

DO DOUGLAS-FIR BRANCHES AND ROOTS HAVE JUVENILE WOOD?

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ABSTRACT

We sampled boles, branches, and roots of four Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) trees to learn a) whether branches and roots have a zone of juvenile wood, defined as a zone with progressive changes in wood density and/or tracheid length from the pith outward at successively greater cambial ages, and if so, b) whether the radial patterns in branches and roots are similar to those in boles. Samples came from the following positions: bole, 30 cm aboveground; branch, 30 cm outward on the lowest live branch, and root, 1–3 m from the bole. Average sample cambial ages were bole, 60 years; branch, 30 years; and root, 48 years. Roots and branches had higher density wood than did the bole at the positions studied, and roots had the longest tracheids followed by the bole and then the branches. All three positions exhibited juvenile wood but with different radial patterns. All positions had their highest density near the pith, which was followed by a steep decline in the boles and a more gradual decline in the roots and branches. Boles and roots, but not branches, then showed an increase in density after this decline. Boles and branches had short tracheids near the pith followed by a gradual increase to an asymptotic value. In contrast, tracheid length in roots was relatively constant from pith to bark, although there was a dip of about 20% from about cambial ages 14 to 24. This study shows that the vascular cambium of this species is not constrained to produce one sole radial pattern of wood properties as it matures. The presence of different radial patterns in boles, branches, and roots supports the hypothesis that juvenile wood in the bole is an adaptive feature rather than an unavoidable developmental consequence. Further work should investigate more fully the different physiological or mechanical roles of the various wood types within the context of the position in the tree at which they occur.

Keywords: Density, juvenile wood, Douglas-fir, tracheid length, specific gravity, root, branch.

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INTRODUCTION

The presence of juvenile wood is a universal feature of the bole of softwood trees (reviewed in Zobel and Sprague 1998). Juvenile wood is “the zone of wood extending outward from the pith where wood characteristics undergo rapid and progressive changes in successively older growth rings” (Larson et al. 2001). Juvenile wood is present from the base to the tip of the tree, although with somewhat varying characteristics by height (Groom et al. 2002; Mott et al. 2002; Burdon et al. 2004; Xu and Walker 2004). In this paper, we asked whether roots and branches have the same radial patterns of tracheid length and wood density as does the bole in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) trees. We refer to the roots, branches, and boles as ‘positions’ in this paper. By knowing whether the vascular cambium produces a specific radial pattern of wood types, we can infer more about the role of juvenile wood in trees. If we find that branches (away from the compression wood) and/or roots have different radial patterns of tracheid length and wood density than does the bole, then we would infer that juvenile and mature wood have position-specific roles in the tree. Once scientists understand the functional roles of different wood types for living trees, then tree breeders can safely breed for traits that improve wood quality without danger of inadvertently altering traits that are important for tree survival.

For most structural applications, juvenile wood is inferior to mature wood, and given that its incidence is increasing due to economic pressures to harvest trees at younger ages, there is much interest in improving the juvenile wood’s end-use quality. Not only does juvenile wood have different anatomical and chemical characteristics than does mature wood (Senft et al. 1985), but the rate of change of characteristics from one growth ring to the next in juvenile wood is higher than the rate of change in mature wood (Abdel-Gadir and Kraemer 1993a, b). The properties of juvenile wood and the size of both the bole and the juvenile core affect the value of products that are recovered. For example, a

piece of lumber that is predominantly mature wood may still have significant warp if one edge is made up of juvenile wood.

Comparisons of xylem anatomy from branches, roots, and boles are rare in the literature, and many of the studies do not control for cambial age in comparing positions and species. The earliest comprehensive treatment (Fegel 1941) did not separate results by species. The most robust trends in conifers are that branches are usually denser than the bole (Fegel 1941; Howard 1973; Domec and Gartner 2002; Dunham et al. 2007) and that branches have shorter tracheids than the bole (Fegel 1941; Patel et al. 1971; Manwiller 1972; Dunham et al. 2007). The root trends are not as universal: root may be less dense than the bole (Fegel 1941; Howard 1973) or similar if compared at similar cambial age (Dunham et al. 2007). Root wood may have shorter or longer tracheids than the bole (Fegel 1941; Dunham et al. 2007). Not surprisingly, the values of density and tracheid length vary from place to place within a given plant part (root, bole, or branch) (Dunham et al. 2007), so more precise knowledge of the sampling position will help clarify the trends for trees of a given species and environment.

