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The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood

Received: 2 October 2000 / Accepted: 5 February 2001 / Published online: 15 March 2001
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Abstract Specific conductivity (k_s , $\text{m}^2\text{s}^{-1}\text{MPa}^{-1}$) describes the permeability of xylem and is determined by all aspects of xylem anatomy that create resistance to the flow of water. Here we test the hypothesis that k_s is a function of radial and vertical position within the stem, rather than solely a function of cambial age (ring number from the pith), by measuring k_s on samples excised from 35-year-old Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] trees at six heights and two or three radial positions. Sapwood k_s decreased from the cambium to the heartwood boundary, and the difference between outer and inner sapwood increased with height in the tree. Beneath the live crown, inner sapwood had 80–90% the k_s of outer sapwood, but only 55% just 10 m higher in the stem (about 10 nodes down from the tree top). Outer sapwood k_s peaked near the base of the crown and declined toward both the base and top of the stem. These patterns can be explained by two superimposed effects: the effect of cambial age on the dimensions of tracheids as they are produced, and the effect of xylem aging, which may include accumulation of emboli and aspiration of bordered pits. Tracheid lumen diameter and earlywood and latewood density and width, all factors known to vary with cambial age, were measured on different trees of the same age and from the same stand. Lumen diameter increased with cambial age, whereas the proportion of latewood and growth ring density increased after an initial decrease in the first 5 years. Our results suggest that the effect of cambial age on xylem anatomy is not sufficient to explain variation in k_s . Instead, physical position (both vertical and radial) in the

stem and cambial age must be considered as determinants of conductivity.

Keywords Cambial age · Specific conductivity · Wood anatomy · Wood density · Juvenile wood

Introduction

The anatomical structure and composition of xylem within a tree stem is spatially heterogeneous, and as a result, the physical and mechanical properties of wood vary with position in a stem (Gartner 1995). The ability of xylem to conduct water is critical to the overall function of a woody plant, both for the delivery of nutrients, and because it is related directly to carbohydrate assimilation through stomatal control. Sap flux density varies spatially (and of course, temporally) within stems, most often with flux density peaking in the outermost growth rings and declining toward the heartwood boundary (Phillips et al 1996; Zang et al. 1996; Schäfer et al. 2000; Wullschleger and King 2000). Studies with fine resolution have shown that in some cases sap flux density increases inward from the cambium and peaks in the first few growth rings, followed by a gradual decline toward the heartwood boundary (Cohen et al. 1985; Čermák et al. 1992; Granier et al. 1994, 2000). This latter decline may be more abrupt in ring-porous hardwoods (Čermák et al. 1992). The process by which sapwood ceases to function in water transport is poorly understood.

Sap flux density at a particular position in the stem is a function of sapwood conductivity and the leaf area (and corresponding transpiration rates) that is connected hydraulically to sapwood in that region. Transpiration rates are in turn a function of soil water availability, evaporative demand within the crown, and the ratio of leaf area to sapwood area, all of which determine the local water potential gradient. The degree to which old sapwood is connected to actively transpiring foliage, relative to new sapwood in the outermost growth rings, has received very little attention. In contrast, many studies

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report within-stem patterns of conductivity, but they differ in their methods and do not always agree on general trends. Comstock (1965) first reported a radial decrease in axial conductivity toward the heartwood boundary, but an increase with tree height. Others have reported no clear radial differences in conductivity but an increase with tree height (Booker and Kininmonth 1978). Still others report a decrease in conductivity toward the heartwood boundary at a single height (Markstrom and Hann 1972; Booker 1984; Ellmore and Ewers 1986), and a general decrease with tree height within the crown (Whitehead et al. 1984). Finally, Sellin (1993) reports a decline in conductivity toward both the tip and base of stem and branch axes. Disagreement in the literature is not surprising given that different species were studied, and that in many cases the water content of samples during measurements differed from the water content in the tree (Booker and Kininmonth 1978; Booker 1984; Pothier et al. 1989a, b). Sampling techniques also differed in the amount of damage caused to samples and their ability to accommodate spiral grain.

