Effects of live crown on vertical patterns of wood density and growth in Douglas-fir

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Abstract: It would be valuable economically to know what are the biological triggers for formation of mature wood (currently of high value) and (or) what maintains production of juvenile wood (currently of low value), to develop silvicultural regimes that control the relative production of the two types of wood. Foresters commonly assume the bole of softwoods produces juvenile wood within the crown and mature wood below. We tested that assumption by comparing growth ring areas and widths and wood density components of the outer three growth rings in disks sampled from different vertical positions of 34-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees. The 18 trees were sampled from one site and had a wide range of heights to live crown. Most of the variance (63–93%) in wood characteristics (growth ring area: total, earlywood, latewood; growth ring width: total, earlywood, latewood; latewood proportion: by area, width; and ring density: total, earlywood, latewood) was due to within-tree differences (related to age of the disk). Stepwise regression analysis gave us equations to estimate wood characteristics, after which we analyzed the residuals with a linear model that included whether a disk was within or below the crown (defined as the lowest node on the stem with less than three live branches). After adjusting for tree and disk position, only 2–10% of the residual variation was associated with whether the disk was in or out of the live crown. There were no statistically significant differences at $p = 0.05$ between a given disk (by node number) in versus out of the crown for any of the factors studied. Moreover, the wood density characteristics were not statistically significant at $p = 0.30$. This research suggests that there was no effect of the crown position on the transition from juvenile to mature wood as judged by wood density. Therefore, we found no evidence to support the concept that tree spacing and live-branch pruning have a significant effect on the cambial age of transition from juvenile to mature wood in Douglas-fir trees of this age.

Résumé : Il serait utile, d’un point de vue économique, de savoir ce qui déclenche la formation du bois mature (considéré présentement comme ayant une grande valeur) et ce qui maintient la production de bois juvénile (considéré présentement comme étant de faible valeur), de façon à développer des régimes sylvicoles pouvant contrôler la production de chacun de ces deux types de bois. Les forestiers assument couramment que la tige des conifères produit du bois juvénile dans la cime et du bois mature dans la partie inférieure. Nous avons testé cette hypothèse en comparant les composantes de l’aire et de la largeur des cernes annuels ainsi que de la densité des trois cernes annuels extérieurs dans chacun des disques prélevés à diverses positions en hauteur sur des douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) âgés de 34 ans. Les 18 arbres ont été échantillonnés sur le même site et présentaient une grande variabilité dans la hauteur jusqu’à la cime. La plus grande partie de la variabilité (63–93%) dans les caractéristiques du bois (surface des cernes annuels: totale, bois initial, bois final; largeur des cernes annuels: totale, bois initial, bois final; proportion de bois final: en surface et en largeur; et densité par cerne annuel: totale, bois initial, bois final) provenait de différences intra-arbres (en relation avec l’âge correspondant aux disques). L’analyse de régression par degrés a fourni les équations permettant d’estimer les caractéristiques du bois, après quoi les résidus furent analysés avec un modèle linéaire prenant en compte le fait que les disques se trouvent dans la cime (définie comme étant le plus bas verticille contenant au moins trois branches vivantes) ou en dessous. Après ajustement par arbre et par position de disque, seulement de 2 à 10% de la variation résiduelle était associée à la position du disque, soit dans la cime ou plus bas. Nous n’avons pas trouvé de différence significative ($p = 0,05$), pour aucun des facteurs analysés, entre les disques (définis par numéro de verticille) qu’ils soient situés dans la cime ou en dessous. Qui plus est, les caractéristiques liées à la densité n’étaient pas significativement différentes, même au niveau de $p = 0,30$. Ces résultats laissent croire qu’il n’existe pas d’effet de cime dans la localisation ou dans la transition du bois juvénile vers le bois mature en ce qui concerne la densité du bois. Par conséquent, nous n’avons trouvé aucune preuve pour supporter l’idée que l’espacement ou l’élagage des branches vivantes puisse avoir un effet significatif sur l’âge cambial de transition entre le bois juvénile et le bois mature chez des douglas de Menzies de cet âge.

