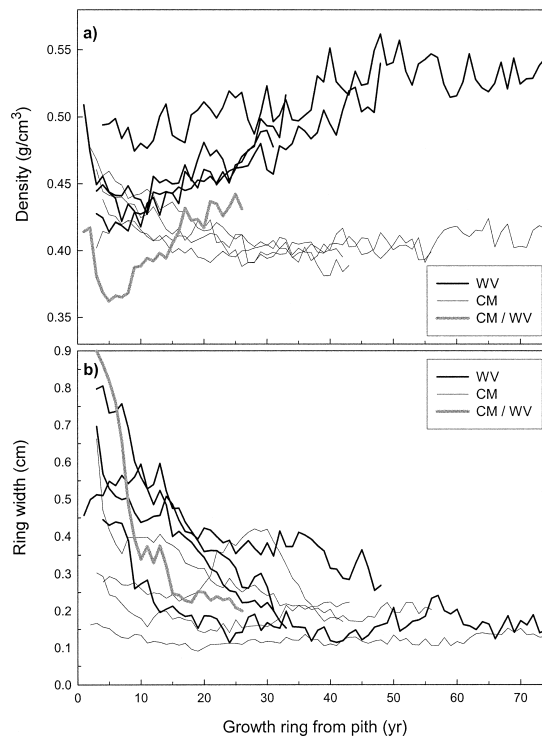


FIG. 1. Site means of growth ring characteristics as a function of growth ring number from the pith for sites from the Willamette Valley (WV), the Cascade Mountains (CM), and a Cascade Mountain seed source grown in the Willamette Valley (CM/WV). a) Total ring density, b) growth ring width. Each line is the mean value for one site ($n = 10\text{--}23$ trees/site). The longest cores are from the sites that were compared for hydraulics.

Mountains (CM) (Figs. 1a, 2a). This difference is about 20% for rings 27 to 31 (Table 3). For the sites that had older cores, the density difference between the WV and the CM was even larger beyond ring 31 (Figs. 1a, 2a): rings 60–75 had average density of 0.53 for WV site 6, and 0.41 for CM site 8, a difference of 29%. The trees from the CM seed source grown in the WV (CM/WV) had low-density wood (Table 3). All sites within a region (WV vs. CM) had remarkably similar wood density curves (Fig. 1a), except for the WV Sweet Home site, which had denser wood up to ring 40 than did the other WV sites. No statistical tests were performed on the similarity of curves of sites within regions, as the similarities were apparent from inspection.

