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DISTRIBUTION AND VITALITY OF XYLEM RAYS IN RELATION TO TREE LEAF AREA IN DOUGLAS-FIR

by

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SUMMARY

The factors that determine sapwood width and volume in a tree are not known. This study asked whether sapwood width is related to a need for stem storage sites. Experiments were conducted on 12 34-year-old Douglas-fir [(*Pseudotsuga menziesii* (Mirb.) Franco] trees with a 6–7 fold range of leaf areas and leaf area/sapwood volumes. Because of declining ray frequency but constant average ray area, ray volume declined for the first 6–10 growth rings, then remained constant, and did not vary with height (breast height vs. 10 nodes from the top). Fewer of the ray parenchyma cells had nuclei in inner than outer sapwood. Inner sapwood had ray parenchyma with smaller rounder nuclei than did outer sapwood, and there was no effect of height. There was a positive relationship between leaf area and the relative volume of ray in outer sapwood at breast height ($r = 0.646$, $p = 0.02$), supporting the hypothesis that Douglas-fir trees with larger leaf areas have higher ray volume than do trees with smaller leaf areas. However, correlations of leaf area/sapwood volume with leaf area at either height were not significant, nor were correlations of either leaf area or leaf area/sapwood volume with measures of ray vitality (nuclear frequency in outer sapwood, or the ratio of nuclear frequency in the middle/outer sapwood or in inner/outer sapwood). These latter correlations give no evidence that Douglas-fir trees determine their sapwood volume based on a need for quantity of vital xylem rays.

Key words: Ray parenchyma, heartwood formation, ray volume, leaf area, sapwood area, *Pseudotsuga menziesii*.

INTRODUCTION

Sapwood width is characteristic of a species, but can change within a tree, with environment, age, and vigor. We do not know whether a tree operates according to some 'design criteria' for sapwood transverse area (or for sapwood volume), or whether the area (or volume) is determined by independent processes responsible for sapwood production and heartwood formation. The common assumption that sapwood area is determined by a need for water transport is simplistic and faulty in many cases. For example, there was a non-proportional reduction in sapwood area relative to leaf area

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after pruning in *Abies balsamea* trees (Margolis et al. 1988), and *Ulmus americana* trees maintain several years of sapwood, but > 90% of the water is transported in the outer ring. Better knowledge of the mechanisms responsible for sapwood area will advance our understanding of tree physiology. It will also improve our efficiency at processing trees into products and then utilizing them because sapwood and heartwood often differ greatly in their properties (color, permeability, surface chemistry, decay resistance, and moisture content).

One explanation for sapwood quantity that has not been explored is the potential relationship between tree size and available storage sites in the stem. Tree leaf area is used as the unit of size by which to compare trees because it approximates potential carbon gain, and it is a good index of the tree's potential for growth, recovery, and reproduction. If there is such a relationship, then one could expect a positive correlation between tree leaf area and parenchyma abundance and activity in the stem.

Our hypothesis assumes that the main role of parenchyma is storage of organic compounds (i.e., Dickson 1991). Actually, its roles undoubtedly depend on the evolved response of a species to the environment and to conditions during the plant's life. Other reported roles of xylem parenchyma include radial gas transport (Hook et al. 1972), alteration of concentrations of materials in the xylem stream (Sauter et al. 1973; Pate & Jeschke 1995; Van Bel 1995), and providing passive (Shain 1995) or active defense (Shigo 1984; Boddy 1992; Schmitt & Liese 1993; Smith & Shortle 1993), tissue for production of callus after injuries (Fisher & Ewers 1989), radial strength (Burgert et al. 1999), shear resistance (Myer 1922), and padding (Haberlandt 1914; Fisher & Ewers 1989; Putz & Holbrook 1991).

From the little that has been published on conifers, we know that from pith to bark there appears to be no change or a decline in ray frequency (number of rays/mm^2 tangential area; Gregory & Romberger 1975; Lev-Yadun 1998) and an increase in size of individual rays (Bannan 1937, 1954; Gregory & Romberger 1975). By vertical position in a tree, there may be little variation in ray frequency or ray height (Jaccard 1915, as cited in Larson 1994) or a modest decrease in ray frequency (Bannan 1965).