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Introduction

Many studies suggest that the location of the crown affects the quality and quantity of wood produced along the bole in conifers (e.g., Larson 1963; Underwood 1967; DiLucca 1989; Sundberg et al. 1993; Fabris 2000). Hormonal signals (plant growth regulators) produced by the foliage and the apical meristems are thought to move downward toward the base of the tree and to control factors such as earlywood and latewood width, cell wall thickness, and cell expansion. It is thought that below the crown, there is less effect of the plant growth regulators, and so mature wood, which has less earlywood, narrower tracheids, and thicker cell walls, is produced (Larson 1962, 1969, 1973). Some silviculturists and modelers use the “rule of thumb” that the tree produces juvenile wood within the crown and mature wood below that level (e.g., Riou-Nivert 1989; Maguire et al. 1991; Josza 1995; Hann et al. 1997). There is conflicting evidence regarding the cause for the purported lowered effect of the plant growth regulators below the crown versus within the crown in softwoods (e.g., Sundberg et al. 1993; Little and Pharis 1995; Funada et al. 2001; Savidge 2001). It may result from differences by season and (or) vertical location in pool sizes of the plant growth regulators (Larson 1962, 1969; Aloni and Zimmermann 1983; Uggla et al. 1998; Funada et al. 2001), receptivity to the plant growth regulators (Sundberg et al. 1993; Little and Pharis 1995), the ratio of one plant growth regulator to another (reviewed in Savidge 1996), and (or) radial concentration gradient of the growth regulators near the cambium (Tuominen et al. 1997; Uggla et al. 1998, 2001).

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has a large economic importance for forest products industries of the United States, New Zealand, and parts of Europe. Its primary uses are dimension lumber, piles, plywood (Forest Products Laboratory 1999), and pulp, but it is found in many other solid and composite products as well. In almost all of these capacities its wood density is a good predictor of its economic value and (or) its performance because of density’s correlation with strength or pulp yield. Wood density in this species changes dramatically within the bole from the pith outward toward the bark, from the zone termed “juvenile wood” to the “mature wood”. Numerous researchers suggest that the height of the live crown, which is largely determined by tree spacing or artificial pruning, affects this radial pattern of wood density (Larson 1969; Polge et al. 1973; DiLucca 1989). As the rotation lengths for Douglas-fir shorten, the raw material base is shifting from a low proportion to a much higher proportion of this low-value juvenile wood (Kennedy 1995). Thus, there is potential economic value in predicting the quantity and density of wood from known stand characteristics.

Wood density in Douglas-fir generally declines from the pith outward for 5–10 years, then increases and levels off at a value higher than that near the pith, but occasionally it levels off at a value lower than that near the pith or it continues to increase gradually for more than 50 years (e.g., Megraw 1986*a*; Jozsa et al. 1989). The concept of a threshold for transition from juvenile to mature wood was developed for practical, not biological, usage. For example, we say the age of transition is around 10–20 years, because at this age there are only very small changes in properties between adjacent growth rings, and the wood mechanical properties in those growth rings are usually adequate for wood utilization. However, the curve may not reach a plateau for many decades. In an evaluation of seven individual growth rings in one old tree, Wellwood et al. (1974) found a peak in wood density at 150 years, a decline from 150 to 300 years, and then a leveling off from 300 to 400 years.

The transition point from juvenile to mature wood in Douglas-fir can be variable for a number of reasons: individual variability (DiLucca 1989; Fabris 2000), genotypic variability (McKimmy 1966; Vargas-Hernandez and Adams 1991; Abdel-Gadir and Krahmer 1993), and height in the tree (Fabris 2000). The calculated transition age of Douglas-fir varies depending on the algorithm used for calculations (Fabris 2000) and the wood characteristic studied (Megraw 1986*a*; Fabris 2000). Silvicultural management (Erickson and Harrison 1974; Smith 1980; Megraw 1986*b*; Jozsa and Brix 1989; Fabris 2000) and the site itself (McKimmy 1966; Cown and Parker 1979) can affect wood density values at a given cambial age.

Previous research on Douglas-fir has shown that compared with mature wood, the juvenile wood has wider growth rings, wider earlywood, and lower whole-ring density, latewood density, and latewood proportion (Megraw 1986*a*, 1986*b*; Jozsa et al. 1989; Fabris 2000). In a careful study of Douglas-fir trees from spacing trials in British Columbia, Canada, Fabris (2000) reported an increase in total ring density of 32% going outward from growth ring 6 through growth ring 25 for trees of intermediate crown class. Earlywood density was unchanged for the same interval, and latewood density increased by 15%. Total ring width, earlywood width, and latewood width declined by 75, 77, and 47%, respectively, over the same interval, so latewood proportion increased by a factor of almost two.