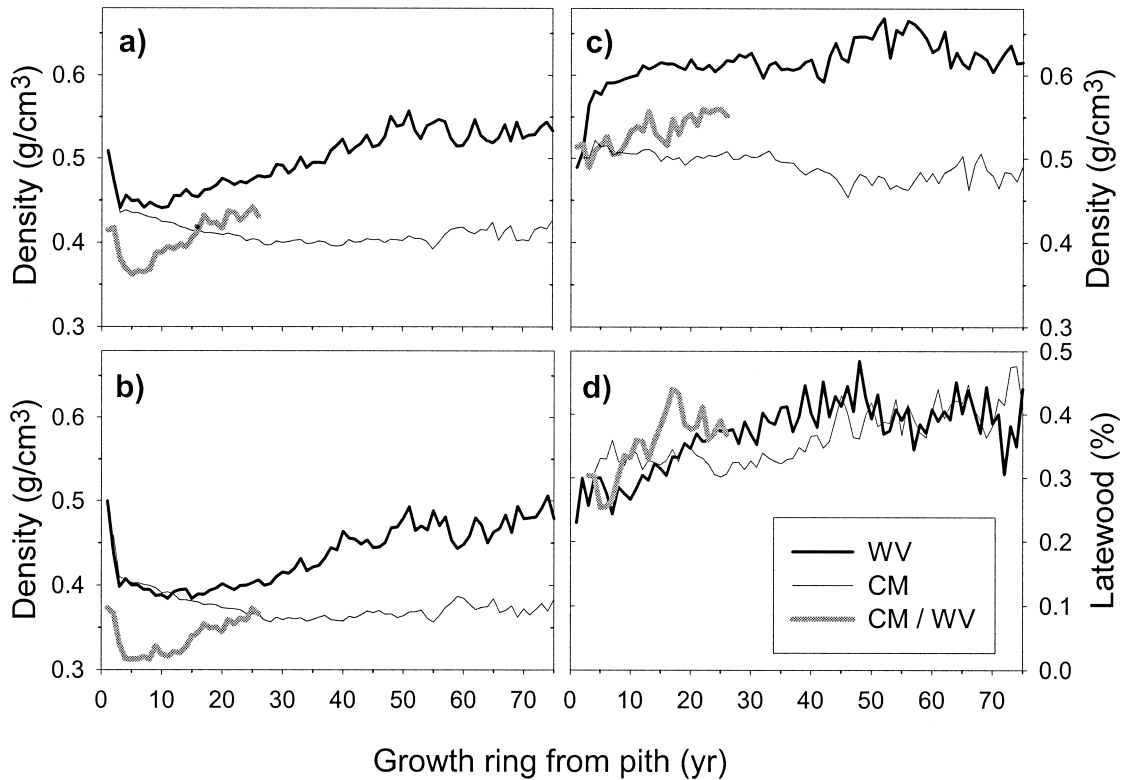


FIG. 2. Regional means of growth ring characteristics as a function of growth ring number from the pith for trees from the Willamette Valley (WV), the Cascade Mountains (CM), and a Cascade Mountain seed source grown in the Willamette Valley (CM/WV). a) Total ring density, b) earlywood density, c) latewood density, d) latewood proportion. Each line is the mean value for one region (n = 4 sites/region except for CM/WV where n = 1).

TABLE 3. Physical properties of ponderosa pine wood from the naturally-regenerated stands in the Willamette Valley (WV; n = 4), the Cascade Mountains (CM; n = 4), and from planted trees of Cascade Mountain seed source in the Willamette Valley (CM/WV; n = 1). Within each row, values with the same letter are not significantly different at P < 0.05. Mean ± SE.

	WV	CM	CM/WV
Slope of wood density ¹ (rings 10–40)	$(20.4 \pm 2.0) \times 10^{-4}$ (b)	$-(8.7 \pm 0.9) \times 10^{-4}$ (a)	
Wood density (rings 27–31; g/cm ³)			
Total	0.48 ± 0.01 (a)	0.40 ± 0.01 (b)	
Earlywood	0.41 ± 0.01 (a)	0.36 ± 0.01 (b)	
Latewood	0.62 ± 0.01 (a)	0.50 ± 0.02 (b)	
Growth ring width (rings 27–31; mm)			
Total	2.54 ± 0.39 (a)	2.36 ± 0.58 (a)	
Earlywood	1.62 ± 0.27 (a)	1.69 ± 0.55 (a)	
Latewood	0.93 ± 0.16 (a)	0.67 ± 0.10 (a)	
Latewood proportion (rings 27–31)	0.37 ± 0.01 (a)	0.32 ± 0.04 (a)	
Slope of wood density ¹ (rings 10–26)	$(1.9 \pm 0.7) \times 10^{-3}$	$(-1.3 \pm 0.3) \times 10^{-3}$	$(3.5 \pm 0.5) \times 10^{-3}$
Wood density (rings 22–26; g/cm ³)			
Total	0.47 ± 0.01	0.41 ± 0.04	0.43

¹ Slope is from the linear regression of the curve of total wood density vs. growth ring number for the growth rings noted.

For rings 10–40, the slope of total wood density differs between regions, being positive in WV and negative in CM (Table 3). This difference in slope is driven by changes in earlywood density and latewood proportion, not latewood density (Fig. 2): for rings 10–40, earlywood density and latewood proportion differ between regions ($P < 0.01$ and $P < 0.05$ respectively), but latewood density does not ($P = 0.22$). The higher wood density in WV than CM was seen in both the earlywood and latewood (Fig. 2b, c, Table 3). The CM/WV trees produced wood of low density, consistent with the CM origin, and with a positive slope, consistent with the WV trees (Table 3).

Growth rings widths (Fig. 1b, Table 3) and latewood proportion (Fig. 2d, Table 3) were similar in the WV and CM sites. Note that one of the CM sites had a large increase in ring width from about years 20–40, with no effect on density. That ring width was associated with a one-entry thinning of site 4 that land managers told us occurred 21–31 years ago, which would correspond to growth rings 16–26 on those cores. The CM/WV site, in spite of its more aggressive vegetation management, had intermediate growth ring widths for all the sites studied (Fig. 1b).

Hydraulic properties

For the hydraulics samples, the wood from the WV site (Sweet Home) was denser than that from the CM site (Crescent), in terms of total density, earlywood density, and latewood density (Table 4). Both sites had similar growth ring widths and latewood proportions (Table 4). The hydraulics samples were similar to the samples taken as radial cores except that the hydraulics samples from WV had a higher proportion of latewood than did those from the CM (Table 4). The hydraulics samples were younger, the trees were shorter, and the stem diameter was smaller at Crescent than Sweet Home (Table 4). The apparent contradiction of having smaller-diameter stems but the same growth ring widths at the Crescent vs. Sweet Home sites must result from growth ring width

being measured only on the small subset of the radius that we tested hydraulically.

The specific conductivity (k_s) of outer sapwood was 68% higher in the CM samples than in WV samples (Table 5). In the WV samples, there was no significant difference between the k_s of outer and inner sapwood (ANOVA, $P > 0.05$), but in the CM samples, inner sapwood had 40% lower k_s than did outer sapwood (ANOVA, $P > 0.05$, Table 5). Sapwood k_s (which is weighted by proportional areas of outer and inner sapwood) is 27% lower in WV than CM (Table 5).

