

## SAPWOOD AND INNER BARK QUANTITIES IN RELATION TO LEAF AREA AND WOOD DENSITY IN DOUGLAS-FIR

by

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### SUMMARY

The relationships between leaf area and sapwood and inner bark quantities (widths, areas, and volumes) were studied in an attempt to understand the design criteria for sapwood quantity in eighteen 34-year-old Douglas-fir (*Pseudotsuga menziesii*) trees with a wide range of leaf areas, sapwood areas, and dry masses of leaf, xylem, bark, and branch. Cumulative leaf area increased from the tip to the base of the crown, and then was constant; none of the other variables had the same distribution, and so whereas there were many significant correlations, none of the factors can be related to leaf area in a simple, causal manner. Leaf area/sapwood area was extremely variable from tree to tree at a given height, and within a tree from height to height. Sapwood width was relatively constant from the tip down the stem, supporting the hypothesis that sapwood quantity in this species is related to radial gas diffusion causing either a lethal buildup of CO<sub>2</sub> or a lethal depletion of O<sub>2</sub> at the sap/heart boundary. However, there was no significant correlation between leaf area and either total sapwood density (dry weight/green volume) or the average latewood density in the sapwood which were used as proxies for radial diffusion rate; further research on actual radial gas diffusion in green wood may be informative.

**Key words:** Sapwood area, leaf area, phloem, wood density, heartwood.

### INTRODUCTION

The quantity of sapwood that a tree contains is important to physiologists (Margolis et al. 1995; Ryan et al. 1995; Becker et al. 2000), ecosystem scientists (Callaway et al. 1994; Berninger & Nikinmaa 1997) and wood technicians (Wellwood 1955; Tjoelker 1990; Morrell et al. 1996; Semple & Evans 2000). The ability to predict sapwood's occurrence from tree characteristics will help us better characterize a forest, whether to manage its growth, to understand its carbon budget, or to better predict value and suitability of the xylem for conversion into products. The purpose of this paper is to test several structural relationships between leaf area, widths and volumes of sapwood and inner bark, and sapwood density to help improve our understanding of how and why a certain amount of sapwood and inner bark are maintained in young Douglas-fir (*Pseudotsuga menziesii*) trees.

Most investigators believe that the need for water transport governs the sapwood quantity. They assume that 1) leaf area per sapwood area is constant and 2) within an individual, all sapwood has the same permeability and all leaves have the same evapotranspiration rates. In a rough way, the first assumption appears correct. In many studies, sapwood area is linearly related to the distal leaf area for a given species (reviewed in Margolis et al. 1995). However, the relationship often varies by growth rate (Wellwood 1955; Albrektson 1984; Espinosa Bancalari et al. 1987), crown class (Dean & Long 1986; Thompson 1989; Sellin 1996), fertilization (Brix & Mitchell 1983), age (Sellin 1996), stand density (Keane & Weetman 1987), elevation and geographic region (Lassen & Okkonen 1969), climate (Mencuccini & Grace 1995), sampling location with respect to the crown (Shelburne et al. 1993; Kershaw & Maguire 2000), and whether the stem is self-supported or leaning on another object for support (Gartner 1991). When a tree is pruned, the sapwood area will diminish, although not necessarily in direct proportion to the loss of leaf area (Margolis et al. 1988; Långström & Hellqvist 1991). There are also numerous examples that suggest that water transport is not the only factor determining sapwood area. For example, ring-porous trees often maintain many years of sapwood (Table 1 & 2 in Panshin & De Zeeuw 1980), but only one or two rings provide the majority of the water transport (Ellmore & Ewers 1986; Cermak et al. 1992). Sapwood contains an average of 20% air by volume (Gartner et al. 2001), a value that far exceeds what an engineer would specify if he or she were designing a tissue solely for water transport.

The second assumption, that transpiration of all leaves and permeability of all sapwood are constant, is certainly incorrect, although the within-individual variabilities may not be important if one is looking at a non-mechanistic scale. Clearly different parts of the canopy transpire at different rates depending on their branch age and foliage age, exposure, and water supply (e.g., Hanba et al. 1997; Hubbard et al. 1999). Likewise, different parts of sapwood have different permeabilities, based on radial position (Comstock 1965; Puritch 1971; Spicer & Gartner 2001), vertical position (Whitehead et al. 1984; Pothier et al. 1989; Spicer & Gartner 2001), and presence of reaction wood (Spicer & Gartner 1998) or embolisms (e.g., Tognetti et al. 1998). Thus, a motivation for the study was to find if there are better correlates with sapwood quantity than the leaf area/sapwood area ( $A_l/A_s$ ) relationship.

Leaf area could have a more direct relationship with inner bark area (= phloem area) than with sapwood area. Inner bark area is made largely of live, metabolically active cells, whose transport demands could be related to the tree leaf area where photosynthate is produced. However, in the tropical genus *Bauhinia*, the correlation of xylem area and leaf area was stronger than that of phloem area and leaf area for trees and shrubs ( $r = 0.86$  vs.  $r = 0.76$ , respectively, Ewers & Fisher 1991).

Leaf area could be dependent on *volume* of sapwood ( $V_s$ ) or inner bark ( $V_b$ ) rather than their *area* if trees have had stronger selection for requirements for storage quantity/leaf area than for transport/leaf area. Non-living spaces in the sapwood could store stem water and air. Living spaces could store water and/or nutrients, and contain cells that could become meristematic upon wounding, cells for defense, and cells that exchange chemical constituents with the xylem stream. In the inner bark, all the

storage would most likely be in living cells. However, Ryan (1989) has shown that  $A_1/V_s$  increases as tree size increases, and Kaufmann and Watkins (1990) have shown that  $A_1/V_s$  varied substantially in their study trees, and was not correlated with tree vigor.