In Douglas-fir boles, juvenile wood typically has high density near the pith, it declines for the next several growth rings, and then it rises to an asymptotic value (e.g., Megraw 1986; Abdel-Gadir and Kraemer 1993b; Fabris 2000; Gartner et al. 2002). Latewood proportion often has a similar pattern, a high value rapidly declining and then a gradual increase to an asymptote (Megraw 1986; Abdel-Gadir and Kraemer 1993a; Gartner et al. 2002), although Fabris (2000) found a gradual increase in latewood proportion with no sign of leveling off in 33-year-old breast-height disks. Tracheids in Douglas-fir boles are short near the pith, and increase with cambial age to an asymptote (e.g., Megraw 1986; Hamm 1989). This radial pattern of tracheid length is extremely common in boles of woody plants, although the magnitudes of the initial and final tracheid lengths vary by species (reviewed in Zobel and van Buijtenen 1989).

There are few reports on radial patterns of

density or tracheid lengths in root or branch wood in conifers. In branches of *Pinus sylvestris*, Sanio (1872) reported an increase in tracheid size (length and diameter) up to an asymptote after which length was relatively constant. He reported a more complex pattern in roots: long tracheids at 8–13 years, declining to about age 30 and then increasing before reaching an asymptote. A similar pattern was implied in a low sample-size study of root wood in *Pinus radiata* and *Pinus nigra* (Matsumura and Butterfield 2001): tracheid length was high within the first centimeter of the pith, and then in the one *P. radiata* sample and in two of the three *P. nigra* samples, tracheid length declined and then rose again. The following anecdotal report by Bannan (1941) is consistent with having long tracheids near the pith that then decline in length: he wrote that in lateral roots of some of the samples he studied of eight species of conifers, the widest tracheids and the lowest late-wood proportions occurred in the growth rings closest to the pith. In contrast, Patel (1971) found no radial variation in tracheid length in roots of *Pinus radiata*, whereas the stem showed the typically seen radial pattern of increasing tracheid length.

We adopted the null hypothesis that roots and branches will have similar radial patterns to those observed in the bole for basic wood density and tracheid length. Moreover, we expected that the branches would have higher wood density and shorter tracheids than the bole, and that the roots would have lower wood density and longer tracheids than the bole.

METHODS

Plant materials and study site

We studied wood from four Douglas-fir trees in the central Coast Range of Oregon near Edyville, Oregon. The stand is in private ownership of Dr. Michael Newton, a silviculture professor at Oregon State University, who kept detailed records on the plantation. It originated from natural regeneration on a pasture site that had been abandoned in 1940, 64 years before the

study. The trees grew slowly at first, but then their growth accelerated due to management that aimed to give the trees much space. The site was thinned 45, 28, and 17 years before this study was undertaken (in 1959, 1976, and 1987, respectively). The thinning 45 years before the study left only the smallest trees (diameter <20 cm). The thinning 28 years before the study left a relatively open stand of about 140 trees/ha and with basal area of about 45 m²/ha. At the time of the study, trees in the stand were large for their age, averaging 51 m tall and 76 cm diameter at breast height (Mike Newton, pers. communication).