The curves that were fit to the data on loss of conductivity vs. the negative of applied pressure produced a high value of r^2 (0.98). However, the curves did not pass directly through all of the data (Fig. 3a). ANOVAs of the parameters derived from the fitted curve (Ψ_{12} , Ψ_{50} , Ψ_{88} and slope) showed no significant differences between the two sites ($P < 0.23$, Table 5). When the measured values of loss of conductivity vs. applied pressures (Fig. 3b) were compared for the two sites, the PROC MIXED analysis showed significant differences in the values at -3.0 MPa, with the CM showing 34 ± 6 vs. $19 \pm 2\%$ more loss of conductivity than the WV.

Sigmoidally fit curves were also compared for loss of relative water content vs. the negative of applied pressure (Fig. 3c). C_{\max} and $\Psi_{\max/2}$ did not differ significantly by site (Table 5). The maximum loss of RWC possible (Max) was 72% and 90% in the CM and WV, respectively (data not shown). In a comparison of the measured data (rather than the fit curves) of loss of RWC vs. the negative of applied pressure (Fig. 3d), wood from the CM site lost significantly more of its relative water content at -4.0 MPa than did the wood from the WV site.

DISCUSSION

The ponderosa pine wood from the Willamette Valley (WV) was denser than wood from the Cascade Mountains (CM). This result was surprising because there was no strong *a priori*

TABLE 4. Physical properties of ponderosa pine wood from the two stands that were compared for hydraulic properties, Willamette Valley (Sweet Home) and Cascade Mountains (Crescent). Within each row, values with the same letter are not significantly different at $P < 0.05$. Mean \pm SE ($n = 6$).

	WV (Sweet Home)	CM (Crescent)
Hydraulics samples		
Wood density (g/cm ³)		
Outer sapwood ¹	0.53 \pm 0.02 (a)	0.41 \pm 0.01 (b)
Inner sapwood	0.48 \pm 0.01 (a)	0.39 \pm 0.01 (b)
Growth ring width (mm)		
Outer sapwood ¹	1.06 \pm 0.25 (a)	1.21 \pm 0.20 (a)
Inner sapwood	1.44 \pm 0.20 (a)	1.86 \pm 0.20 (a)
Latewood proportion		
Outer sapwood ¹	0.36 \pm 0.02 (a)	0.20 \pm 0.01 (b)
Inner sapwood	0.34 \pm 0.01 (a)	0.18 \pm 0.03 (b)
Tree height (m)	26.2 \pm 1.4 (a)	12.4 \pm 0.4 (b)
Disk diameter (inside bark; cm)	33.1 \pm 2.8 (a)	19.2 \pm 0.8 (b)
Age where sampled (yr) ²	86 \pm 7 (a)	49 \pm 1 (b)
Sapwood rings (no.)	69 \pm 6 (a)	41 \pm 2 (b)
Sapwood area (cm ²)	815 \pm 150 (a)	192 \pm 28 (b)
Heartwood area (cm ²)	73 \pm 14 (a)	9.5 \pm 2.9 (b)
Proportion of outer sapwood ¹	0.63 \pm 0.01 (a)	0.67 \pm 0.01 (b)
Radial density trees		
Wood density (rings 60–75; g/cm ³)		
Total	0.53 \pm 0.02 (a)	0.41 \pm 0.01 (b)
Earlywood	0.47 \pm 0.02 (a)	0.37 \pm 0.01 (b)
Latewood	0.62 \pm 0.02 (a)	0.48 \pm 0.02 (b)
Growth ring width (rings 60–75; mm)		
Total	1.62 \pm 0.31 (a)	1.33 \pm 0.17 (a)
Earlywood	0.99 \pm 0.21 (a)	0.82 \pm 0.14 (a)
Latewood	0.63 \pm 0.12 (a)	0.51 \pm 0.05 (a)
Latewood proportion (rings 60–75)		
Total	0.40 \pm 0.04 (a)	0.42 \pm 0.04 (a)
Age at breast height (yr)	83 \pm 5 (a)	81 \pm 6 (a)

¹ Outer sapwood represents the outer half of the sapwood width.