A totally different design criterion for sapwood quantity is contained in the hypothesis that sapwood width is determined by either a build-up of  $\text{CO}_2$  or a depletion of  $\text{O}_2$  to levels that are lethal for the xylem parenchyma cells. This hypothesis is similar to Carrodus' (1971) hypothesis that elevated  $\text{CO}_2$  is responsible for the formation of heartwood-like polyphenols in an *Acacia* species. Because there are few pits in the radial direction, I expected the relationship to be driven by wood density, in which case higher density wood would be associated with a lower radial gas diffusion rate and thus narrower sapwood. Evidence in support of this hypothesis is that Douglas-fir trees have quite constant sapwood widths from their base upward toward where the first heartwood is produced (Brix & Mitchell 1983; Megraw 1986; Espinosa Bancalari et al. 1987) and that buttressed trees of a variety of species often have wider sapwood in the extremities of the buttresses (which have more surface area) than in the grooves (personal observation). Moreover, the width of sapwood is influenced by silvicultural practice (Granier 1981; Brix & Mitchell 1983; Mörling & Valinger 1999), crown class (Wellwood 1955; Smith et al. 1966) and crown vitality (De Kort 1993), with fertilized, thinned, and/or dominant trees having the widest sapwood. These trees likely have a higher proportion of earlywood and lower wood density than do trees that are not fertilized, thinned, or dominant.

First, this paper describes the vertical distribution of mass, leaf area, cross-sectional areas and volumes of stem tissues, and other tree characteristics of a group of 34-year-old Douglas-fir trees, chosen to represent a wide range of crown sizes. Second, it evaluates whether  $A_1$  is related to  $A_s$ ,  $A_b$ ,  $V_s$ , or  $V_b$  in any consistent way to shed light on the design criteria for sapwood and inner bark quantities. Third, the paper evaluates whether sapwood width is related to sapwood density.

## MATERIALS AND METHODS

### *Plant materials*

In March 1995, I felled Douglas-fir trees [*Pseudotsuga menziesii* (Mirbel) Franco] at the H.J. Andrews Experimental Forest in the central Cascades of Oregon, USA (site L107, 44° 15' N, 122° 10' W, 705 m elevation). To insure a wide range of tree sizes and allocation patterns I sampled 18 trees from three adjacent research plots. I treated the trees as individuals with no blocking by plot, analyzing the trees for their variable form, not as representations of the plot treatments (see 'Data analyses', below). Two-year-old seedlings had been planted in 1963. The trees grew in an unthinned plot (3460 trees/ha in 1982), or one of two thinned plots (thinned to 600 trees/ha in 1982), one of which was fertilized in 1982 and 1984 (Velazquez-Martinez et al. 1992). Thus, plots had been manipulated (thinned and/or fertilized) 11–13 years before our harvest.

### *Harvests*

After felling the trees, I marked the center of each of the internodes 5, 10, 15, and 20 nodes down from the tree tip, and breast height (1.3 m, about node 25), and the tree base (0.3 m; about node 30). The height to each of these marked nodes was recorded, and then several replicate disks were taken from each marked location. Disks were referred to as disk 5, 10, etc.

I tracked information between these marked internodes separately, designating each area as a 'zone'. The six zones were from nodes 0–5, 6–10, 11–15, 16–20, and 21–breast height, and breast height to the tree's base. I calculated a seventh zone from the tree's base to the ground.

### *Volume, area, and mass estimates of the bole*

It was relatively simple to collect biomass data given the sampling I undertook for leaf area and for volumes and areas of sapwood and inner bark. The mass data are presented to more fully describe the sampled trees and to show the relative dry mass in each of the categories used.

I drew two perpendicular diameters on a fresh disk from each zone and tree. The boundary between sapwood and heartwood was highlighted with the indicator stain Alizarine-Red (Kutscha & Sachs 1962), which generally corresponded to the boundary of the natural coloration. I then used a razor blade to surface the bark and pith along the designated diameters to make it easier to see the boundaries. I measured the width of outer bark, inner bark, sapwood, heartwood, and pith along these diameters, and then averaged values for the four radii. Geometry was used to estimate cross-sectional areas and volumes of each of the tissue types for each zone and tree. Because I had no diameter data from the tree at ground level (at 0.0 m), I assumed it had the same diameters and tissue areas as the basal disk (at 0.3 m).

Density of xylem and bark were used to estimate xylem and bark mass from the volume estimates. I estimated density of xylem and bark on a wedge-shaped sample whose edges converged on the pith, of about 45° and 3–4 cm thick. After the wedge was cut, I removed the bark with a chisel. The geometry of these samples ensured that I weighted the different radial parts of the xylem correctly. Mass and volumes were determined on oven-dry samples (103 °C), then volumes were converted to wet volume using the shrinkage/swelling values for Douglas-fir xylem (Table 3–5 in Forest Products Laboratory 1999). Volume was determined by submerging the samples into water that was on a balance, recording the change in output on the balance (where an increase in 1 g indicates the sample has 1 cm<sup>3</sup> volume), and correcting for the water that the samples absorbed.

Values were summarized as the mean ± standard error and range for the 18 trees. To visualize the vertical distribution of mass, I plotted a composite average of mass, standardized by tree height. I first calculated the mass/length of stem for each zone. That is, if the zone had 300 g of leaf dry mass and was 3 m long, its mass/length was 100 g/m. Then I divided the stem's height into the 50 zones and, for each zone, took the average value of mass/length of the 18 trees. I was then able to summarize mass per length (by height) of leaf, branch (xylem plus bark), bole xylem, and bole bark for the average of the 18 trees.

### *Branch mass and leaf areas*

I took one third of all the branches for determination of branch mass and leaf area, keeping material separate for the different zones and trees. This sampling scheme was accomplished by keeping every third primary branch (and all the mass distal to it) encountered, regardless of the branch's size. Samples were kiln-dried at 60 °C, and then re-dried before weighing. Mass was separated into needle and branch (including bark).

To convert needle (leaf) mass to needle area, during the harvest I collected subsamples of fresh needles (one subsamples for each zone per tree). I used an image analysis system to estimate one-sided needle area for each of the subsamples (about 0.5 g dry mass). These subsamples were then oven-dried and weighed, the conversion from needle mass to area was calculated, and then whole-tree leaf areas were estimated.

### *Sapwood density*

Samples were X-rayed to derive within-ring profiles of wood density, but only data from the sapwood region were used. I X-rayed one 1.9-mm thick radial sample from each zone and tree using a direct-scanning X-ray densitometer (Hoag & McKimmy 1988). Before samples were scanned, their resin was extracted using toluene and ethanol, and they were equilibrated to a constant moisture content (Gartner et al. 2002). Data were taken for a 200- $\mu\text{m}$  diameter spot every 200  $\mu\text{m}$  from the pith to the bark. Using the Beer-Lambert equation I estimated wood density (as dry mass per green volume) for each of these 200- $\mu\text{m}$  segments, and then estimated total ring width, earlywood width, latewood width, latewood proportion, total ring density, earlywood density, and latewood density for sapwood growth rings. I also calculated sapwood earlywood area and sapwood latewood area for the breast height disk.