The hydraulic (or specific) conductivity of sapwood is determined by xylem anatomy. Although radial variation in xylem structure is well characterized, it results from two distinct processes that are rarely considered separately: ‘cambial maturation’ and ‘sapwood aging’. New xylem cells are produced by divisions in cambial initials, the meristematic cells forming a thin (one-cell-thick) layer between the xylem and phloem. Cambial maturation describes a developmental process that results in a change in the dimensions of cambial initials over time, which in turn affects the dimensions of xylem cells produced by the cambium (e.g., longer initials produce longer tracheids in conifers). Rapid change in the cambium occurs for the first 5–25 years, depending on the species, and produces xylem referred to as ‘juvenile wood’. In contrast, xylem produced by a mature cambium (‘mature wood’) is relatively uniform in anatomical properties (Panshin and de Zeeuw 1980; Senft et al. 1985; Zobel and van Buijtenen 1989; Cown 1992). In conifers, mature wood is composed typically of longer cells with thicker walls and larger lumens, and a greater proportion of latewood relative to wood from a young cambium (Erickson and Harrison 1974; Panshin and de Zeeuw 1980; Abdel-Gadir 1993; Lindström 1997). Cambial maturation is also affected by height within the tree (Oleson 1978; Panshin and de Zeeuw 1980; Fabris 2000). Separate from the process of cambial maturation is ‘sapwood aging’, which may include changes in relative water content due to accumulation of emboli (Chalk and Bigg 1956; Sellin 1991; Sperry et al. 1991; Shupe et al. 1995), blockage of vessels by tyloses (Bamber and Fukazawa 1985), aspiration and incrustation of bordered pits (Krahmer and Cote 1963; Panshin and de Zeeuw 1980), and loss of integrity or flexibility of pit membranes (Sperry et al. 1991). These changes result in the reduction of functional (water-conducting) sapwood area on a fine scale.

Here we test the hypothesis that specific conductivity (k_s) is a function of both radial and vertical position

within the stem, rather than solely a function of cambial age (ring number from the pith), in 35-year-old Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] trees. Using a new method, we measure k_s on samples excised from different heights and radial positions within the stem. We then compare within-stem patterns of k_s with aspects of xylem anatomy known to be a function of cambial age. Our results should improve our understanding of sapwood function and how aging affects the flow of water through woody stems.

Materials and methods

Specific conductivity

Plant material

Six approximately 35-year-old Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] trees were sampled from each of two adjacent stands in a research plantation on the H.J. Andrews Experimental Forest in the Blue River Ranger District, Willamette National Forest (44°15'N, 122°10'W), Oregon, USA. The plantation was established in 1963 with 2–0 seedlings following clear-cutting and slash burning. Stands within the plantation were then thinned to different densities in 1981 (Velazquez-Martinez et al. 1992). In July 1995, three randomly selected trees were harvested from each of two stands, one moderately thinned (about 600 trees/ha in 1981) and one unthinned (about 3,460 trees/ha in 1981). In June 1997, three more trees were harvested from each stand for a total of 12 trees.

Six heights were sampled in each tree by removing a 10-cm-thick disk from near the base (0.3 m aboveground), at breast height (1.3 m aboveground), and from the center of each internode (the region between nodes, where each node is a branch whorl) 5, 10, 15 and 20 nodes from the top of the tree. Trees were harvested early in the morning to minimize tension in the xylem and disks were placed in plastic bags with damp towels for transport to the laboratory. Total tree height, diameter at breast height, and heights to each disk and to the base of live crown were recorded. Tree characteristics are summarized in Table 1.

Sample preparation

Alizarine-red dye (Kutscha and Sachs 1962) was used to mark the heartwood/sapwood boundary on fresh disks along two perpendicular diameters, along which the thickness and number of rings of sapwood were recorded. Two samples for k_s were outlined in pencil on each disk, one from the innermost sapwood (adjacent to, but not including, the heartwood/sapwood boundary), and one from the outermost sapwood (adjacent to, but not including, the cambium and current year's growth ring, if present). For the breast height disk only, a third sample was drawn midway between the inner and outer sapwood positions. All samples were drawn to be about 1.5 cm² in cross-section, have true radial surfaces (in the

Table 1 Tree height, diameter at breast height (1.3 m aboveground), and location of base of live crown for Douglas-fir trees ($n=12$)