² At breast height (1.4 m) in WV, and at 1.6 m in CM.

reason to expect a density difference. The WV sites were much wetter than the CM sites. On a species basis, higher density is usually associated with dry rather than wet sites (e.g., Nicholls and Wright 1976 for softwoods; Barajas-Morales 1987 for hardwoods), possibly because denser woods may have narrower lumens and/or thicker cell walls, which are better able to handle the mechanical stress of transporting water during drought (Carlquist and Hoekman 1985). Within ponderosa pine, however, irrigation of a dry site in eastern Washington produced higher wood density, with a more gradual transition to latewood and

a higher latewood proportion (Howe 1968). The WV sites are also at lower elevation than the CM sites, and in some conifers (including one provenance study of ponderosa pine, Echols and Conkle 1971), the populations at or from lower elevation had denser wood than those at high elevation (discussed in Zobel and van Buijtenen 1989, pp. 38–47). However, the cause of an elevation effect is unclear because elevation is usually confounded with temperature and precipitation. Even though the annual radial growth rates were within the same range in the WV and CM regions, the timing of the annual growth is likely to be quite dif-

TABLE 5. Hydraulic properties of ponderosa pine wood from the Willamette Valley (Sweet Home) and the Cascade Mountains (Crescent; see text). Each tree and position is the mean of two values (mean \pm SE, n = 6 trees).

	WV (Sweet Home)	CM (Crescent)	P
k_s (10^{-12} m ²)			
Outer sapwood	3.4 \pm 0.4	5.7 \pm 0.5	0.01
Inner sapwood	3.6 \pm 0.2	2.9 \pm 0.4	0.23
Total sapwood	3.5 \pm 0.4	4.8 \pm 0.5	0.09
Values of parameters of the fitted sigmoidal curves			
Loss of conductivity			
Ψ_{12} (MPa)	-2.7 \pm 0.2	-2.2 \pm 0.1	0.49
Ψ_{50} (MPa)	-3.6 \pm 0.1	-3.3 \pm 0.1	0.23
Ψ_{88} (MPa)	-4.6 \pm 0.2	-4.5 \pm 0.2	0.23
Slope (loss of k_s /MPa)	58 \pm 9	44 \pm 7	0.98
Loss of RWC			
$\Psi_{\max/2}$ (MPa)	-4.8 \pm 0.1	-4.0 \pm 0.2	0.16
C_{\max} (loss of RWC/MPa)	18.7 \pm 1.4	18.5 \pm 1.2	0.10

ferent in the two regions, and so the trajectory of that growth may be quite different (Downes et al. 1999). Nonetheless, one study found no

relationship between growth rate and wood density in ponderosa pine (Myers 1960).

The CM seed source grown in the WV re-

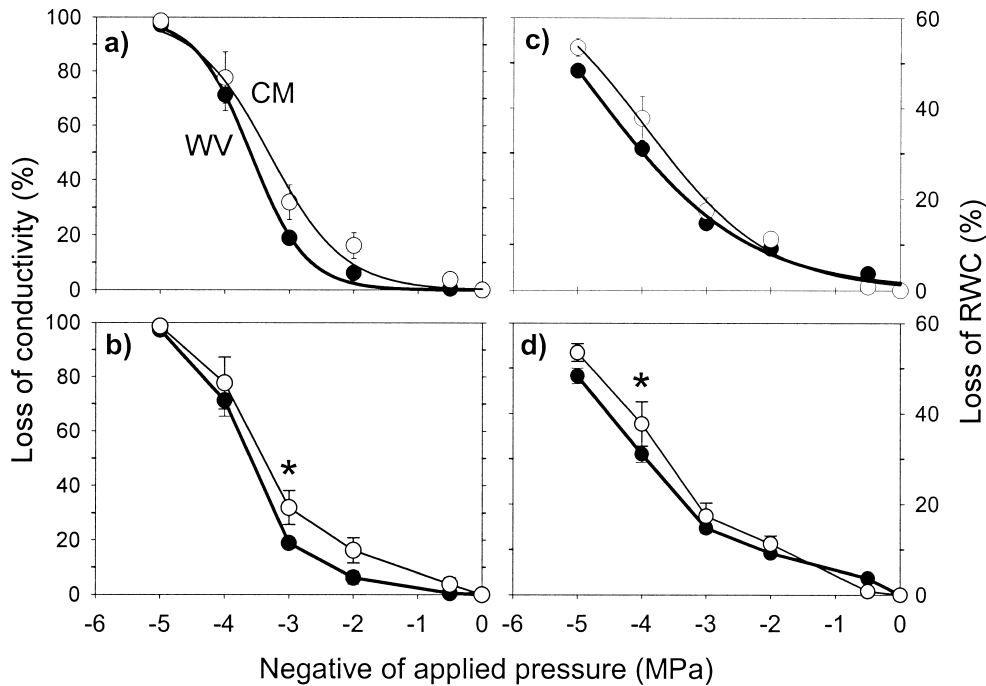


FIG. 3. Loss of conductivity and loss of relative water content vs. the negative of applied air pressure in wood from Willamette Valley (Sweet Home) and Cascade Mountain (Crescent) ponderosa pines (mean \pm SE, n = 6). a) and c) Sigmoidal curves fitted on measured values; b) and d) measured values connected linearly. Asterisks show significant differences at $P < 0.05$.

gion produced wood of low density, consistent with the CM origin, and had a positive slope, consistent with the native WV trees. The results are suggestive that the seed source is responsible for the low-density values, and the environment is responsible in some unknown ways for the positive slope. Site differences between WV and CM include precipitation, elevation, temperature, competing vegetation, and soils.