### *Sapwood width in relation to sapwood density*

To infer whether the density of sapwood controls how thick is the sapwood, I correlated average latewood density and average total wood density of the sapwood with sapwood width for each of the five disk locations (disk 10, 15, 20, breast height, and base) separately. Disk 5 was excluded because it had no heartwood. These components were chosen because total ring density describes the solid mass through which the gas needs to diffuse, and the latewood, being the densest part of the growth rings, may be the part of sapwood that would provide the most resistance for diffusion. For simplicity, values were weighted linearly with depth, rather than by actual growth ring area over the disk; only very small differences would have resulted had I weighted samples by area.

### *Data analyses*

I chose to treat each tree as an individual and to disregard treatment from which it came, for three reasons. First, the three treatments were in relatively narrow adjoining plots that were considered to have the uniform conditions prior to treatment (Velazquez-Martinez et al. 1992). All trees came from  $\leq 200$  m of one another. Sec-

ond, stands were last manipulated 11–13 years before this study. There had been substantial mortality and natural regeneration in the meantime. Thus, individuals within treatments may no longer have been reacting to the environment imposed by the treatment. Third, previous analyses of wood density, ring width, and ring area (and their components: earlywood value, latewood value, total ring value) for the average of the outer three growth rings, found that 63–93% of the variation was due to disk within tree (Gartner et al. 2002). In ring density, for example, only 7–10% of the total variance was due to treatment.

Correlation analyses were performed to describe the relationships between total leaf area of the tree and each of the following characteristics: sapwood area (at breast height, at base of live crown), earlywood sapwood area (at breast height), latewood sapwood area (at breast height), total sapwood volume of the bole, inner bark area (at breast height, at base of live crown), and total inner bark volume.

To show the variability in the relationships between disk height and leaf area/sapwood area or leaf area/inner bark area, I plotted the data distribution, showing the median value and the percentile distribution around that median for each height. I used analysis of variance to look at the effect of disk (representing height) on leaf area/sapwood area and leaf area/inner bark area. For these analyses, leaf area was the cumulative leaf area above the disk. P-values were adjusted using the Bonferroni method for multiple comparisons. I then computed correlation coefficients for leaf area/sapwood area or leaf area/inner bark area at each of the heights, separately, to learn whether the relationship changes with height.

Lastly, I correlated sapwood width and density of sapwood or density of the latewood sapwood, for each of the five heights separately. All statistical tests were done using SAS System software (1996 SAS Institute Inc., Cary, NC, USA).

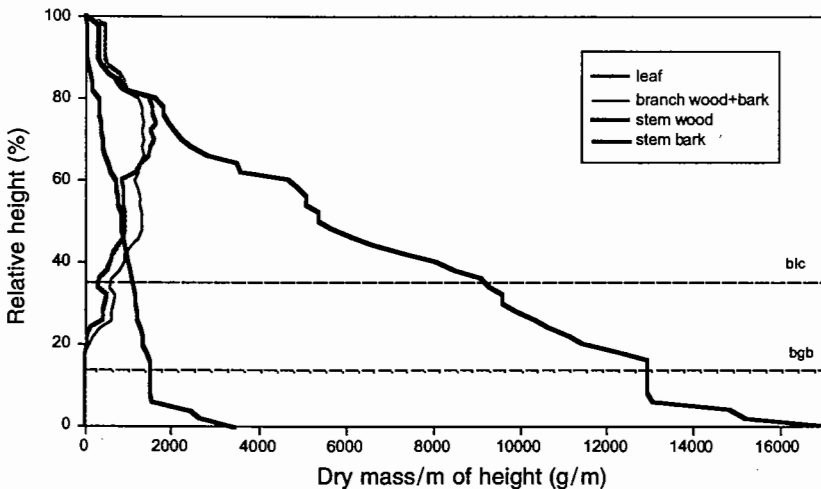


Fig. 1. Mean dry mass distribution by relative height (0% is base, 100% is tip) for eighteen 34-year-old Douglas-fir trees, showing leaf mass, branch mass, bole bark, and bole xylem mass. The dashed lines show average base of live crown (bhc) and lowest green bark (lgb).

## RESULTS

***Vertical distributions of mass, sapwood, and heartwood***

The sampled trees had a wide range of sizes and geometries (Table 1 and Appendix), particularly crown length, tissue volumes and masses, leaf area, and sapwood and heartwood quantities (as shown by their widths, areas, and volumes). The composite average of mass (standardized by tree height) shows that about half of the branch mass was leaf, and that the average crown base was higher than the average location of the lowest green bark (Fig. 1, Table 1). Leaf area distribution follows leaf dry mass distribution closely (data not shown).

Inner bark and sapwood width were relatively constant from the base upward to node 10 (about 13 m), and then decreased to node 5 (about 17 m, Fig. 2a). Heartwood and outer bark width decreased from the tree base to its tip (Fig. 2a), whereas pith width increased from the base upwards (Appendix).

The areas of sapwood, heartwood, and outer bark decreased relatively steadily with height, whereas inner bark was relatively constant for a long distance along the lower bole, then decreased above the base of live crown (Fig. 2b). Cumulative leaf area, of course, was constant below the base of the live crown, and decreased upward toward the tip of the tree (Fig. 2b).