Characteristic	Mean ± SE
Tree height (m)	21.1±0.6
dbh (cm)	21.8±0.6
Base of live crown (m)	8.1±1.1
Base of live crown (nodes from top)	16±1

Table 2 Vertical and radial sample locations and total cross-sectional sapwood area (mean \pm SE, $n=12$)

Internode from top	Height aboveground (m)	Sapwood area (cm ²)	Mean growth ring from pith	
			Inner sapwood	Outer sapwood
5	17.2 \pm 0.7	25 \pm 3		4.0 \pm 0.2
10	12.9 \pm 0.6	81 \pm 6	6.0 \pm 0.2	9.3 \pm 0.2
15	8.5 \pm 0.5	122 \pm 9	9.5 \pm 0.4	13.9 \pm 0.3
20	4.1 \pm 0.4	155 \pm 12	13.2 \pm 0.3	18.8 \pm 0.2
Breast height	1.3	168 \pm 13	16.3 \pm 0.6	22.7 \pm 0.8
Base	0.3	201 \pm 18	17.0 \pm 0.5	25.0 \pm 0.4

plane of the rays), and to include complete growth rings in the radial direction. The number of rings per sample ranged from three to five, depending on position in the tree. Compression wood and other abnormalities were avoided. Where a light-colored ring (the 'transition zone') was present adjacent to the heartwood, it was not included in the inner sapwood sample. Sample locations and growth ring composition are shown in Table 2.

Samples were first sawn from disks with a small bandsaw, and then radial and tangential surfaces were obtained with chisels while keeping the sample wet with water. About 2 cm was sawn off each axial end leaving a sample about 6 cm long. The ends (cross-sectional surfaces) were cut with a razor blade and samples were stored in water until measured for k_s . Repeated measures on several samples indicated that k_s was not affected by the amount of time a sample was stored in water, at least for up to 1 week. Although soaking in water is likely to have increased the water content of the outermost tracheids (those cut open in preparation), there was no evidence that it increased the water content of the entire sample. Samples run continuously for up to 3 h also showed no increase in flow rate. This allowed samples to be run at their 'native' state of embolism. Typically, samples were run within 24 h of excision from the disk.

Conductivity measurements

Specific conductivity (k_s) describes the permeability of a sample and is defined by Darcy's law as:

$$k_s = \frac{Ql}{A_s \Delta P}, \quad (1)$$

where k_s is in m²s⁻¹MPa⁻¹, Q is the volume flow rate (m³/s), l is the length of the segment (m), A_s is the sapwood cross-sectional area (m²), and ΔP is the pressure difference between the two ends of the segment (MPa). All conductivity calculations were corrected to 20°C to account for changes in fluid viscosity with temperature.

A technique modified from Spicer and Gartner (1998) was used to measure k_s of segments excised from whole disks with minimal damage to the sample, and one that is robust against grain deviation. Samples were fitted with tubing connectors at both ends and sealed inside a membrane-lined pressure sleeve apparatus during volume flow rate measurements. An air pressure of about 0.1 MPa held the membrane against the sides of the sample to prevent leakage, and a dilute solution of oxalic acid (10 mol/m³, filtered to 0.22 μ m) was delivered to one end under a gravitational pressure head of 0.005 MPa. Oxalic acid has been shown to prevent the decline in conductivity with time that is commonly observed during long measurement periods using distilled water (Sperry et al. 1988). A 1 ml graduated pipette was attached to the other end and volume flow rate was measured by timing the movement of the meniscus across 0.1 ml graduations. The mean of at least five timed periods was used to calculate volume flow rate. Fluid temperature was recorded to correct for changes in viscosity. Repeated measures on the same sample showed that direction of flow did not affect results.

The cross-sectional area of samples could be approximated by an isosceles trapezoid and was calculated as:

$$A = \frac{1}{2}h(a+b), \quad (2)$$

Table 3 Random effects models for comparison among fixed positions within stems, treating trees as blocks

Effect	Type	df	P-value ^a
Model to test for differences in k_s among vertical and radial positions			
Tree	Random	11	
Disk ^b	Fixed	4	0.0001
Disk \times tree	Random	44	
Radial position	Fixed	1	0.0001
Radial position \times tree	Random	11	
disk \times radial position	Fixed	4	0.0032
Disk \times radial position \times tree	Random	44	
Total df 119			
Model to test for differences in the difference between inner and outer sapwood k_s among heights within the stem			
Tree	Random	11	
Disk	Fixed	4	0.0034
Disk \times tree	Random	44	
Total df 59			

^aMixed models only provide P -values for fixed effects

^bOnly five heights are included in the model because the disk 5 internodes from the tree top has only one radial position (outer sapwood)

where A is the area, h is the height in the radial direction, and a and b are the widths in the tangential direction. For several samples the two ends differed in size, in which case the mean area of both ends was used.