The stand was thinned again in July 2004, when we sampled four trees from the stand. The choice to sample only four trees was based on our judgment that four trees is sufficient to assess the general patterns in branches and roots, given the stability of patterns in the bole (with the same reasoning used by Matsumura and Butterfield in their 2001 study on root radial patterns); and the knowledge that it was already time-consuming to conduct the 1100 macerations and 168,000 tracheid measurements for the adopted sample size of four trees. We chose trees on the basis of whether they had an acceptable root to sample within 1 to 3 m of the bole. Roots were not acceptable if within that zone they were inaccessible (e.g., covered with slash or growing at a steep downward angle); were forked; had rapid taper, indicating a large mechanical role (Wilson 1975); were exposed to sunlight; or showed damage from being in former skid trails. After an acceptable root was found, we took two adjacent disks from that root, two disks from the stump (about 30 cm above ground), and two disks from the lowest live branch starting at 30 cm distance from the bole. Branch and root disks were 4 cm thick and bole disks were 7 cm thick.

While samples were still fresh, we cut a radial strip from each of the two disks from each position, end-matching the strips. One radial strip was used for X-ray densitometry and the other was used for macerations for tracheid length determination. The radial strips were chosen to avoid knots, compression wood zones, and other

irregularities in grain to the extent possible. Lengths of the strips are in Table 1. In the branches, samples were taken from the lateral wood (mid-way between the compression wood and the opposite wood). Samples were then air-dried.

X-ray densitometry

The samples for X-ray densitometry were initially cut to 5 mm × 5 mm (radial and longitudinal directions, respectively). They were then extracted by soaking in acetone for 30 hours at room temperature, and air-dried in a hood (Weyerhaeuser Technology Center protocol, Greg Leaf, pers. communication). Samples were then re-cut to 0.98 mm in the longitudinal direction and X-rayed at Weyerhaeuser Technology Center (Federal Way, WA) using their direct-scanning X-ray densitometer (QRTS-01X Tree Ring Analyzer and Scanner, Quintek Measurement Systems, Inc., Knoxville, TN) with a beam size of 0.025 mm by 0.500 mm (radial and tangential directions, respectively) and a step size of 0.02 mm.

For the bole, the data from the X-ray were earlywood width, latewood width, growth ring width, latewood proportion, and basic density (g/cm^3 , oven-dry mass/green volume) of earlywood, latewood, and the total growth ring for each growth ring. For branch and root, which had quite narrow rings relative to the step size of the X-ray, the data collected were growth ring width and basic density of the growth ring. Several growth rings had compression wood, so we replaced their data with the mean of the rings before and after the compression wood. Because the growth rings in some of the root and branch samples were very narrow, we sanded the X-rayed samples, measured ring widths, and adjusted ring numbers for the X-ray data accordingly. If an extra ring was found, we assigned it the density of the average of the five rings before and five rings after it in cambial age. For this process ring widths were measured using the Tree Ring Measuring Device, which is a black and white video camera (Pulnix TM-745) and monitor attached to a dissecting microscope

(Nikon SMZ-2T). The sample is located on a moving stage that has a linear encoder for distance measurements (Acu-Rite Incorporated, Jamestown, NY). Adjusted numbers of growth rings for each sample are shown in Table 1; samples averaged 60, 30, and 48 years old for bole, branch, and root, respectively.

Maceration

The radial strips for tracheid length determination were separated into chunks (hereafter called samples) using a chisel, hammer, and razor blade, starting at the pith. For the bole, all the samples included two growth rings. For the branches and roots, if there were >2 growth rings/mm, all of the growth rings in that millimeter were taken as one sample; otherwise, samples included two growth rings. Following standard procedures, these samples were further divided to produce matchstick-sized pieces that were placed in labeled test tubes, one for each sample. Samples therefore included both earlywood and latewood in the proportion in which they were present in the growth rings.

For maceration, samples were first soaked in distilled water for at least 24 hours, and then the water was poured off. Samples were submerged in 6% sodium chlorite, and then test tubes were heated in a water bath to 85°C. When the water bath reached this temperature, we added 6–7 drops of acetic acid to each test tube then left the samples in the heated water bath for 4–5 hours further. The macerating solution was then poured off, samples were rinsed and then submerged in a 1% aqueous solution of safranin-O for at least 12 hours, rinsed again, and spread on glass slides.