Table 1. Characteristics of the 34-year-old Douglas-fir trees studied (n = 18).

characteristics	mean $\pm$ s. e.	range
height (m)	20.6 $\pm$ 0.5	15.5–23.7
diameter at breast height (cm)	20.4 $\pm$ 0.5	17.6–24.8
base of live crown (distance from ground, m)	7.8 $\pm$ 0.9	1.5–14.4
crown length (nodes)	16.8 $\pm$ 1.0	10–24
crown length (m)	12.8 $\pm$ 0.7	7.0–16.9
lowest green bark (distance from ground, m)	3.1 $\pm$ 0.5	0.7–8.1
extent of bole with green bark (nodes)	22.4 $\pm$ 0.7	17–27
bole volume (cm <sup>3</sup> )		
pith	162 $\pm$ 16	51–298
sapwood	208,946 $\pm$ 14,647	117,881–339,230
heartwood	95,110 $\pm$ 8,113	38,723–182,125
inner bark	29,126 $\pm$ 3,699	13,664–83,200
outer bark	10,240 $\pm$ 1,880	1,711–35,031
dry mass (g)		
leaf	13,401 $\pm$ 1,540	4,117–25,943
branch (xylem and bark)	14,618 $\pm$ 2,063	2,991–29,860
xylem (bole)	138,103 $\pm$ 8,657	85,171–221,889
bark (bole)	18,884 $\pm$ 1,741	8,075–35,058
leaf area (m <sup>2</sup> )	78.9 $\pm$ 9.4	24.7–163.1

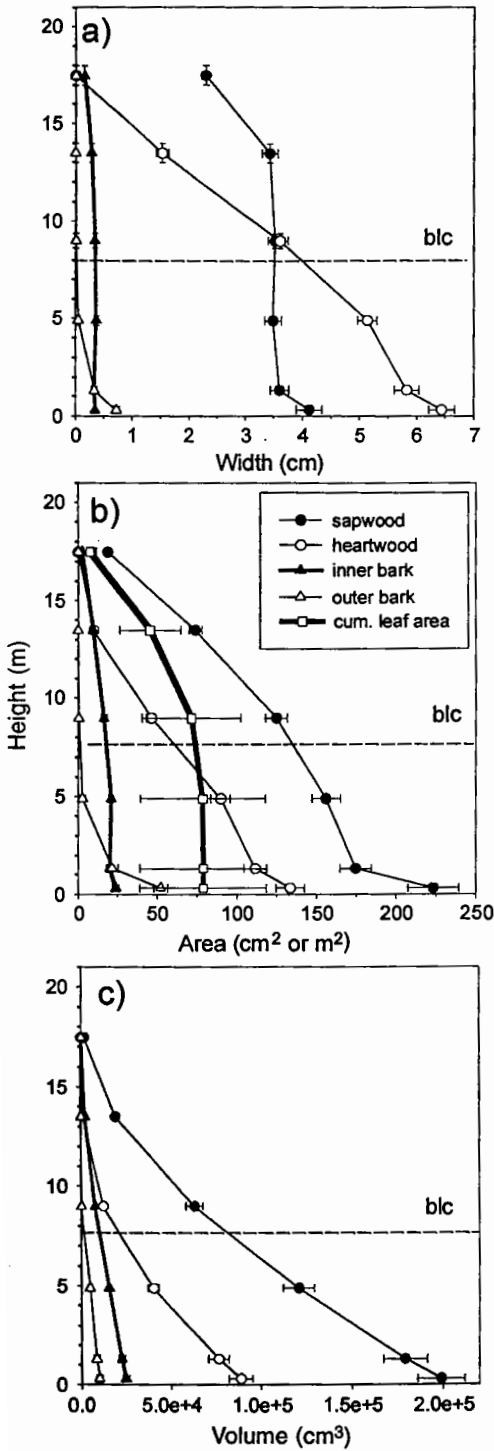


Fig. 2. Within-tree characteristics by height for 34-year-old Douglas-fir trees, average height 20.6 m.

**a)** Widths of heartwood, sapwood, inner bark, and outer bark.

**b)** Areas of heartwood, sapwood, inner bark, outer bark, and leaf (cumulative). Note that leaf area is shown in m<sup>2</sup>, and all other areas are in cm<sup>2</sup>.

**c)** Cumulative volumes of heartwood, sapwood, inner bark, and outer bark.

Values show the mean  $\pm$  s.e. (n = 18); s.e. for height is shown only in panel a). Note that the heights represent specific nodes (see 'Harvests' sub Material and Methods). The dashed line shows the average base of the live crown (blc).



Table 2. Ratios of leaf area to sapwood or inner bark quantities and the correlation of leaf area with the sapwood or inner bark quantity for 34-year-old Douglas-fir trees ( $n = 18$ ). Abbreviations:  $A_1$  (leaf area),  $A_s$  (sapwood area),  $V_s$  (sapwood volume),  $A_b$  (inner bark area),  $V_b$  (inner bark volume).

variable	$A_1$ / variable		correlation of $A_1$ with variable	
	mean $\pm$ s.e.	range	r	p
$A_s$ , base of live crown ( $m^2/cm^2$ )	0.52 $\pm$ 0.04	0.23–0.99	0.7289	<b>0.0006</b>
$A_s$ , breast height ( $m^2/cm^2$ )	0.44 $\pm$ 0.04	0.19–0.92	0.6234	<b>0.0057</b>
earlywood $A_s$ , breast height ( $m^2/cm^2$ )	0.71 $\pm$ 0.09	0.32–1.51	0.5029	<b>0.0334</b>
latewood $A_s$ , breast height ( $m^2/cm^2$ )	1.25 $\pm$ 0.13	0.44–2.40	0.5531	<b>0.0173</b>
$A_b$ , base of live crown ( $m^2/cm^2$ )	4.9 $\pm$ 0.4	1.5–7.9	0.7320	<b>0.0006</b>
$A_b$ , breast height ( $m^2/cm^2$ )	4.3 $\pm$ 0.7	1.1–13.1	0.3786	0.1213
$V_s$ ( $m^2/cm^3$ )	0.0014 $\pm$ 0.0002	0.0007–0.0037	0.4165	0.0855
$V_b$ ( $m^2/cm^3$ )	0.012 $\pm$ 0.002	0.005–0.033	0.5004	<b>0.0344</b>

The cumulative volumes of sapwood, heartwood, inner bark, and outer bark all decreased exponentially from the base upward (Fig. 2c).

#### *Sapwood and inner bark quantities relative to leaf area*

The ratio of leaf area ( $A_1$ ) to sapwood and inner bark quantities as well as their correlation coefficients are given in Table 2. Cumulative  $A_1$  was correlated significantly with sapwood area ( $A_s$ ) at both the base of the live crown or at breast height, and with inner bark area ( $A_b$ ) at the base of the live crown. These correlations were moderately strong ( $r$  of 0.62 to 0.73). At breast height, the correlation of  $A_1$  was stronger with  $A_s$  than with either earlywood  $A_s$  or latewood  $A_s$ .  $A_1$  was also correlated with inner bark volume ( $V_b$ ), but not with sapwood volume ( $V_s$ ) or  $A_b$  at breast height.