Activity of ray parenchyma is higher in outer than inner sapwood most of the year (with a few exceptions, i.e., Shain & Mackay 1973). This assertion is based on examination of cell storage contents (Hillis et al. 1962), uptake of tetrazolium (Fahn & Arnon 1963), callus production in tissue culture (Allen & Hiatt 1994), respiration rates (Pruyn et al. 1999), and shape, size, and abundance of nuclei in the ray parenchyma. In general, the outer sapwood has more frequent ray nuclei than the inner sapwood presumably because in inner sapwood many ray cells are dead and have no nuclei. Nuclei in the outer sapwood are large and oblong-elliptical, becoming rounder, smaller (Frey-Wyssling & Bosshard 1959; Nair & Chavan 1983), and more irregular in outline (Yang 1993) from the outer to inner sapwood. Ray parenchyma cells in outer sapwood are more likely to have a nucleus than those in inner sapwood, and the nuclei are absent in heartwood. The radial patterns of these characteristics across the sapwood are generally gradual, but the shape of the curve varies among species (Nobuchi et al. 1979; Yang 1993). The only study to compare heights was conducted in only one individual (Yang et al. 1994). The vigor of the ray parenchyma cells of the

outer sapwood (as defined by an index of nuclear shape) was highest at the base of the live crown, and decreased from there toward both the tree base and tip.

There have been few studies that relate tree vigor to parenchyma quantity in conifers. In some coniferous species, dominant trees had taller rays and a higher ray frequency than did the co-dominant or suppressed trees (Schultze-Dewitz 1961). Some studies report positive correlations between growth ring width and ray height (Bannan 1937, 1954, 1965; Gregory & Romberger 1975) or ray frequency (Bannan 1954; Gregory & Romberger 1975). Other studies, however, report no relationship between growth ring width and ray height (Lev-Yadun 1998) or ray frequency (Bannan 1965), or a negative relationship (summarized in Larson 1994: 375).

The following are the hypotheses tested in the coniferous species Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] with the goal of learning if there is evidence that a need for storage sites drives sapwood width and volume.

1) There is a pith-to-bark increase in ray volume (as a proportion of tissue) due to higher ray frequency (no./area) and no change in ray area, and there is no change with disk height.
2) There is no change with height but a pith-to-bark decrease in ray vitality, as judged by nuclear frequency in ray parenchyma (no./area of ray) and in nuclear length and width.
3) There is a positive relationship between both the tree leaf area and the tree leaf area/sapwood volume, and both nuclear frequency and the vitality of ray parenchyma.

MATERIALS AND METHODS

Plant materials

In March 1995, we felled 12 trees 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, trees were sampled from two adjacent research plots, one thinned (about 600 trees/ha in 1981), and one unthinned (about 3460 trees/hectare in 1981). Trees were 20 years old when thinning occurred (Velazquez-Martinez et al. 1992) and 34 years old at the time of harvest. Permanent subplots had been set up within each research plot and needed to remain intact, so we first determined the mean diameter at breast height (dbh) of trees within the subplot and marked trees outside the subplot that had dbh ± 10% of that mean. Six marked trees were then selected randomly from each research plot (outside the subplot) for harvest.

After felling the trees, we marked the main stem just above the 5th, 10th, 15th, and 20th node from the top, at breast height, and at the base (1.3 m and 0.3 m from the ground, respectively). The marked locations are hereafter referred to as being at the node, although they are actually just distal to it. The height to each of these marked nodes was recorded (Table 1) and then several replicate disks were taken from each marked location. We tracked information between these marked internodes separately, designating each interval 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.

Table 1. Descriptive characteristics of the sampled 34-year-old *Pseudotsuga menziesii* trees (n = 12 trees).

Variables	Mean ± s.e.	Range
Height above the ground (m)		
Tree tip	20.2 ± 0.7	15.5–23.7
Node 5	17.3 ± 0.7	13.5–20.7
Node 10	13.3 ± 0.7	10.0–16.6
Node 15	8.7 ± 0.5	6.2–11.2
Breast height	1.3	
Basal disk	0.3	
Diameter at breast height (cm)	19.5 ± 0.5	17.5–22.5
Sapwood width (cm, breast height)	3.4 ± 0.2	2.4–4.4
Sapwood area (cm^2, breast height)	159 ± 10	145–298
Total volume of sapwood in the trunk (m^3)	0.186 ± 0.015	0.118–0.284
Total leaf area (m^2)	76.3 ± 12.9	25–163
Leaf area/sapwood area (m^2/cm^2, breast height)	0.44 ± 0.06	0.17–0.76
Leaf area/sapwood volume (m^2/m^3, breast height)	397 ± 75	160–1049