TABLE 1. *Radius length and number of growth rings detected in the bole, branch, and root samples examined.*

	X-rayed radius (cm)			Growth rings detected (no.)		
	Bole	Branch	Root	Bole	Branch	Root
Tree 1	38.0	3.5	5.9	58	31	43
Tree 2	35.8	2.3	7.8	52	26	41
Tree 3	40.7	3.8	3.7	64	31	49
Tree 4	40.6	2.9	7.4	65	30	60

Three slides were made from each sample. For each slide we measured the lengths of 50 tracheids using an image analysis system consisting of a digital camera (Photometrics CoolSNAP digital camera, Tucson, Arizona), the dissecting microscope, RS Image v.1.9.2 software (Roper Scientific) to capture images, and Scion Image Beta 4.0.2 (www.scioncorp.com) software to analyze images. We took care to avoid measuring broken or cut tracheids.

Data analysis

Both X-ray and maceration data were compiled as a function of cambial age (growth ring number from the pith) for each of the positions. We graphed the data (total ring density, tracheid length, and latewood proportion for the boles) as a function of cambial age for each tree individually for inspection, and then averaged the values for all four trees with no data smoothing. We cut off the curves where there were data for fewer than three individuals. Graphs were inspected visually.

RESULTS

The shape of the curves of density vs. cambial age differed among the three positions (Fig. 1A). Root and bole density were high at cambial age 1, declined, and then increased gradually toward a value at which they appeared to be leveling off, but the rates of change were different in roots than boles. Like roots and boles, branches had high density at cambial age 1, but then branch density declined and did not later increase. Density declined most steeply in boles, less steeply in roots, and the least steeply in the branches. In boles the lowest density was at cambial age 5 ($0.35 \pm 0.01 \text{ g/cm}^3$, mean \pm s.e., $n=4$). The mean value increased relatively steadily from cambial age 5 to about cambial age 40 and then appeared to level off, with a density of $0.42 \pm 0.01 \text{ g/cm}^3$ at cambial age 58.

The basic density of the wood was either higher in branches than roots, or similar in branches and roots, depending on the cambial age range compared (Fig. 1A). Branches and

roots had higher wood density than did bole at almost every cambial age sampled (Fig. 1A). At cambial age 21, the bole had 85% the density of the branch and 79% the density of the root.

Latewood percentage in the bole increased gradually from cambial age 3 ($24 \pm 2\%$) to cambial age 58 ($38 \pm 4\%$) (Fig. 1B). The high latewood percentage values in the first two growth rings probably are not meaningful because at the youngest cambial ages the anatomy does not always lend itself to defining earlywood and latewood, even with microscopy.

The shapes of the curves of tracheid length vs. cambial age were similar for boles and branches, with a gradual increase toward a value at which they leveled off (Fig. 1C). In contrast, the curve of tracheid length vs. cambial age had a very different shape for roots (Fig. 1C). Root tracheids were long near the pith as well as near the bark, and showed a dip of about 20% in the mid-range of the cambial ages studied (about ages 10–26). The plot of the individual tree means (Fig. 2) showed two trends that were obscured in the common mean plot (Fig. 1C). First, the mid-range dip in tracheid length was less evident in Fig. 2 than Fig. 1C even though the data from which they were derived are the same. Secondly, the trend of long tracheids near the pith was present in all of these samples, and was not driven by an outlier.

Mean tracheid lengths were greatest in the root followed by the bole and then the branch. Tracheids in the root were almost two times longer than tracheids in the branch at cambial age 21. Mean tracheid length in roots was 4.2, 3.8, and 3.9 mm at cambial ages 1, 32, and 43, respectively. Mean tracheid length in boles was 1.6, 3.3, and 3.3 mm at cambial ages 1, 32, and 58, respectively. Mean tracheid length in branches was 1.2 and 2.1 mm, respectively at cambial ages 1 and 32, respectively.

DISCUSSION

Wood characteristics underwent rapid and progressive changes at successively greater cambial ages for wood density (bole, branches, and roots) and/or tracheid length (bole and branch).