The values of  $A_1/A_s$  and  $A_1/A_b$  were quite variable from tree to tree and within trees by height (Fig. 3–5). The mean value of  $A_1/A_s$  was lowest at the tip and base of the tree, and peaked near the middle of the crown (Fig. 4a). The base and the tip (disk 5) had significantly lower  $A_1/A_s$  ratios than did disk 10 ( $p = 0.0122$  and  $p = 0.0011$ , respectively). There were no significant differences in  $A_1/A_b$  between disk heights (Fig. 4b).

The correlation between  $A_1$  and  $A_s$  was highest at the base of the live crown (Fig. 5). The correlation between  $A_1$  and  $A_b$  was also highest at the base of the live crown, but it was not as strong as the  $A_1/A_s$  correlation (Fig. 5)

#### *Sapwood width vs. sapwood density*

There were no significant correlations between sapwood width and either the average latewood density in the sapwood or the average density of the sapwood, at any of the heights (Table 3). Note that sapwood varied greatly in width. For example, at the base, it varied from 2.6 to 6.5 cm in width (see also Appendix).

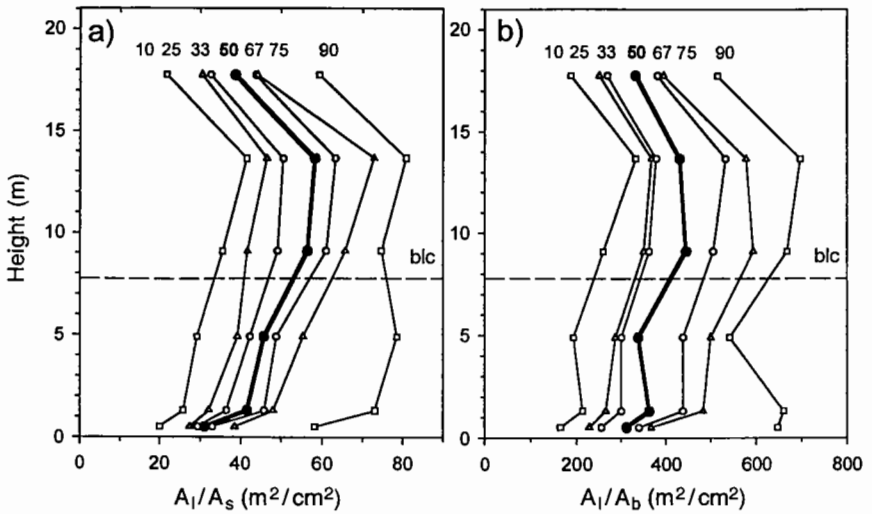


Fig. 3. Value distribution of a) cumulative leaf area/sapwood area ( $A_1/A_s$ ) and b) cumulative leaf area/inner bark area ( $A_1/A_b$ ) with height in 34-year-old Douglas-fir trees ( $n = 18$ ). Different curves on the same graph show the percentile of values by height, with 50 representing the median. Note that the heights represent specific nodes (see 'Harvests' sub Material and Methods). The dashed line shows the average base of the live crown (blc).

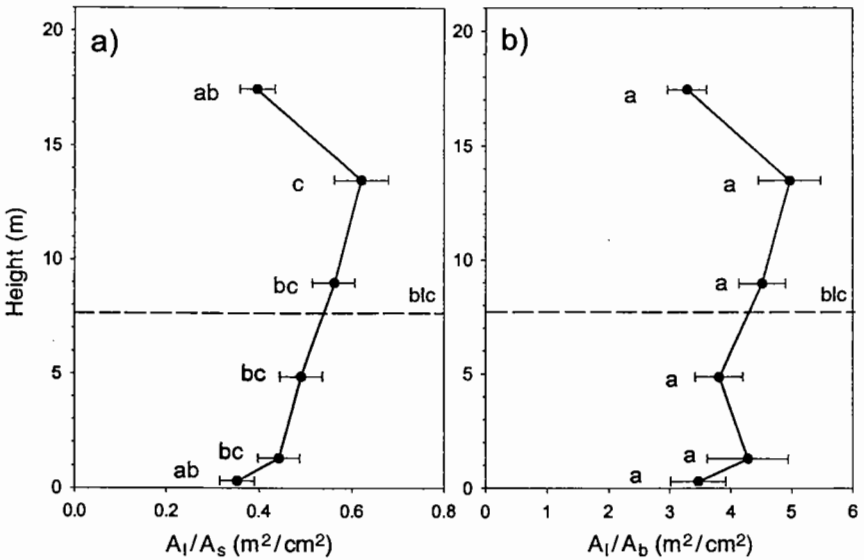


Fig. 4. Values with height of a) cumulative leaf area/sapwood area ( $A_1/A_s$ ) and b) cumulative leaf area/inner bark area ( $A_1/A_b$ ) for Douglas-fir trees (mean  $\pm$  s. e.,  $n = 18$ ; the same letter at different values signifies that values do not differ significantly at  $P < 0.05$ ). Note that the heights represent specific nodes (see 'Harvests' sub Material and Methods). The dashed line shows the average base of the live crown (blc).