The current study investigated the effect of the position of the tree crown on wood density and ring areas and widths of the most recently produced wood. We used eighteen 34-year-old Douglas-fir trees from one site but with a wide range of crown depths. If crown position affects these wood characteristics as described above, then we would expect that after adjustment for disk age, wood within the crown will have wider growth rings, wider earlywood, less dense latewood, and lower latewood proportion than wood below the crown.

Materials and methods

Plant materials

In March 1995, we felled trees at the H.J. Andrews Experimental Forest in the central Cascades of Oregon, U.S.A. (site L107, 44°15′N, 122°10′W, 705 m elevation). To ensure a wide range of sizes and allocation patterns across trees of the same age, we sampled research plots at one site that had been planted with 2-year-old seedlings in 1963, then treated or left untreated in 1981–1984, which was 11–14 years before our harvest. Treatment consisted of thinning in 1981 from about 3460 to 600 trees/ha or thinning as described plus fertilizing in 1982 and again in 1984. The amount of fertilizer applied depended on tree size, with a mean application of 51, 11, 10, 7, 4, and 0.3 kg/ha of N, P, K, Ca, S, and Fe, respectively (Velazquez-Martinez et al. 1992). Six trees were harvested from each of the three treatments: unthinned unfertilized, thinned unfertilized, and thinned fertilized.

The original researchers established a subplot of 50 reference trees within each treatment. We chose our trees from outside that subplot but with diameter at breast height (DBH) within ±10% of the subplot mean. We marked 10 such trees in each plot, then selected the first six of those trees per treatment that could be felled without compromising future research on the subplots.

Harvests

After felling the trees, we marked the center of each internode 5, 10, 15, and 20 nodes from the tree top and also marked breast height and the tree's base (about 25 and 30 internodes from the top, respectively). The marked locations are hereafter referred to as disks 5, 10, 15, and 20 at nodes 5, 10, 15, and 20, respectively, although they are actually just distal to (above) the respective node. A disk was taken for this study from each of the marked locations. Tree height, DBH, and height to each of the nodes were recorded. The position of the crown was defined as the lowest whorl with less than three live branches. We also whittled through the outer bark to find the lowest point on the bole that one could still find green tissue (phelloderm), and noted the corresponding node as the base of the green bark.

Wood density, growth ring widths, and growth ring areas

The disks were air-dried for several weeks then oven-dried at 60°C. We sawed one randomly selected radial strip 1.9 mm thick (longitudinal direction) from each disk. We did not have a soxhlet apparatus of sufficient length to accommodate the strips, so we extracted them instead by submersion in boiling solutions in a deep beaker for four periods of 2 h each. The first and second periods were in 67% toluene and 33% ethanol. The third period was in 67% ethanol and 33% toluene, and the fourth period was in 100% ethanol (method modified from TAPPI 1987).

After extraction, the samples were weighted to prevent warping, while they conditioned to the equilibrium moisture content of the X-ray room. They were line scanned by X-ray with a direct-scanning X-ray densitometer, which produced a data value every 200 μm along the 200-μm wide scan. The X-ray beam comes from a fine-focus copper-targeted X-ray tube and is beta filtered to be relatively monochromatic (H.R. Holbo and B.L. Gartner, unpublished data). Precise sample thickness was measured with a digital caliper at three locations per sample, which then were averaged for each sample. Data were deconvoluted using standard methods (Liu et al. 1988) to give estimates of the density of the wood at each 200-μm position along the sample in dry mass per green volume (g/cm^3). Then, using DendroScan software (Varem-Sanders and Campbell 1996) we found the growth ring and earlywood–latewood boundaries, verified them by comparison of graphs to samples, then summarized data for each growth ring to give the following values: growth ring width (total, earlywood, and latewood), latewood proportion, and growth ring density (total, earlywood, and latewood). Growth ring area (total, earlywood, and latewood) was calculated assuming growth rings were concentric and that the radius we scanned was characteristic of all the radii. DendroScan assigns growth ring boundaries at the steepest point in density versus distance curves between the maximum latewood density of one year and the minimum earlywood density of the next year. It assigns the earlywood–latewood boundary as the distance point within one growth ring that has the mean density between minimum earlywood and maximum latewood densities.