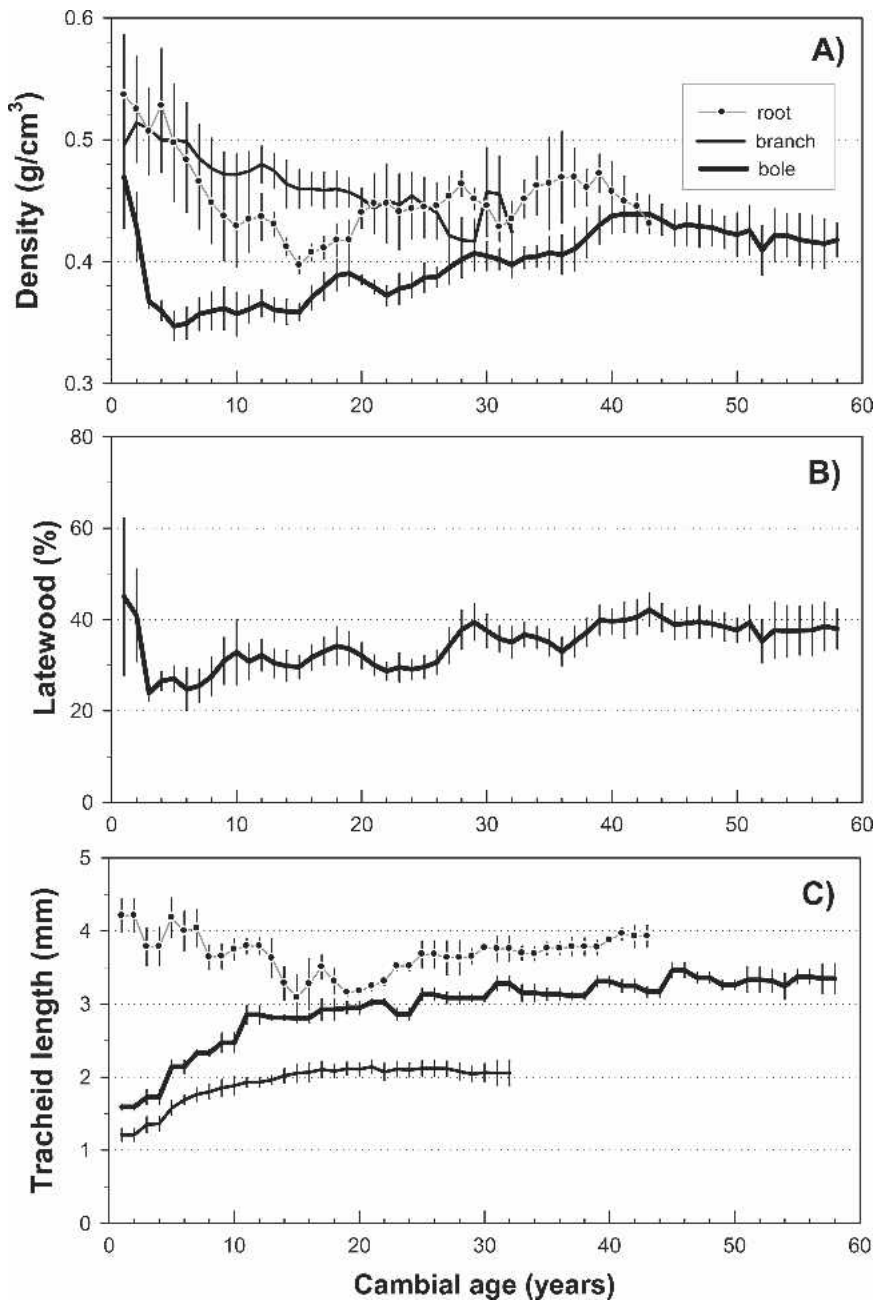


FIG. 1. a) Total ring basic density, b) latewood proportion, and c) tracheid length of bole, branch, and root as a function of cambial age for coastal Douglas-fir trees (mean \pm s.e., $n=4$).

On the basis of this small sample size, one can define a juvenile wood region in each position (bole, branch, root), but the basis of the definition is position-specific.