Following conductivity measurements, samples remained in the pressure-sleeve apparatus and were perfused with a filtered (0.22 μ m) 0.5% (w/v) aqueous safranin-O solution for 10 min. For 16 of the 60 inner sapwood samples dye perfusion showed the innermost growth ring (i.e., the ring adjacent to the heartwood/sapwood boundary) to be partially or wholly non-conductive. In these cases the cross-sectional area was recalculated to exclude the non-conductive region.

Statistical analyses

Differences in k_s were tested using a random effects model to account for correlation between disks within trees and radial positions within disks following a split-plot experimental design (Table 3). The disk that was five internodes from the top was excluded because it contained only one radial position (outer sapwood). A second random effects model was used to test for an effect of disk on the difference in k_s between inner and outer sapwood positions (Table 3). Paired t -tests were used to compare inner, middle and outer sapwood positions within breast height disks. All statistical tests were done using SAS System software (1996 SAS Institute, Cary, N.C., USA).

Xylem physical properties

Plant material

In March 1995, six trees from each of the same two stands described for k_s measurements were harvested for characterization of xylem properties in a total of 12 trees. Trees were sampled at six heights identical to those described for k_s by removing a 1-cm-thick disk from the midpoint of each target internode. Disks were air dried and used for both density and tracheid measurements.

Xylem density

Air-dried disks were oven-dried for 72 h at 60°C. Radial strips about 1.9 mm thick (longitudinal direction) \times 7 mm wide (tangential direction) \times disk radius were sawn from each disk and extracted in boiling solutions of toluene and ethylene (four periods of 2 h each). The first and second periods were in 67% toluene, 33% ethylene; the third in 67% ethylene, 33% toluene; and the fourth in 100% ethylene. After extraction, samples were weighted to keep from warping while conditioning to the equilibrium moisture content of the X-ray room. After equilibration, samples were line-scanned along a 200- μ m wide path with a direct-scanning system X-ray densitometer that produced a data value every 200 μ m along the radial transverse line. The X-ray beam came from a fine-focus copper-targeted X-ray tube and was beta-filtered to be relatively monochromatic (H. R. Holbo and B. L. Gartner, unpublished data).

Thickness of each sample was measured at three locations with a digital micrometer, and we used the average of the measures for each sample. Data were deconvoluted with standard techniques (e.g., Hoag and McKimby 1988) using Beer's Law to give estimates of the density of the wood at each 200 μ m position along the sample in dry mass per green volume (g/cm^3). Using the software DendroScan (T. M. L. Varem-Sanders and I. D. Campbell) we established the growth ring and earlywood/latewood boundaries in the dataset, verified them by comparison of graphs to actual samples, and summarized data for each portion of each growth ring to give total ring width, earlywood width, latewood width, latewood proportion, total ring density, earlywood density, and latewood density.

Tracheid lumen diameter

Two radial sections (1 cm \times 1 cm \times disk radius) were sawn from each breast-height and node-10 disk and divided into approximately 1-cm³ samples from the pith to the bark. One radial section was divided to analyze wood produced in 1964, 1968, 1972, etc. whereas the other one was divided to analyze wood produced in 1966, 1970, 1974, etc. Samples were softened by soaking in boiling water and sectioned (25 μ m thick) transversely with a sliding microtome. Sections were stained in a 1% solution (w/v in absolute ethanol) of safranin-O following a dehydration series and mounted with a permanent mounting medium.