Estimates of leaf area and sapwood volume

Heartwood and sapwood areas were determined on a fresh disk from each height for each tree. We drew two perpendicular diameters, highlighted the boundary area with the indicator stain Alizarine-red (Kutscha & Sachs 1962), measured sapwood and heartwood widths, and then averaged values for the two diameters. We then used geometry to estimate sapwood cross-sectional area for each disk and sapwood volume for each zone of the 12 trees. Sapwood area was taken as the area of the disk (excluding bark) minus the area of the heartwood. Sapwood volume was the volume of the stem segment (excluding bark) for the zone, minus the volume of the heartwood (knowing areas of sapwood and heartwood at the base and tip of each zone and knowing zone length).

To estimate leaf (= needle) biomass, we removed one third of all primary branches of each tree, separating by zone. After the branches were dried, leaves were remove and their oven-dry mass (48 hrs at 60° C) was determined. During the harvest a subsample of fresh leaves was also collected (one subsample per zone per tree). One-sided leaf area was estimated for each subsample using an image analysis system. Subsamples were oven-dried and weighed, and the conversion from leaf mass to area was calculated. An average value was calculated per zone for each of the plots and used to estimate whole-tree leaf area (unpublished). The distal leaf area is all the leaf area attached to the tree distal to (above) a disk.

The sampled trees represent a wide range of sizes, although they were all the same age (Table 1). The widest ranges were in tree leaf area, leaf area/sapwood area, and

leaf area/sapwood volume (which varied by factors of 6, 5, and 7, respectively), but even sapwood area at breast height and total volume of sapwood in the trunk varied by factors of two in the sample studied.

Ray size and distribution

Disks from node 10 ('disk 10') and breast height were air-dried and then oven-dried at 60 °C. One radial strip was removed from each disk, and then it was cut into blocks two growth rings deep. Tangential sections were made with the microtome in the middle of the earlywood on every other growth ring from the bark, starting with the ring formed in 1994. Thus, for disk 10, which had 10 growth rings, we sampled five rings (those produced in 1994, 1992, 1990, 1988, and 1986) and for the breast-height disk, which usually had about 26 growth rings, we sampled about 13 rings. Four tangential sections were made per sampled ring, stained in safranin, and permanently mounted.

Ray area, frequency and volume (a proportion) were estimated using an image analysis system. Slides were viewed through a compound microscope (Nikon Labophot-2) with a 10× objective lens and a color video camera (Sony CCD/RGB) that projected the image onto a color monitor (33 cm diagonal distance, Sony Trinitron) and onto a computer monitor (Apple Macintosh Quadra 800) by way of a digitizing card. Two fields of view (1.00 mm × 0.80 mm each) were randomly selected for each tangential section made, for a total of eight fields per sampled ring. Using the software NIH Image v. 1.60 (Rasband 1996), we highlighted all rays within each field of view with the program's paint tool. Entire rays (simple and fusiform, including epithelial cells and ray tracheids) were highlighted, including cell walls but excluding the canal itself. Fusiform rays were not distinguished from uniseriate rays in this research.

Ray area, then, includes cell wall, ray tracheids, and ray parenchyma, and excludes resin canals. Ray frequency is the number of rays per mm^2 tangential section. Ray volume is the proportion of tangential area occupied by ray (calculated for each growth ring as the sum of all ray areas divided by the sum of the areas viewed). Because we assume that the same result would be found at any nearby depth, this relative area is a good estimate of the volumetric proportion of tissue that is ray.

It would have been preferable to have quantified the longitudinal parenchyma as well, and to have excluded ray tracheids and probably radial and longitudinal epithelial cells. However, those details would have required too much labor. Bannan (1965) reported for the same species that 10% of the rows of fusiform rays were due to ray tracheids in outer wood at breast height; there were no data for the uniseriate rays or for proportion of rays occupied by epithelial cells.

Ray parenchyma vitality

Additional disks from node 10 and breast height were used to characterize nuclear frequency, length, width, area, and slenderness ratio, all of which were used as indices of parenchyma vitality. These disks were kept cold and moist ≤ 24 hours until we could remove a radial strip that extended from the cambium to one growth ring into

Table 2. The growth rings that were sampled for parenchyma vitality at two heights (the disk 10 nodes from the top of the tree and the disk at breast height) in 34-year-old *Pseudotsuga menziesii* trees (mean ± s.e., n = 12 trees; range). Values are the growth rings that were sampled, counting inward from the cambium.