The radial pattern in boles is very similar to what has already been reported. The first several rings had high density and then the density declined and then rose again before leveling off.

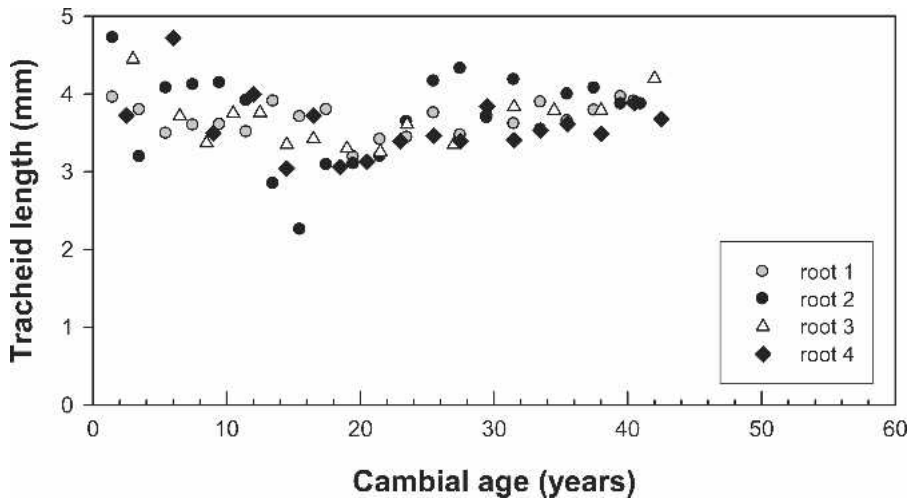


FIG. 2. Mean tracheid length for roots as a function of cambial age for each of the four Douglas-fir trees sampled. Each point represents the mean of 150 tracheids.

This pattern is the check-shaped pattern often reported for Douglas-fir (e.g., Megraw 1986; Abdel-Gadir and Krahmer 1993b), although often there are some individuals that lack the initial high density, instead exhibiting low density near the pith that increases and levels off (Fabris 2000). The curve for bole density vs. cambial age in the current study was similar to that reported by Megraw (1986), although his sample had higher absolute values. He sampled 45 trees at breast height, and reported the lowest density at cambial age 6 (0.37 g/cm^3). At cambial age 60, the mean density value was 0.46 g/cm^3 . The radial increase in tracheid length in boles also follows the patterns already reported for Douglas-fir. Megraw (1986) sampled tracheid length of 55-year-old Douglas-fir trees at stump height (about 60 cm) from Washington ($n = 32$), and found mean tracheid length of 1.6 and 3.2 mm at cambial ages 3 and 40, respectively. These values are nearly identical to those in the current study. Lastly, the radial pattern of latewood proportion increases gradually in the current study. In many studies, the increase is more pronounced but follows the same general shape. Megraw (1986) shows a minimum value of about 22% latewood at cambial age 5 that fluctuated around the value of 40% from cambial

age 40 to 60, again very similar to the 38% seen in the current study at cambial age 58.

In branches, wood density appeared to decline from the pith to the bark, possibly to an asymptote, although more data are needed to pursue this question. The radial patterns of tracheid length in branches were similar to those in the bole: low values near the pith with a gradual increase to an asymptote.

In roots, the radial pattern of wood density started high, declined to about 80% of the initial value and then climbed again to about the initial value. This finding of long tracheids near the pith with little radial variation in Douglas-fir roots is quite interesting because it contrasts to the pattern of increasing conduit dimensions from the pith to an asymptote that has been reported for wood of hundreds of other species of hardwoods and softwoods, with very few exceptions: root wood of *Pinus radiata* (Patel 1971), stem wood of two of five mangrove species investigated (Sun and Suzuki 2001), and some rosette-forming species (i.e., Carlquist 1962), and species with storeyed cambia. The data in the current study are also consistent in curve shape to Sanio's report on *Pinus sylvestris* (1872) in which root tracheid length was high, decreased, and then increased again.