Transverse sections were viewed with a compound microscope using the 10 \times objective and images were captured through a black and white video camera with a digitizing card. Images were analyzed with NIH Image v. 1.6 (public domain software, Rasband 1996) on a Macintosh Quadra 800 computer by measuring the length of lines drawn across tracheid lumens with the line tool. For alternating growth rings (i.e., every other year), 5 radial files of tracheids were randomly selected and the first 10 tracheids in each file (i.e., the first 10 earlywood tracheids produced outward from the growth ring boundary) were measured for diameter. In this way a total of 50 earlywood tracheids were measured per sample for every second growth ring.

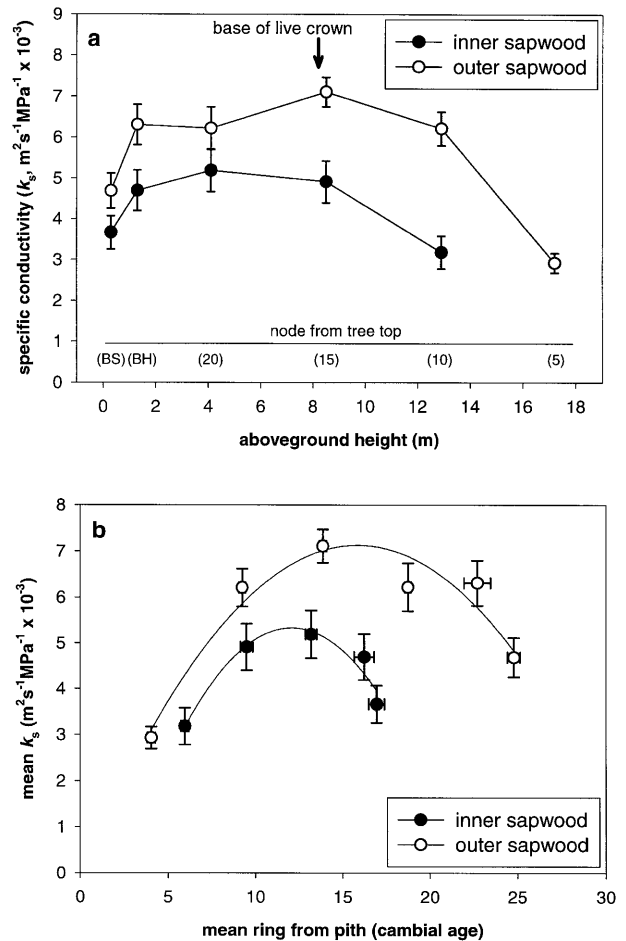


Fig. 1 **a** Specific conductivity (k_s) of outer and inner sapwood versus vertical position in the tree, and **b** k_s of outer and inner sapwood versus cambial age of sample for 35-year-old Douglas-fir trees ($n=12$ trees)

Results

Specific conductivity

Trees from the two stands had similar k_s values for the same radial and vertical positions, and stand was not significant as a blocking factor (data not shown), so results reported here are for all 12 trees pooled together. Specific conductivity (k_s) reached a peak at the 15th (outer sapwood) and 20th (inner sapwood) internode from the top, and declined toward the top and base of the tree (Fig. 1a). Peak k_s in the outer sapwood corresponded to the location of the base of the live crown (Table 1).

The inner sapwood had consistently lower k_s than the outer sapwood (Fig. 1a), but the effect of radial position on k_s depended on the vertical position within the stem (i.e., the disk \times position interaction was significant, P -value=0.003, Table 3 a). The difference between inner and outer sapwood k_s decreased toward the tree base, with a significantly smaller difference at the base (0.3 m from

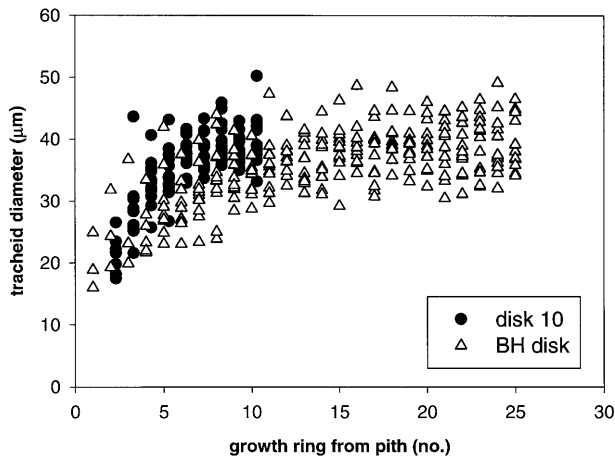


Fig. 2 Diameter of earlywood tracheid lumens by growth ring from the pith for samples from a disk 10 internodes down from the top (disk 10) and at breast height (BH disk) in 35-year-old Douglas-fir trees. Each point represents the mean of 50 measurements for one growth ring and tree; there were 12 trees sampled for each growth ring and height