The radial patterns of wood density differed between the two regions after about the first five rings. In the CM region, the radial density pattern was relatively constant, but in the WV it increased toward the bark. In the CM region, the pith-to-bark decline in density (not typical of hard pines, e.g., Megraw 1985; Larson et al. 2001) was caused by a decline in both earlywood density and latewood density (not typical of hard pines). In the WV region, the pith-to-bark increase in density (typical of hard pines) was caused by an increase in earlywood density (not typical of hard pines), latewood density (typical of hard pines), and latewood proportion (typical of hard pines). The contrast between a flat radial density trend in the CM and an increasing one in the WV is somewhat surprising within one species, albeit a genetically diverse one, although there are many precedents for both types of pattern (e.g., pages 79–84, Zobel and Sprague 1998).

The wood from the WV region had lower specific conductivity (k_s) than did the wood from the CM, consistent with its higher wood density. In the radial core samples, the WV's higher density was caused by higher density of both the earlywood and latewood, but not by a difference in latewood proportion between the two regions, which makes the WV population especially interesting to study hydraulically. Unfortunately, in the hydraulics samples, the WV samples had a higher latewood proportion than did the CM samples, making it hard to interpret results too strongly. Other studies in ponderosa pine found that higher temperature, whether in a greenhouse (Maherali and DeLucia 2000b) or in a comparison of desert vs. montane populations

(Maherali and DeLucia 2000a), induced development of wood with wider tracheids and therefore higher k_s . Those results are not consistent with the lower k_s and higher wood density in the WV than the CM regions, and suggest that the regional difference in wood density that we observed results at least in part from having narrower lumens in the WV than the CM region. In the WV region, the outer and inner sapwood had similar k_s , which contrasts to previous reports that show higher k_s in outer than inner sapwood in coniferous species that have been studied: ponderosa pine (Domec and Gartner 2003), *Pinus radiata* (Booker 1984), *Pseudotsuga menziesii* (Markstrom and Hann 1972; Spicer and Gartner 2001), *Tsuga canadensis* (Comstock 1965), and *Pinus contorta* and *Picea engelmannii* (Markstrom and Hann 1972). There was also one report of no significant differences in k_s of inner and outer sapwood in *Pinus radiata*, but the report's authors believed the result was caused by compression wood in many of their samples and increased latewood proportion in the outer rings (Booker and Kininmonth 1978).

Trees in dry regions usually have a lower leaf area/sapwood area than do trees from more mesic regions (reviewed in Margolis et al. 1995; Mencuccini and Grace 1995), which provides them less transpiring surface area per conducting area. The disadvantage to a relatively large sapwood area is the higher respiratory costs of the sapwood parenchyma cells (e.g., Ryan 1990; Pruyn et al. 2002). This pattern of lower leaf area/sapwood area in drier sites was shown in ponderosa pine from the desert sites vs. from cool, moist montane areas (Callaway et al. 1994). Once the tracheids are developed, the tree can lose some of the original k_s as the sapwood ages, or they can maintain the k_s . Maintenance of the high k_s across the sapwood, as seen in the WV pine (oldest sapwood ring averaging 69 years), is a different way to provide high conductive capacity, and other factors being equal, suggests that the WV populations are more drought-adapted than the CM populations. This difference is

reversed from what one would expect from climate. However, higher drought adaptation in WV than CM trees would be adaptive if, for example, the CM trees stop their water transport when the seasonal drought arrives, thus effectively becoming dormant during the drought. The WV trees, in contrast, may remain active throughout a longer season, cycling in and out of drought and actually sensing more water stress than the CM trees. Physiological investigations of seasonal and daily photosynthetic activity, stem water potential, and leaf area/sapwood area in the contrasting regions would help clarify these issues, although it already has been shown that ponderosa pine is quite sensitive to water stress, shutting stomata at water potentials around -2.0 MPa (Hubbard et al. 1999). It would also be instructive to sample the WV in both dry and wet sites.

The wood was less vulnerable to embolism at about -3.0 MPa in the WV trees than in the CM trees, which also suggest that the WV trees are more able to withstand drought (because WV trees maintain more of their water transport capacity at a given water potential). The higher latewood proportion in the WV hydraulics samples is unlikely to affect these results, because, at least in Douglas-fir, the shape of these curves is almost entirely influenced by the earlywood, not the latewood (Domec and Gartner 2002b). The importance of the shape of these curves is always subject to question because the bulk water potential (which we assume approximates local water potentials) does not fall into the range of the lower part of the curve (lowest water potentials in Montana were -2.0 MPa, Piñol and Sala 2000). More striking than the difference between the loss of conductivity curves, however, is their similarity in such different habitats. The curves were also similar for the ponderosa pines compared from a hillslope vs. a riparian area (Stout and Sala 1999) and from desert vs. montane sites (Maherali and DeLucia 2000a). In a study comparing xylem cavitation of several Pinaceae in Montana (inland western USA), Piñol and Sala (2000) hy-