	Growth rings sampled	Range
Disk 10		
outer sapwood	1	1
middle sapwood	3.3 ± 0.1	3–4
inner sapwood	6.3 ± 0.2	5–7
Breast height disk		
outer sapwood	1	1
middle sapwood	5.8 ± 0.2	5–7
inner sapwood	11.3 ± 0.4	10–14

the heartwood (as determined with the indicator stain). Strips were about 2 cm tangentially and 2 cm longitudinally. Strips were fixed and stored in 3% glutaraldehyde in phosphate buffer solution (pH 7.0, Glauert 1974).

We cut each radial strip into smaller segments of 2–4 growth rings, then sectioned them radially 22 µm thick. Sections were stained with Harris's hematoxylin (Johansen 1940) to highlight cell nuclei. They were mounted in glycerine for study then observed through the image analysis system described above.

Outer, middle, and inner sapwood were studied. The outer sapwood was the outermost growth ring. The inner sapwood was the innermost ring in which the earlywood contained nuclei. The middle sapwood was the growth ring mid-way between inner and outer sapwood (in terms of years, not distance, Table 2).

To estimate nuclear frequency (no. of nuclei/mm^2 of ray as seen in radial sections), we counted the nuclei in 20 areas of ray 400 µm × 150 µm (for a total area of 1.20 mm^2) directly off the Sony monitor for each of the three sapwood locations for the node-10 and the breast-height disks. To estimate the size and shape of nuclei, we viewed slides with the compound microscope using a 40× objective and displayed the image on the computer screen. We measured length and width of the magnified nuclei with a line tool (NIH Image v. 1.60) for 100 nuclei from the earlywood of each of the three sapwood locations for the node-10 and the breast-height disks.

Nuclear area was estimated using the formula of an ellipse with length and width as the major and minor axes. Slenderness ratio was calculated as nuclear length/width (Frey-Wyssling & Bosshard 1959). The nuclear elongation index is the nuclear length/parenchyma cell length (Yang 1986). It was not used in the current study because determining the full length of ray parenchyma cells was usually not possible in our preparations.

Data analyses

The data on ray distribution (ray area, ray frequency, and ray volume) were plotted to show the radial trends. They were plotted from pith to bark rather than from the

cambium inward to facilitate comparison of curves from the two heights. We assumed that the innermost ring analyzed was ring two, whereas it may have been ring one in some individuals because we had collected the data for every two years from the cambium inward. Inspection of plots showed no differences between the initial treatment (thinned and unthinned blocks) so data from both blocks were combined. Paired comparisons of the two heights were made with t-tests using Tukey-Kramer adjustments. All statistical procedures were conducted with Statistical Analysis Systems software (SAS Inc., 1996). Unless otherwise noted, values were considered statistically significant if $p < 0.05$.

The data on ray vitality (nuclear frequency, length, width, area, and slenderness ratio) were analyzed using a mixed model to account for correlation between disks (heights) within the same tree, and between radial positions within the same disk. The two plots (thinned and unthinned) were treated as blocks. Multiple comparison adjustments for the p-values were made using the Tukey-Kramer method when considering pairwise comparisons.

Correlation analysis was used to relate ray volume and parenchyma vitality to tree characteristics for each height separately. Here, the initial treatment (blocks) was ignored, with the assumption that each of the twelve trees was an independent observation. The correlations performed were the following: leaf area (at node 10 or breast height) or leaf area/sapwood volume (at node 10 or at breast height), vs. ray volume in the outer sapwood, nuclear frequency in the outer sapwood, the ratio of nuclear frequency in middle/outer sapwood, and the ratio of nuclear frequency in inner/outer sapwood.

RESULTS

Position effects on ray volume, area, and frequency

The average area of rays was independent of the growth ring number from the pith (Fig. 1a), but both ray frequency (Fig. 1b) and ray volume (Fig. 1c) declined for about the first 10 growth rings from the pith and then reached a plateau. There were no significant effects of height on ray area or ray volume (paired t-tests for matched growth rings, Fig. 1a, c) but for ray frequency, disk 10 was higher than the breast height disk near the pith, and lower toward the bark (Fig. 1b).