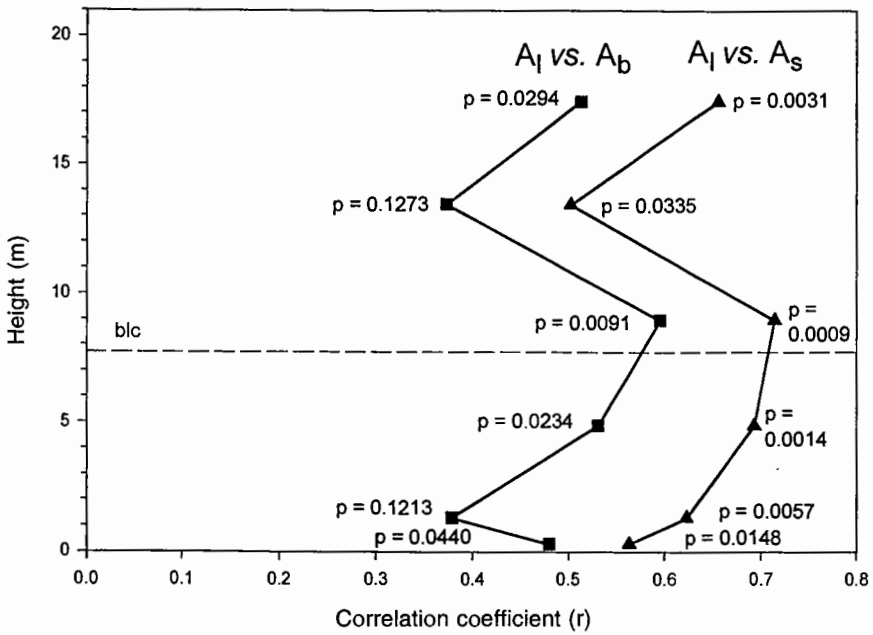


Fig. 5. Correlation coefficients between 1) leaf area ( $A_l$ ) vs. sapwood area ( $A_b$ ) or 2) leaf area ( $A_l$ ) vs. inner bark area ( $A_s$ ) at different heights for Douglas-fir trees ( $n = 18$ ). The P-value for the correlation is shown next to each data point. Note that the heights represent specific nodes (see 'Harvests' sub Material and Methods). The dashed line shows the average base of the live crown (blc).

Table 3. Correlation ( $r$ ) of sapwood width vs. density of sapwood or density of sapwood latewood by height in 34-year-old Douglas-fir trees ( $n = 18$ ).

	Disk Location				
	10	15	20	bh	base
Sapwood width vs. sapwood density					
$r$	-0.429	-0.078	-0.113	-0.118	-0.184
$p$	0.086	0.760	0.655	0.641	0.481
Sapwood width vs. latewood density					
$r$	-0.411	0.210	0.388	0.169	0.347
$p$	0.101	0.403	0.112	0.502	0.172

## DISCUSSION

*Relationship of leaf area to other tissue areas and volumes*

Inspection of Figure 2 shows that none of the measured variables can scale linearly with cumulative leaf area ( $A_1$ ) because none of them have the same shaped curve. Cumulative  $A_1$  (Fig. 2b) increases from tip toward an asymptote at the base of the crown, whereas both sapwood area ( $A_s$ ) and inner bark area ( $A_b$ ) increase continuously from tip to base. All the tissue volumes increase exponentially from the tip to the base (Fig. 2c). Therefore, although there were significant correlations between  $A_1$  and  $A_s$ ,  $A_b$ , and  $V_b$ , the relative shapes of the curves suggest that there is no simple causal relationship between  $A_1$  and of the other variables ( $A_s$ ,  $A_b$ ,  $V_b$ ). Both  $A_s$  and  $A_b$  at the base of the crown were equally good predictors of  $A_1$ . As expected,  $A_s$  and  $A_b$  were more strongly correlated with cumulative  $A_1$  if taken at the base of the live crown than at breast height (e.g., Waring et al. 1982; Blanche et al. 1985).

Leaf area/sapwood area ( $A_1/A_s$ ) was not constant with height in these young Douglas-fir trees: it was lowest at the base and tip and highest near the crown base. The same pattern was shown in other studies on young *Pseudotsuga menziesii* (Brix & Mitchell 1983; Espinosa Bancalari et al. 1987) and *Pinus contorta* (Dean & Long 1986). Similar to the current study, *Pinus taeda* also showed differences in  $A_1/A_s$  with height, with increasing values from breast height to the base of the crown (the only segment of stem studied; Shelburne et al. 1993). However, several studies have reported constant  $A_1/A_s$  with height, both in *Pseudotsuga menziesii* (Long et al. 1981; Waring et al. 1982) and in other species: *Picea engelmannii*, *Pinus contorta*, *Populus tremuloides* (Kaufmann & Troendle 1981), *Abies grandis*, *Abies amabilis*, *Tsuga heterophylla*, *Picea engelmannii*, *Pinus ponderosa* (Waring et al. 1982). One needs to use caution in the above comparisons, however, because the results obtained depend on the locations of the heights compared (for example, whether one looks at base and/or tip, or only intermediate locations) and also the criteria one uses to say whether the relationship is linear. In *Picea sitchensis* and *Pinus contorta*, for which  $A_1/A_s$  is not constant with height, if one takes into account the variable sapwood permeability with height, one finds a constant  $A_1/(A_s * \text{sapwood permeability})$  with height (Whitehead et al. 1984). However, sapwood permeability has little or no effect on the relationship in other species such as *Pinus taeda* (Shelburne et al. 1993), *Pinus sylvestris* (Mencuccini & Grace 1995), and *Abies balsamea* (Coyea & Margolis 1992).

The mean  $A_1/A_s$  at breast height for this site ( $0.44 \text{ m}^2/\text{cm}^2$ ) is in the middle of the range of Douglas fir means summarized by Margolis et al. (1995):  $0.38\text{--}0.70 \text{ m}^2/\text{cm}^2$ . However, there is so much variability in the current study that the mean does not describe the trees very well (Fig. 3a). In the same species, Espinosa Bancalari et al. (1987) found about 30% higher  $A_1/A_s$  in a fast-grown stand than in the stands with intermediate or slow growth rates at both the crown base and at breast height. At breast height, the  $A_1/A_s$  of these trees ranged from 0.19 to  $0.91 \text{ m}^2/\text{cm}^2$ , which almost spans the reported stand averages summarized for 20 conifer species (Margolis et al. 1995) of 0.08 (*Juniperus monosperma*) to 0.75 (*Abies lasiocarpa*). *Pinus contorta* is also reported to vary widely in its  $A_1/A_s$ . A study of twenty 270-year-old trees from

one site found  $A_1/A_s$  ranging from 0.09 to 0.88  $m^2/cm^2$  (Kaufmann & Watkins 1990; Margolis et al. 1995). In contrast, however, there were no significant differences in  $A_1/A_s$  for *Pinus ponderosa* trees of different crown classes, although the relationship was different by geographic region (O'Hara & Valappil 1995).