pothesized that ponderosa pine xylem would be more resistant to embolism than Douglas-fir xylem because the pine is native to a drier range of habitats than is Douglas-fir. Their comparison of branch wood of co-occurring individuals at one site showed, contrary to expectation, that the pine had significantly less resistance to embolism than the Douglas-fir, and it also had higher k_s . Piñol and Sala (2000) concluded that high k_s , the tight control over stomatal conductance (e.g., their study and Lopushinsky and Klock 1974; Hubbard et al. 1999), and the species' plasticity in leaf area/sapwood area (Callaway et al. 1994) precluded a need to evolve drought-adapted wood. That research is an excellent example of why the study of ecological wood anatomy must be undertaken in the context of the whole plant's physiology: changes in phenology (such as date of bud burst relative to frost events), water availability (from factors such as rooting depth), loss of water (from changes in foliage area or patterns of stomatal conductance), and the need for water storage in the stem can all have significant impacts on the optimal wood structure and sapwood quantities needed.

CONCLUSIONS

This research shows that the wood of ponderosa pine in the Willamette Valley ("valley pine") differs from the wood of the same species in the Cascade Mountains in terms of its wood density, the pattern of radial change of wood density, and its specific conductivity for axial water transport. Given the volume of timber that will be produced in the next decades and given that the wood varies markedly from the Cascade Mountain ("east side") ponderosa pine, it will be important to determine appropriate end uses for this wood. The higher density of the WV wood may make it more suitable for structural uses and may make it more attractive for pulp, and the higher density of its earlywood may make the wood suitable for peeling into veneer.

The unusual difference in radial wood density between the populations (especially the

increasing earlywood density with growth ring from the pith in the Willamette Valley vs. the decreasing earlywood density in the Cascades) provides opportunities for physiological studies on the importance of earlywood properties for water transport. The apparent drought adaptations of the Willamette Valley merit further physiological study to understand how and why those populations have more drought adaptations than do the populations growing in the drier sites, the Cascades.

ACKNOWLEDGMENTS

We wish to thank Crown Pacific, the Willamette Valley Ponderosa Pine Conservation Association, and especially Bob McNitt and Howard Dew for discussion and help in obtaining samples. We appreciate the support of Claire Neema and Brad St. Clair at the project's inception, and the discussions with Randy Johnson throughout the project. The manuscript was improved by comments from Eini Lowell and Michael Wiemann. The research was partially supported by both a special USDA grant to Oregon State University for wood utilization research and by USDA CSREES 96-35103-3832.

REFERENCES

- BARAJAS-MORALES, J. 1987. Wood specific gravity in species from two tropical forests in Mexico. *IAWA Bull.* n.s. 8:143–148.
- BASSMAN, J. H. 1988. Photosynthesis and water relations of ponderosa pine. Pages 45–69 in *Ponderosa pine: The species and its management*; symposium proceedings. Sept. 29–Oct. 1, 1987, Spokane, WA. Washington State University, Pullman, WA.
- BLATNER, K. A., AND R. L. GOVETT. 1988. Ponderosa pine lumber market. Pages 7–9 in *Ponderosa pine: The species and its management*; symposium proceedings. Sept. 29–Oct. 1, 1987, Spokane, WA. Washington State University, Pullman, WA.
- BOOKER, R. E. 1984. Dye-flow apparatus to measure the variation in axial xylem permeability over a stem cross section. *Plant Cell Environ.* 7:623–628.
- , AND J. A. KININMONTH. 1978. Variation in longitudinal permeability of green radiata pine wood. *New Zealand J. For. Sci.* 8:295–308.
- BURDON, R. D., AND C. B. LOW. 1991. Performance of *Pinus ponderosa* and *Pinus jeffreyi* provenances in New Zealand. *Can. J. For. Res.* 21:1401–1414.
- CALLAWAY, M., E. H. DELUCIA, AND W. H. SCHLESINGER. 1994. Biomass allocation of montane and desert ponderosa pine: An analog for response to climate change. *Ecology* 75:1474–1481.
- CARLQUIST, S., AND D. A. HOEKMAN. 1985. Ecological wood anatomy of the woody southern California flora. *IAWA Bull.* n.s. 6:319–347.
- COCHARD, H., P. CRUIZIAT, AND M. T. TYREE. 1992. Use of positive pressure to establish vulnerability curves: Further support for the air-seeding hypothesis and implications for pressure-volume analysis. *Plant Physiol.* 100:205–209.
- COMSTOCK, G. L. 1965. Longitudinal permeability of green eastern hemlock. *Forest Prod. J.* 15:441–449.
- CONKLE, M. T., AND W. B. CRITCHFIELD. 1988. Genetic variation and hybridization of ponderosa pine. Pages 27–43 in *Ponderosa pine: The species and its management*; symposium proceedings. Sept. 29–Oct. 1, 1987, Spokane, WA. Washington State University, Pullman, WA.
- 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.
- , AND ———. 2002a. Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: Inferring the design criteria for Douglas-fir wood structure. *Tree Physiology* 22:91–104.
- , AND ———. 2002b. How do water transport and water storage differ in coniferous earlywood and latewood? *J. Exp. Botany* 53:2369–2379.
- , AND ———. 2003. Relationship between growth rates and xylem hydraulic characteristics in young, mature, and old-growth ponderosa pine trees. *Plant, Cell and Environment* (in press).
- DOWNES, G., C. BEADLE, AND D. WORLEDGE. 1999. Daily stem growth patterns in irrigated *Eucalyptus globulus* and *E. nitens* in relation to climate. *Trees* 14:102–111.
- ECHOLS, R. M. 1972. Patterns of wood density distribution and growth rate in ponderosa pine. Pages H1–H16 in *Symposium on the Effect of Growth Acceleration on the Properties of Wood*. Forest Products Laboratory, Madison, WI.
- , AND M. T. CONKLE. 1971. The influence of plantation and seed source elevation on wood specific gravity of 29-year old ponderosa pines. *Forest Sci.* 17:388–394.
- FOREST PRODUCTS LABORATORY. 1999. Wood handbook: Wood as an engineering material. Gen. Tech. Rep. FPL-GTR-113. USDA, Forest Serv. Forest Prod. Lab. Madison, WI: 463 pp.
- GARTNER, B. L. 1995. Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. Pages 125–149 in B. L. Gartner, ed. *Plant stems: Physiology and functional morphology*. Academic Press, San Diego, CA.
- GOODING, G. D. 1998. Genetic variation and mating system of ponderosa pine in the Willamette Valley of