It is possible that roots and branches did not produce rings every year in the xylem that we sampled; that is, they may have had 'missing rings.' In western Washington, Douglas-fir trees ranging in age from 35 to 70 years had 8 to 10 missing rings in their lower branches, with a maximum of 15 missing rings (Reukema 1959). Wilson (1964) and Fayle (1968) reported that growth rings are often non-continuous around the root circumference, and thus they could be missing on any given radius. If true age were used rather than age determined by number of growth rings, the root and branch curves would be stretched along the X-axis, but their basic shapes would not change substantially.

Undoubtedly the relative densities of the bole, branch, and root are related to where in the tree the wood was sampled. For example, Dunham et al. (2007) sampled 54-year-old Douglas-fir trees ($n = 32$), comparing outer wood properties from seven positions on the tree. Outer wood of the bole had average densities of 0.48, 0.41, and 0.40 g/cm^3 for 52-, 25-, and 5-year-old wood, respectively. This pattern reflects the typical juvenile wood pattern of lower density in the wood with lower cambial age. The root samples had densities of 0.44 and 0.39 g/cm^3 for 44- and 22-year-old wood, showing the juvenile wood pattern again, and also displaying that the 44-year-old root wood was denser than 25-year-old bole wood. The branch samples had densities of 0.47 and 0.49 g/cm^3 for 20- and 7-year-old branch wood, not showing a recapitulation of the juvenile wood pattern, but showing that this relatively young branch wood was similar in density to the oldest bole wood, and was denser than the root wood. Actual values undoubtedly also depend on the amount of mechanical support that the roots, branches, and bole are called upon to provide, which will depend on the soil structure (for its anchorage ability and for the geometry it permits the root system to have), soil moisture content and atmospheric vapor pressure deficit (for mechanical properties of the soil and for the amount of tension in the water column that the xylem will experience), the stand structure (for the amount of wind and light that enter), and other environmental factors (such as wind expo-

sure and mass of snow the plant may need to support).

The relative lengths of tracheids in different positions were as hypothesized, with branches having shorter tracheids than the bole, and roots having longer tracheids than the bole. The physiological or developmental drivers for these patterns are unknown, but they are consistent with Murray's Law, which predicts that the most efficient transport systems (those systems that transport the most water for a given driving force and a given mass invested in conduits) have fewer but more conductive conduits in their boles than in their more distal parts (McCulloh et al. 2003, 2004; McCulloh and Sperry 2005).

The current study does not support the hypothesis that the cambium is constrained to produce short cells when it is young (immature), and that after a certain time period of radial growth it produces 'better' wood (i.e., more efficient at transporting water and having higher density and lower microfibril angle for increased strength parallel to the grain). The existence of long cells near the pith in roots suggests that the cambium is capable of producing long cells from the very first year. Moreover, the inverse linkage of microfibril angle and cell length does not hold in all situations, such as in the root wood of two pine species (Matsumura and Butterfield 2001). These authors also showed that the radial decline in microfibril angle occurred at much lower cambial age in roots than in the boles of the two pine species studied.

The fact that Douglas-fir trees produce wood of different characteristics in all three positions implies that the positions have different physiological or mechanical roles, and that these roles have resulted from natural selection. It would be quite useful to focus on the bole, and make quantitative models to evaluate the potential importance of these radial changes for both the hydraulics and the mechanics of juvenile and mature wood. These models need to consider not only whether a feature is of adaptive value where it is found, but why the radial change is important, as well. For example, if it is of adaptive value to have long, wide, highly conductive tracheids in mature wood, why does the tree not

produce long, wide, highly conductive tracheids in the juvenile wood, as well? The results for some roots and for some mangroves show that the cambium is capable of producing relatively uniform products even when young.

A more thorough understanding of why the cambium produces different wood types in different species, positions, and developmental stages will permit new thinking in silviculture and breeding. With such understanding, we will be more able to predict how wood quality will be affected by silviculture regimes, and we will be able to better target important traits to include in breeding programs with the aim of increasing the efficiency at growing high volumes of high quality wood.

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