Table 4 Specific conductivity (k_s , $\text{m}^2\text{s}^{-1}\text{MPa}^{-1} \times 10^{-3}$) and mean growth ring number from pith of inner, middle and outer sapwood positions at breast height (mean \pm SE). Values within the same row followed by the same letter in italics are not significantly different (P -value >0.05 , one-tailed paired t -test)

	Inner sapwood	Middle sapwood	Outer sapwood
k_s ($\text{m}^2\text{s}^{-1}\text{MPa}^{-1} \times 10^{-3}$)	4.7 ± 0.5 <i>a</i>	5.6 ± 0.5 <i>b</i>	6.3 ± 0.5 <i>c</i>
Ring number from pith	16.3 ± 0.6	19.6 ± 0.5	22.7 ± 0.8

ground) and 20 internodes from the tree top, relative to the 10th internode from the top (adjusted P -values = 0.008 in both cases, Tukey-Kramer adjustment). The middle sapwood position in breast height disks had intermediate k_s and differed significantly from both the inner and outer positions (Table 4; P -values = 0.04 and 0.02, respectively, paired t -test). Sample position affected the k_s for a given cambial age, such that samples of the same cambial age (i.e., same ring number from the pith) but higher in the stem had higher k_s than samples at a lower position in the stem (Fig. 1b).

Xylem physical properties

Tracheid lumen diameter increased for about the first 10 years from the pith, and then remained constant (Fig. 2). The same pattern was observed at breast height and 10 nodes down from the tree top (about 13 m from the ground), although tracheids tended to be slightly wider at the top of the tree (disk 10) than at breast height for the same cambial age.

For all heights sampled except the tree base, the proportion of latewood increased with cambial age, after

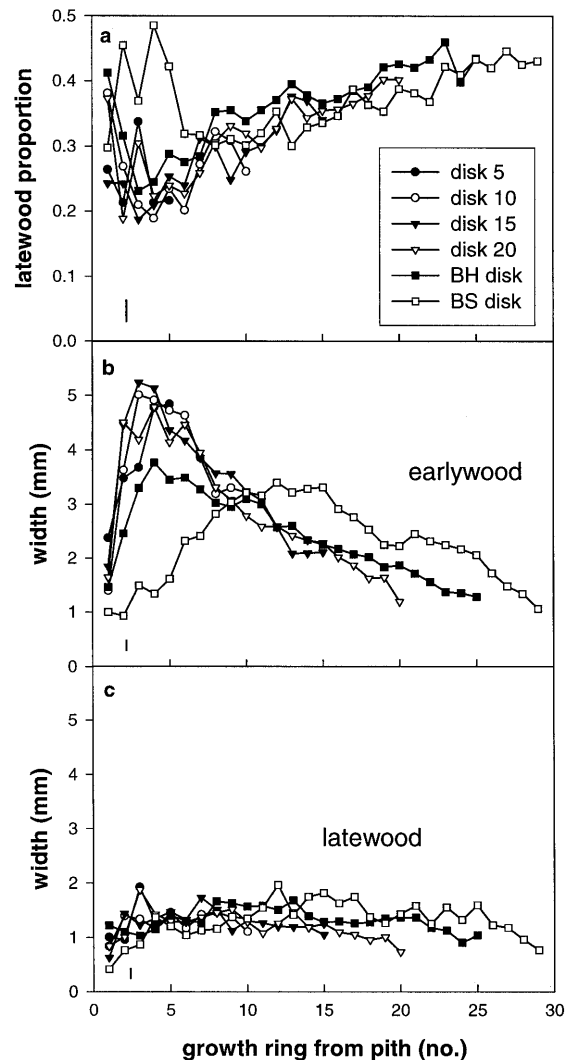


Fig. 3 a Proportion of latewood, b width of earlywood, and c width of latewood in growth rings from the base to the top of the tree in 35-year-old Douglas-fir trees. Each data point is the mean of 12 trees. The bar at bottom left represents the mean standard error for all data points

an initial rapid decrease in the first 3–5 years (Fig. 3a, b). In contrast, there was a sharp increase in latewood proportion in the first few rings from the pith near the tree base. Changes in latewood proportion were largely a function of changes in earlywood width (Fig. 3a, b).