Both earlywood and latewood  $A_s$  had weaker correlations with  $A_1$  than did total (earlywood + latewood)  $A_s$ . Had either earlywood or latewood  $A_s$  produced a stronger correlation with  $A_1$  than with total  $A_s$ , I would have inferred that  $A_s$  is at least in part determined by a need for water transport. In the case of earlywood, I would have inferred that water transport was a strong determinant of  $A_1$ . Had latewood  $A_s$  produced a stronger correlation, I would have inferred that the conducting tissue when under extreme drought stress (the latewood) may be the strong determinant of  $A_1$ , for it is possible that the latewood transports water when the rest of the hydrosystem is embolized: it has not been shown conclusively whether the earlywood or latewood part embolizes under xylem tension. In *Picea abies*, needle mass per earlywood  $A_s$  did not differ significantly in any of the conditions investigated, whereas needle mass per total  $A_s$  did differ (Eckmüller & Sterba 2000). This experiment suggested that in *P. abies* the transport system in the earlywood is closely related to the  $A_1$  that the tree carries, because a constant needle mass per earlywood  $A_s$  was maintained among three crown classes, among three age-class categories, and among three crown-condition classes.

The variables that were correlated with  $A_1$  are undoubtedly auto-correlated. The significant correlation between  $A_1$  and  $A_b$  may simply follow the correlation of  $A_1$  with  $A_s$ , for there may be a developmental requirement to produce a near-constant ratio of  $A_s$  to  $A_b$ . The correlation of  $A_1$  with  $A_b$  is surprising given the larger error associated with estimated  $A_b$  than  $A_s$  because of its smaller size. This result suggests that one could sample the inner bark, rather than the xylem, to estimate  $A_1$  if one wanted a less invasive method.

The significant correlation between  $A_1$  and  $A_b$  may suggest that flux through the phloem has some role in determining leaf area or vice versa. The significant correlation between total tree  $A_1$  and tree  $V_b$  may suggest that in addition to flux through the phloem, some function of phloem volume (such as storage capacity) may also have a role in determining  $A_1$ .

The relationship of  $A_1/V_s$  was not significant in the current study at  $p < 0.05$ , but it was significant at  $p = 0.086$ . If sapwood quantity were determined by a need for storage cells, then one could have expected that trees with higher  $A_1$  would have more sapwood, a higher proportion of xylem tissue that was parenchyma cells, and/or a greater depth of survival of the sapwood parenchyma cells. Neither of the latter two effects in a subset of 12 of these 18 trees from the current study were found (Gartner et al. 2000).

Kaufmann and Watkins (1990) looked at  $A_1/V_s$  in ten trees of *Pinus contorta*, expecting that the most vigorous trees would have the highest ratios. However, they found overlap in the  $A_1/V_s$  values among the trees that had short crowns and appeared to have low vigor compared to the trees with long full crowns that appeared to have high vigor. Their result showed that  $A_1/V_s$  was highly variable within that one stand,

and thus it did not appear that the tree is designed to keep this ratio constant from individual to individual.

#### *Relationship of sapwood width to wood density*

Both sapwood width and inner bark width were quite constant throughout most of the height of the tree, with the exception of the tip, where they decreased. The constancy of sapwood width with height in Douglas-fir has also been described in 22-year-old trees (Espinosa Bancalari et al. 1987), in 55-year-old trees (Megraw 1986), and in 59- to 78-year-old trees (Wellwood 1955). However, contrary to our hypothesis, there was no correlation between sapwood width and the average wood density of the sapwood, or the density of the latewood at any height in these trees. This data analysis of the current study was designed to ask if there was an indication that diffusion of oxygen into the wood, or diffusion of CO<sub>2</sub> out of the wood is related to sapwood formation, with the assumption that dry wood density of the sapwood would be negatively correlated with their radial diffusions. It would be interesting to study the wood to learn if there are radial interstitial spaces that can function for gas or water conduction. Many coniferous species have such interstitial spaces alongside the rounded edges of the ray cells (reviewed in Bolton et al. 1975).

#### CONCLUSIONS

The quantity of sapwood in Douglas-fir does not appear to be related causally to leaf area, even though the sapwood area and leaf area are correlated. Neither does sapwood quantity appear to be correlated with the density of the sapwood itself. The most striking pattern that emerged was that sapwood width was relatively constant from the base upward toward the tip. These data further support the contention that we do not know the design criteria for sapwood quantity in Douglas-fir. However, I urge caution in making inferences from this study to other species because there are species-specific relationships that explain how the tree determines its sapwood quantity.

This research has treated sapwood as if it were homogeneous, whereas actually it can vary considerably in its mechanical, hydraulic, and respiratory capabilities with radial position and height. An improved understanding of sapwood heterogeneity should help us understand physiologically what sapwood does, and may eventually help us understand the design criteria used by trees to determine their sapwood quantity. The ability to better predict sapwood and heartwood quantity in a stand will help silviculturists make better-informed decisions regarding forest management and harvesting, help tree-owners ensure fair prices for the logs, and help mills plan for the wood that they will be processing.

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## Appendix

Tree descriptions (means, s.e., range, n = 18 for each measurement). Tree height was  $20.6 \pm 0.5$  m (range of 15.5–23.7). Note that zones are of variable lengths. It was assumed that the ground level had the same values as the base level for calculations that required areas or densities.