Position effects on ray parenchyma vitality

There were no significant effects of height on nuclear frequency, length, width, or slenderness ratio (using the mixed model for height and radial position, $p < 0.05$, Table 3). However, nuclear area was significantly higher at breast height than at disk 10.

The outer and middle sapwood had higher nuclear frequency than did inner sapwood. The slenderness ratio of nuclei was higher in outer than inner sapwood (Table 3) because the outer nuclei were both longer and narrower than the inner nuclei. The size of individual nuclei, as estimated by the area of an ellipse, was greatest in the outer sapwood, followed by the inner and then the middle sapwood (Table 3).

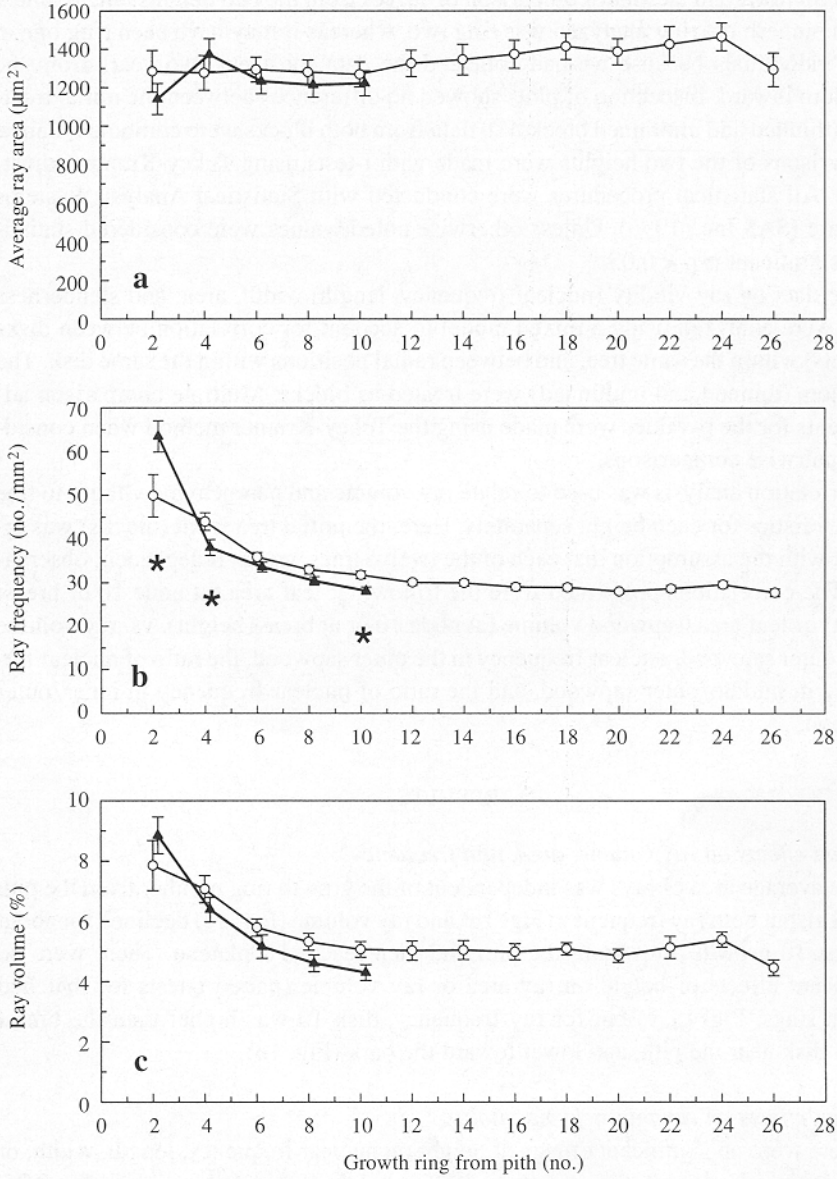

Fig. 1. Parenchyma characteristics vs. approximate number of growth rings (± 1) outward from the pith at two heights, disk 10 (filled triangles) and breast height (open circles), for 34-year-old *Pseudotsuga menziesii* trees (n = 4 to 12, depending on growth ring). Stems were sampled and analyzed in the tangential plane. An asterisk denotes significant differences between data points ($p > 0.05$, paired t-tests with Tukey-Kramer adjustments). a) Average ray area (µm²). b) Ray frequency (no./mm²). c) Ray volume (ray area/total area, %).