Wood density decreased for several rings from the pith and then increased thereafter (Fig. 4). Earlywood density decreased and latewood density increased in the first 5–10 rings from the pith, followed in both cases by a gradual increase (Fig. 4a).

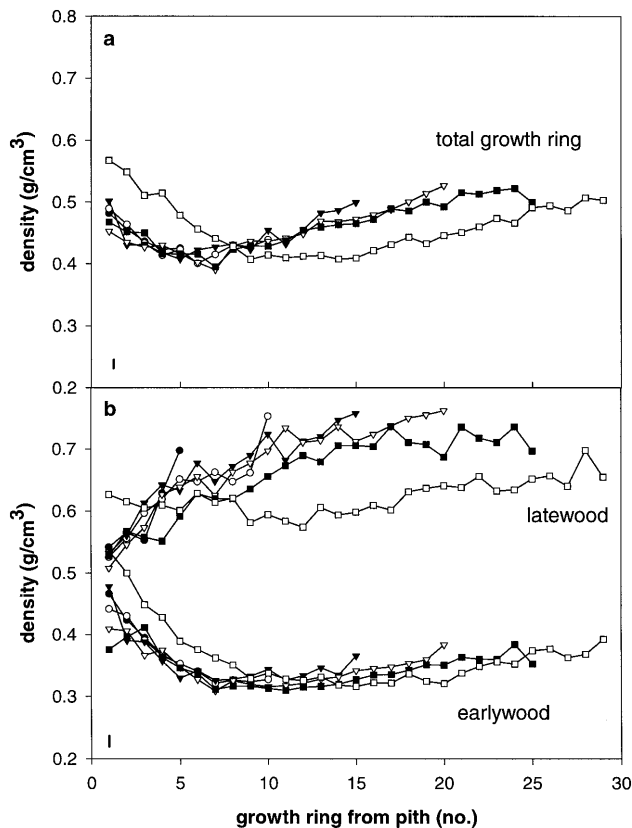


Fig. 4 **a** Relative density of wood and **b** relative density of earlywood and latewood from breast height and from 10 nodes from the tree top as a function of growth ring from the pith in 35-year-old Douglas-fir trees. Each data point is the mean of 12 trees. The bar at the bottom left represents the mean standard error for all data points

Discussion

The within-stem patterns of k_s reported here for mature Douglas-fir trees are complex, and suggest that cambial age, defined by ring number from the pith, is not sufficient to explain variation in k_s . Instead, k_s also depends on both height and radial position within the stem. That k_s decreases toward the heartwood boundary at a given height is not surprising given previous reports (e.g., Comstock 1965; Markstrom and Hann 1972; Booker 1984) and our understanding of xylem anatomy (Gartner 1995). However, the decrease in the difference between inner and outer sapwood k_s toward the base of the stem has implications for how sapwood function changes with age, and to our knowledge has never been reported. It is not known if radial patterns of sap flow show a similar effect of height.

Changes in xylem anatomy associated with cambial maturation (i.e., production of juvenile vs mature wood) should contribute to differences between inner and outer sapwood k_s , but primarily at higher levels in the tree, where the most pronounced radial changes in anatomy occur. For instance, the maximum difference between inner and outer sapwood k_s occurred 10 internodes down

from the top of the stem (inner and outer positions were 6 and 9 rings from the pith, respectively), where there was a marked radial (centrifugal) increase in tracheid diameter. Tracheid length is also likely to increase during this period of rapid cambial maturation (Panshin and de Zeeuw 1980). This observed increase in k_s occurred despite a decrease in earlywood width and corresponding increase in both the proportion of latewood and total ring density, suggesting that the use of density as an index of k_s is inappropriate.