	disk 5	disk 10	disk 15	disk 20	breast height	base	ground
<b>height of node (at the base of zone, m)</b>	$17.5 \pm 0.5$ (13.5–20.7)	$13.5 \pm 0.5$ (10.0–16.6)	$9.0 \pm 0.4$ (6.2–11.4)	$4.9 \pm 0.3$ (3.2–6.7)	1.3	0.3	0
<b>length of zone (m)</b>	$3.1 \pm 0.2$ (2.0–4.0)	$4.0 \pm 0.1$ (3.1–5.1)	$4.5 \pm 0.2$ (3.4–6.0)	$4.1 \pm 0.2$ (1.1–5.2)	$3.6 \pm 0.3$ (1.9–5.4)	1	0.3
<b>dry biomass in zone distal to node (g)</b>							
leaf	$1494 \pm 183$ (380–3430)	$6550 \pm 750$ (2190–13170)	$4260 \pm 680$ (317–9010)	$1070 \pm 370$ (0–6100)	$31 \pm 31$ (0–570)	0	0
branches 0–1 cm diameter	$890 \pm 100$ (190–1850)	$3020 \pm 280$ (940–5760)	$2600 \pm 380$ (350–5350)	$890 \pm 280$ (0–4180)	$17 \pm 17$ (0–300)	0	0
branches 1–2 cm diameter	$210 \pm 40$ (0–590)	$2170 \pm 360$ (33–5350)	$2360 \pm 460$ (0–6180)	$820 \pm 320$ (0–4640)	0 (0)	0	0
branches 2–3 cm diameter	0 (0)	$360 \pm 160$ (0–2070)	$1020 \pm 450$ (0–5080)	$260 \pm 110$ (0–1390)	0 (0)	0	0
trunk xylem	$918 \pm 94$ (514–1,792)	$7,930 \pm 623$ (4,340–12,355)	$24,059 \pm 1,653$ (9,680–36,908)	$38,946 \pm 3,079$ (14,376–61,517)	$45,973 \pm 4,110$ (18,562–96,713)	$15,204 \pm 784$ (10,622–21,688)	$5,074 \pm 289$ (3,395–7,307)
trunk bark	$178 \pm 32$ (62–510)	$1,516 \pm 166$ (682–3,005)	$3,656 \pm 420$ (1,419–8,119)	$4,515 \pm 452$ (1,635–9,611)	$5,327 \pm 641$ (1,600–13,336)	$2,659 \pm 250$ (1,232–5,289)	$1,033 \pm 88$ (474–1,856)
<b>leaf area in zone distal to node (m<sup>2</sup>)</b>	$7.7 \pm 3.9$ (2.0–16.7)	$37.8 \pm 18.2$ (13.5–77.2)	$26.0 \pm 18.7$ (2.1–56.5)	$7.1 \pm 10.9$ (0–43.3)	$0.2 \pm 1.0$ (0–3.9)	0	0
<b>volume in zone distal to node on the bole (cm<sup>3</sup>)</b>							
sapwood	$2,092 \pm 214$ (1,200–4,174)	$17,425 \pm 1,435$ (8,524–28,328)	$43,561 \pm 3,233$ (15,886–70,503)	$57,591 \pm 4,733$ (20,295–89,122)	$58,559 \pm 4,894$ (27,443–105,662)	$19,843 \pm 1,274$ (12,811–31,544)	$6,696 \pm 488$ (4,339–11,152)

	disk 5	disk 10	disk 15	disk 20	breast height	base	ground
<b>heartwood</b>	0 (0-8)	1,409 ± 151 (0-2,542)	11,232 ± 895 (5,566-19,302)	27,619 ± 2,404 (7,287-49,382)	36,039 ± 3,329 (8,793-72,722)	12,243 ± 769 (5,907-17,730)	4,012 ± 274 (2,451-6,184)
<b>inner bark</b>	291 ± 49 (106-765)	2,264 ± 236 (1,039-4,326)	5,652 ± 557 (2,359-10,731)	7,445 ± 644 (3,237-14,248)	7,180 ± 612 (3,677-12,291)	2,215 ± 179 (1,102-3,853)	719 ± 59 (327-1,312)
<b>outer bark</b>	0	0	112 ± 86 (0-1,489)	417 ± 184 (0-2,182)	4,555 ± 1,039 (0-17,125)	3,646 ± 381 (1,186-7,485)	1,562 ± 134 (637-2666)
<b>density (g/cm<sup>3</sup>)</b>							
<b>wood wedge</b>	0.44 ± 0.01 (0.39-0.47)	0.42 ± 0.01 (0.39-0.46)	0.44 ± 0.01 (0.41-0.48)	0.46 ± 0.01 (0.42-0.52)	0.49 ± 0.01 (0.44-0.54)	0.48 ± 0.01 (0.41-0.56)	
<b>bark wedge</b>	0.61 ± 0.02 (0.42-0.74)	0.67 ± 0.02 (0.53-0.87)	0.62 ± 0.01 (0.53-0.69)	0.56 ± 0.02 (0.44-0.69)	0.46 ± 0.01 (0.38-0.56)	0.45 ± 0.01 (0.37-0.51)	
<b>area (cm<sup>2</sup>)</b>							
<b>sapwood</b>	19.0 ± 1.1 (12.8-30.1)	73.9 ± 4.1 (48.6-107.6)	125.1 ± 7.1 (77.9-181.3)	156.1 ± 8.9 (101.2-219.8)	174.5 ± 9.7 (112.0-261.8)	223.2 ± 16.3 (144.6-371.7)	
<b>heartwood</b>	0	9.7 ± 0.9 (0-14.4)	46.3 ± 3.1 (23.6-81.6)	90.0 ± 5.6 (55.4-151.7)	111.8 ± 7.2 (39.0-173.2)	133.7 ± 9.1 (81.7-206.1)	
<b>inner bark</b>	2.6 ± 0.3 (1.2-5.6)	9.6 ± 0.8 (5.4-15.6)	16.6 ± 1.9 (6.9-42.2)	21.2 ± 1.8 (9.9-47.0)	20.4 ± 1.8 (8.5-34.6)	24.0 ± 2.0 (10.9-43.7)	
<b>outer bark</b>	0	0	0.6 ± 0.5 (0.0-8.6)	3.0 ± 1.8 (0.0-30.6)	21.9 ± 3.5 (0.0-61.5)	52.1 ± 4.5 (21.2-88.9)	
<b>width (average radial dimension, cm)</b>							
<b>sapwood</b>	2.30 ± 0.07 (1.88-2.93)	3.43 ± 0.14 (2.60-4.70)	3.53 ± 0.13 (2.43-4.48)	3.49 ± 0.15 (2.45-4.40)	3.60 ± 0.16 (2.40-5.05)	4.12 ± 0.23 (2.60-6.48)	
<b>heartwood</b>	0	1.53 ± 0.11 (0-1.95)	3.62 ± 0.13 (2.50-4.90)	5.14 ± 0.17 (4.00-6.80)	5.83 ± 0.21 (3.48-7.43)	6.44 ± 0.22 (5.10-8.10)	
<b>inner bark</b>	0.16 ± 0.02 (0.08-0.30)	0.29 ± 0.02 (0.18-0.43)	0.35 ± 0.03 (0.15-0.77)	0.37 ± 0.02 (0.20-0.68)	0.33 ± 0.03 (0.12-0.60)	0.35 ± 0.02 (0.18-0.63)	
<b>outer bark</b>	0	0	0.01 ± 0.01 (0.00-0.15)	0.05 ± 0.03 (0.00-0.48)	0.34 ± 0.05 (0.00-0.90)	0.72 ± 0.05 (0.31-1.18)	