- Oregon. M.S. thesis, Oregon State University, Corvallis, OR.
- HACKE, U. G., J. S. SPERRY, W. T. POCKMAN, S. D. DAVIS, AND K. A. MCCULLOH. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461.
- HIBBS, D. E., M. V. WILSON, AND A. L. BOWER. 2002. Ponderosa pine of the Willamette Valley, Western Oregon. *Northwest Science* 76:80–84.
- HOWE, J. P. 1968. Influence of irrigation on ponderosa pine. *Forest Prod. J.* 18:84–93.
- HUBBARD R., B. J. BOND, AND M. G. RYAN. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiol.* 19:165–172.
- LARSON, P. R., D. E. KRETSCHMANN, A. I. CLARK, AND J. D. ISEBRANDS. 2001. Formation and properties of juvenile wood in southern pines: A synopsis. Gen. Tech. Rep. FPL-GTR-129. USDA Forest Serv., Forest Prod. Lab. Madison, WI. 42 pp.
- LINHART, Y. 1988. Ecological and evolutionary studies of ponderosa pine in the Rocky Mountains. Pages 77–89 in *Ponderosa pine: The species and its management; symposium proceedings*. Sept. 29–Oct. 1, 1987, Spokane, WA. Washington State University, Pullman, WA.
- LIU, C.J., J. R. OLSON, Y. TIAN, AND Q. SHEN. 1988. Theoretical wood densitometry: I mass attenuation equations and wood density models. *Wood Fiber Sci.* 20:22–34.
- LOPUSHINSKY, W., AND G. O. KLOCK. 1974. Transpiration of conifers seedlings in relation to soil water potential. *Forest Sci.* 20:181–186.
- MAHERALI, H., AND E. H. DELUCIA. 2000a. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiol.* 20: 859.
- , AND ———. 2000b. Interactive effects of elevated CO₂ and temperature on water transport in ponderosa pine. *Am. J. Bot.* 87:243–249.
- MARKSTROM, D. C., AND R. A. HANN. 1972. Seasonal variation in wood permeability and stem moisture content of three Rocky Mountain softwoods. Research Note No. RM-212, USDA Forest Service, Rocky Mountain Forest and Range Experimental Station, CO.
- MARGOLIS, H., R. OREN, D. WHITEHEAD, AND M. R. KAUFMANN. 1995. Leaf area dynamics of conifer forests. Pages 181–223 in W. K. Smith and T. M. Hinckley, eds. *Ecophysiology of coniferous forests*. Academic Press, San Diego, CA.
- MEGRAW, R. A. 1985. Wood quality factors in loblolly pine: The influence of tree age, position in tree, and cultural practice on wood specific gravity, fiber length, and fibril angle. Tappi Press, Atlanta, GA.
- MENCUCINI, M., AND J. GRACE. 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiol.* 15:1–10.
- MYERS, C. A. 1960. Estimating oven-dry weight of pulpwood in standing ponderosa pines. *J. Forestry* 58:889–891.
- NICHOLLS, J. W. P., AND J. P. WRIGHT. 1976. The effect of environmental factors on wood characteristics. 3. The influence of climate and site on young *Pinus radiata* material. *Can. J. For. Res.* 6:113–121.
- OLIVER, W. W., AND R. A. RYKER. 1990. *Pinus ponderosa* Dougl. ex Laws.: Ponderosa pine. Pages 413–424 in R. M. Burns and B. H. Honkala, Technical Coordinators, *Silvics of North America*, vol. 1, Conifers. Agriculture Handbook 654, USDA Forest Service, Washington, D.C.
- PARKER, J. 1969. Further studies of drought resistance in woody plants. *Bot. Rev.* 35:317–371.
- PIÑOL, J., AND A. SALA. 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. *Functional Ecol.* 14:538–545.
- POTHIER, D., H. A. MARGOLIS, J. POLIQUIN, AND R. H. WARING. 1989. Relation between the permeability and the anatomy of jack pine sapwood with stand development. *Can. J. For. Res.* 19:1564–1570.
- PRUYN, M. L., B. L. GARTNER, AND M. E. HARMON. 2002. Respiratory potential in sapwood of old versus young ponderosa pine trees in the Pacific Northwest. *Tree Physiol.* 22:105–116.
- RYAN, M. G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. *Can. J. For. Res.* 20:48–57.
- SAS INSTITUTE INC. 1997. SAS software release 6.12. SAS Institute, Cary, NC.
- SIAU, J. F. 1984. Transport processes in wood. Springer-Verlag, Berlin, Germany. 245 pp.
- SILEN, R. R. 2002. Ponderosa pine regional races study—1926. Pages 8–10 in *Willamette Valley Ponderosa Pine Conservation Association, 2001 Annual Report*.
- SORENSEN, F. C., AND R. S. MILES. 1982. Inbreeding depression in height, height growth, and survival of Douglas-fir, ponderosa pine, and noble fir to 10 years of age. *Forest Sci.* 28:283–292.
- SPARKS, J. P., AND R. A. BLACK. 1999. Regulation of water loss in populations of *Populus trichocarpa*: The role of stomatal control in preventing xylem cavitation. *Tree Physiol.* 19:453–459.
- SPERRY, J. S., AND M. T. TYREE. 1988. Mechanism of water-stress induced xylem embolism. *Plant Physiol.* 88: 581–587.
- , AND N. Z. SALIENDRA. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant Cell Environ.* 17:1233–1241.
- , M. T. TYREE, AND J. R. DONNELLY. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ.* 11:35–40.
- SPICER, R., AND B. L. GARTNER. 2001. The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. *Trees* 15:222–229.