Table 3. Shape and frequency of ray parenchyma nuclei by height and radial sapwood position in 34-year-old *Pseudotsuga menziesii* trees (mean ± s.e., n = 12 trees). Stems were sampled and analyzed in the radial plane. Means within the same row but with different letters are significantly different ($p < 0.05$, mixed model using Tukey-Kramer adjustment for pairwise comparison).

	height	
	disk 10	breast height
nuclear frequency (no./mm² ray area)	110 ± 4 [a]	110 ± 4 [a]
nuclear length (μm)	30.4 ± 0.8 [a]	32.3 ± 0.8 [a]
nuclear width (μm)	6.7 ± 0.1 [a]	6.9 ± 0.1 [a]
nuclear area (μm²)	203 ± 5 [a]	221 ± 5 [b]
slenderness ratio (nuclear length/width)	4.7 ± 0.2 [a]	4.8 ± 0.2 [a]

	sapwood position		
	outer	middle	inner
nuclear frequency (no./mm² ray area)	114 ± 5 [a]	121 ± 5 [a]	93 ± 4 [b]
nuclear length (μm)	36.3 ± 0.9 [a]	27.8 ± 0.5 [b]	30.0 ± 0.7 [b]
nuclear width (μm)	6.5 ± 0.1 [a]	6.8 ± 0.1 [ab]	7.2 ± 0.1 [b]
nuclear area (μm²)	184 ± 5 [a]	148 ± 3 [c]	169 ± 4 [b]
slenderness ratio (nuclear length/width)	5.8 ± 0.2 [a]	4.2 ± 0.1 [b]	4.3 ± 0.1 [b]

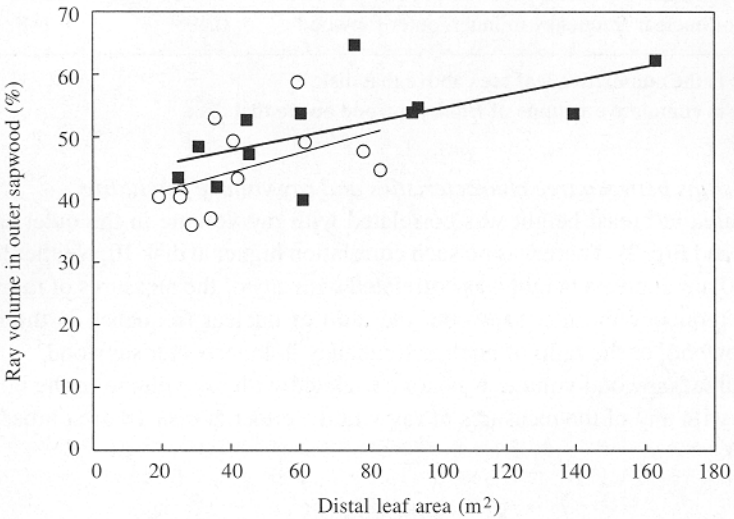

Fig. 2. Distal leaf area vs. ray volume in outer sapwood in 34-year old *Pseudotsuga menziesii* trees at breast height (closed squares, thick line, r = 0.646, p = 0.023) and disk 10 (open circles, thin line, r = 0.489, p = 0.107).

Table 4. Correlations of tree characteristics vs. ray volume and measures of ray parenchyma vitality (Pearson correlation coefficients (r) and probability values (p); n = 12 trees). Values in bold are significant.

Variables	r	p
leaf area[1] at disk 10		
ray volume in outer sapwood	0.489	0.107
nuclear frequency in outer sapwood	0.467	0.126
ratio of nuclear frequency in middle/outer sapwood	–0.403	0.195
ratio of nuclear frequency in inner/outer sapwood	–0.336	0.286
leaf area[1] at breast height		
ray volume in outer sapwood	**0.646**	0.023
nuclear frequency in outer sapwood	–0.043	0.895
ratio of nuclear frequency in middle/outer sapwood	–0.097	0.674
ratio of nuclear frequency in inner/outer sapwood	0.172	0.593
leaf area[1]/sapwood volume[2] at disk 10		
ray volume in outer sapwood	0.017	0.959
nuclear frequency in outer sapwood	0.500	0.097
ratio of nuclear frequency in middle/outer sapwood	–0.236	0.460
ratio of nuclear frequency in inner/outer sapwood	–0.483	0.112
leaf area[1]/sapwood volume[2] at breast height		
ray volume in outer sapwood	0.430	0.163
nuclear frequency in outer sapwood	–0.169	0.600
ratio of nuclear frequency in middle/outer sapwood	0.030	0.927
ratio of nuclear frequency in inner/outer sapwood	0.408	0.188

[1] value is the cumulative leaf area above that disk.
[2] value is cumulative volume of trunk sapwood above that disk.