Lower in the stem, where both inner and outer sapwood are produced by a mature cambium and differ little in anatomical properties, radial changes in k_s may result from 'sapwood aging' rather than 'cambial maturation'. Outer sapwood had higher k_s than inner sapwood even near the base of the tree, despite a centrifugal (pith to bark) increase in latewood proportion and ring density, and a relatively constant tracheid diameter. Although we did not measure tracheid length, it is likely to remain constant after reaching a maximum about 18–20 rings from the pith (Megraw 1985), and would not explain the increase in k_s toward the bark in lower regions of the stem. Although anatomical differences cannot be excluded (e.g., the degree to which pitting between tracheids changes with cambial age is not well documented), we believe that the k_s of inner sapwood is reduced by the presence of non-functional tracheids due to embolism and/or bordered pit aspiration. Water content of conifer sapwood often declines toward the heartwood boundary (Chalk and Bigg 1956; Bamber and Fukazawa 1985; Shupe et al. 1995; Phillips et al. 1996), and is correlated with k_s (Pothier et al. 1989b; Sellin 1991; Sperry et al. 1991). We did not evaluate the extent of 'native' embolism with high pressure flushing (Sperry et al. 1988) or vacuum infiltration because differences in anatomy with cambial age may affect the degree to which emboli can be refilled (if they can be refilled at all). Samples brought to maximum k_s in this manner would then represent different levels of saturation. Clearly it will be important for future studies to quantify the proportion of embolized conduits in different regions of the stem.

In contrast to radial changes, changes in k_s with height are non-linear and are not monotonic, with k_s in both inner and outer sapwood declining toward the tree base and top. The same pattern in k_s was reported in *Picea abies* (Sellin 1993). Previous work with excised stem segments (Comstock 1965; Booker and Kininmonth 1978) may not have included samples from high enough within the tree to see a decline in k_s . We found k_s of the outer sapwood to peak near the base of the live crown and then decline with height. Measurements of k_s within the crowns of *Pinus banksiana* (Pothier et al. 1989a), and *Picea sitchensis* and *Pinus contorta* (Whitehead et al. 1984) showed similar decreases in conductivity from the base of the crown toward the top of tree.

Changes in outer sapwood k_s with height are due largely to cambial age, because the outer samples, which included the outermost three to five growth rings, had

been functioning for about the same length of time. Even within a vertical transect of rings produced in the same year, the anatomical features determining k_s change with height. The decrease in outer sapwood k_s from the base of the live crown toward the tree base is likely a function of the increasing proportion of latewood with cambial age. Although the leaf area distal to the stem remains constant from the tree base to the base of the live crown, the observed increase in k_s along the same transect counteracts a decrease in sapwood area (see Table 2). Specific conductivity then declines from the base of the live crown to the tree top as a result of decreasing tracheid dimensions (due to a young cambium), despite a decrease in the proportion of latewood. That k_s peaks near the base of the live crown may reflect the influence of the crown, through the production of hormones, on the process of cambial maturation (Larsen 1962, 1969). Tracheid length, which is positively correlated with k_s , typically reaches a maximum in the outer sapwood, one-third to one-half of the tree height aboveground (Dinwoodie 1961; Panshin and de Zeeuw 1980), depending on the depth of the crown.

Specific conductivity was much lower near the base of the tree than just one meter above at breast height, despite having a similar proportion of latewood and lower average ring density (due to lower latewood density). Tracheid length has been shown quite universally to be lower at the base of trees than higher up for a variety of conifers, including Douglas-fir (Megraw 1985), which could be related to the observed trend in k_s .

Spatial patterns of k_s are complex, and not attributed easily to one or even several aspects of xylem anatomy. Nevertheless, it is clear that decreasing k_s toward the heartwood boundary in mature stems is not a function of the juvenile-mature wood transition. To begin to understand the series of events leading to cessation of water flow through inner sapwood, it would be useful to couple the approach taken here (measurement of 'native state' k_s) with sap flow studies. Future studies should also consider the flow path connecting actively transpiring foliage to different annual increments, as well as the process of embolism formation (and reversal) in aging sapwood.

Acknowledgements The authors gratefully acknowledge funding from USDA CSREES 96-35103-3832 and 97-35103-5052 and a special USDA grant to Oregon State University for wood utilization research. We wish to thank David Baker, Darren Lerner, Eric North and Rebecca Hess for assistance in the field and laboratory. We also thank two anonymous reviewers for insightful comments.

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