- SQUILLACE, A. E., AND R. R. SILEN. 1962. Racial variation in ponderosa pine. For. Sci. Monogr. No. 2. 27 pp.
- STAMM, A. J. 1970. Variations of maximum tracheid and pit pore dimensions from pith to bark for ponderosa pine and redwood before and after drying determined by liquid displacement. Wood Sci. Technol. 4:81–96.
- STOUT, D. L., AND A. SALA. 1999. Cavitation and xylem vulnerability in *Pinus ponderosa* and *Pseudotsuga menziesii* along a soil moisture gradient. Abstracts of the 84th Annual Meeting of the Ecological Society of America, Aug. 8–12, 1999, Spokane, WA.
- STRATTON, L., G. GOLDSTEIN, AND F. C. MEINZER. 2000. Stem water storage capacity and efficiency of water transport: Their functional significance in a Hawaiian dry forest. Plant Cell Environ. 23:99–106.
- TAYLOR, G. H., AND C. HANNAN. 1999. The climate of Oregon: From rain forest to desert. Oregon State University Press, Corvallis, OR. 211 pp.
- TYREE, M. T., S. D. DAVIS, AND H. COCHARD. 1994. Biophysical perspectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? IAWA J. 15:335–360.
- VAREM-SANDERS, T. M. L., AND I. D. CAMPBELL. 1996. DendroScan: A tree-ring width and density measurement system. Natural Resource Can., Canadian Forest Service, North. For. Cent., Edmonton, Alberta.
- VOORHIES, G. 1969. Specific gravity studies of young-growth southwestern ponderosa pine. Forest Prod. J. 19(6):45–46.
- WARING, R. H., P. E. SCHROEDER, AND R. OREN. 1982. Application of the pipe model theory to predict canopy leaf area. Can. J. For. Res. 12:556–560.
- ZOBEL, B. J., AND J. P. VAN BUIJTENEN. 1989. Wood variation: Its causes and control. Springer-Verlag, Berlin.
- , AND J. R. SPRAGUE. 1998. Juvenile wood in forest trees. Springer-Verlag, Berlin.