Relationships between tree characteristics and ray volume or vitality

Leaf area at breast height was correlated with ray volume in the outer sapwood (Table 4 and Fig. 2). There was no such correlation higher at disk 10. Neither leaf area at disk 10 nor at breast height was correlated with any of the measures of ray vitality: nuclear frequency in outer sapwood, the ratio of nuclear frequency in the middle/outer sapwood, or the ratio of nuclear frequency in inner/outer sapwood.

Leaf area/sapwood volume was not correlated with ray volume in the outer sapwood or with any of the measures of ray vitality, either at disk 10 or at breast height (Table 4).

DISCUSSION

Contrary to hypothesis, the first 6–10 growth rings from the pith had higher proportional volume of ray parenchyma than wood farther from the pith. The radial pattern resulted from a decline in ray frequency with growth ring number from the pith, but

no change in area of individual rays. This result is in contrast to studies showing constant or declining ray frequency (Gregory & Romberger 1975; Lev-Yadun 1998) and increasing ray size from pith outward (Bannan 1937, 1954; Gregory & Romberger 1975). Douglas-fir maintains its needles for 4–6 years in this geographic region, about the same length of time that the stems appear to produce relatively high volumes of xylem storage sites. The two heights did not differ in their ray parenchyma volume for a given growth ring from the pith, implying similar storage capacity in the xylem in a young tree vs. at the tip of an older tree (as shown by the inner wood of the breast height disk vs. the outer wood of disk 10, respectively).

As hypothesized, there was a pith-to-bark decrease in ray vitality and there were no differences between the two heights. The nuclei were larger, longer, and narrower in the outer than in the inner sapwood. Given the reported connection between nuclear morphology and cell activity (Fahn & Arnon 1963), these results suggest that there is a decrease in vigor of ray parenchyma from the outer to the inner sapwood, as reported in numerous other studies (e.g., Frey-Wyssling & Bosshard 1959; Nair & Chavan 1983; Yang 1993; Allen & Hiatt 1994).

We had hypothesized that if these same-aged trees require a certain amount of parenchyma per leaf area, then trees with higher leaf area/sapwood volume would require higher ray volume and/or higher parenchyma vitality. Such relationships were not found either at breast height or the tenth node from the top of the tree. These results suggest that in Douglas-fir there is no causal relationship between tree architectural characteristics (leaf area, sapwood volume) and ray volume or vitality. We interpret these results to suggest that the amount of sapwood that a Douglas-fir tree maintains is not determined by its need for storage sites.

There was, however, a significant positive relationship between leaf area and volume of ray parenchyma in the outer sapwood, suggesting a relationship between leaf area and the properties of the new wood that is produced. The latter result is consistent with the reports that more vigorous individuals and/or those with wider growth rings produce more parenchyma than less vigorous or slower-growing individuals (Schultze-Dewitz 1961; Bannan 1937, 1954, 1965; Gregory & Romberger 1975), and it is contrary to other reports that have found no such effect (Bannan 1965; Lev-Yadun 1998; and summarized in Larson 1994: 375).

Much research is needed to elucidate how trees determine their sapwood quantity and balance the needs for water transport, carbohydrate storage and mechanical support. This study found no evidence that sapwood quantity was determined by a need for storage sites in ray parenchyma. In general, there are three possible approaches to the study of what determines sapwood quantity. One line of research could try to understand the controls and feedbacks over the production of new sapwood relative to competing uses for the photosynthate. Another line of research could elucidate the causes of the conversion of sapwood to heartwood. A third line of research could investigate the tradeoffs for one stem function, such as water transport or storage, at the expense of another function, such as mechanical support. Thus, further research in all three areas – the production of new sapwood, the conversion of old sapwood to heartwood, and the physiology of the existing sapwood – will help us better understand general tree growth and patterns of sapwood quantity.

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