Data analyses

Data were analyzed for two separate purposes, first to show the radial trends at several heights in the trees, and second, to determine how wood characteristics differ depending on the position of the crown. Radial profiles from the pith outwards were produced for each disk, for wood density, growth ring area, growth ring width, and proportion of latewood calculated by ring area or ring width. Each data point was the mean of all trees for that growth ring, but several disks were missing from the data set, so sample size was not always 18. Graphs were inspected for trends. We chose to show the values for the node 10 disk because it was always in the live crown, and the breast height disk, which was always below the live crown and had 25 growth rings, to show a longer trend.

For analyses of wood characteristics versus crown position, we used a ring mean of the values for each wood characteristic for the outer three growth rings. We looked only at these outer rings, because they should be the most influenced by the current crown position.

The overall variation of wood characteristics of the outer three rings was quantified by examining the variance components of the treatment, trees within treatment, and disks within a tree. Variance components were obtained using the VARCOMP procedure of SAS with the REML option (SAS Institute Inc. 1990).

A dummy variable that denoted whether a disk is in the live crown was constructed and called incrown, a value of 0 indicating that the disk was below the live crown and a value of 1 meaning that the disk was within the live crown. The only two positions that had samples both in and out of the live crown were disks 15 and 20, so only data from disks 15 and 20 were used to examine the impact of being in or out of the live crown.

Because the data showed that there were trends in all wood characteristics within the trees (see Figs. 1 and 2) we decided to use the disks from breast height (all out of the live crown) and node 10 (all in the live crown) to estimate the expected value of the wood characteristic at disk positions 15 and 20 for each tree. This procedure allowed us to remove much of the tree-to-tree and within-tree variation. Because distance between disks could influence the association between disks, the initial equation used to estimate the wood characteristic at disk 15 or 20 included both wood characteristics for the breast height disk and disk 10 and the distance (in nodes) from each disk to the disk in question (breast height or disk 10). For each of the wood characteristics an appropriate regression equation was constructed using the REG procedure with the stepwise model-building option. The initial model used in the analysis was

$$\text{Wood characteristic} = \bar{x} + b_1(\text{WC}_{\text{bh}}) + b_2(\text{DFBH}) + b_3(\text{WC}_{10}) + b_4(\text{DF10})$$

Table 1. Characteristics of studied 34-year-old *Pseudotsuga menziesii* trees.

Tree identification*	Base of live crown (nodes from top)	Lowest green bark (nodes from top)	Tree height (m)	DBH (cm)	Tree height/DBH (m/m)
uu 5	10	19	20.7	18.5	112
uu 4	11	25	21.6	18.9	114
uu 2	12	23	22.4	18.7	120
uu 6	12	22	20.3	19.5	104
tu 5	13	19	22.6	22.0	103
uu 3	14	27	23.7	19.9	119
tf 2	17	24	19.5	21.8	89
tf 4	17	24	23.4	22.7	103
tf 6	17	26	20.8	20.4	102
uu 1	18	18	22.2	18.4	121
tu 2	18	24	15.5	17.6	88
tu 6	18	25	17.1	17.6	97
tf 5	18	23	23.0	22.3	103
tu 3	19	24	20.4	21.2	96
tu 4	20	21	18.0	18.4	98
tf 3	21	23	19.7	21.4	92
tu 1	24	17	18.0	22.7	80
tf 1	24	21	21.1	24.8	85
Mean ± SE	16.8±1.0	22.4±0.7	20.5±0.5	20.4±0.5	102±3

*uu, unthinned unfertilized stand; tu, thinned unfertilized stand; tf, thinned fertilized stand.

where $\bar{x}$ is the mean value, WC_{bh} is the wood characteristic measurement for the breast height disk, DFBH is the distance (in nodes) the disk in question is from the breast height disk, WC_{10} is the wood characteristic measurement for the node 10 disk, DF10 is the distance (in nodes) the disk in question is from the node 10 disk, and b_1–b_4 are the regression coefficients for the various terms. Because the data were not balanced (i.e., at each disk position the number of disks in and out of the live crown were not equal), we weighted the disks so that both disk 15 and 20, and in- and out-of-live-crown disks were of equal weight. This ensured that the final equation was not biased because of any imbalance and ensured that the equations did not inadvertently remove any incrown differences. A final model was made after eliminating the variables that were not found significant in this stepwise regression using the default p value of 0.05. These significant variables and the r^2 from these stepwise regressions were tabulated.

The residuals from the above regression models were then analyzed to examine the incrown effect after adjusting for crown position and tree. The general linear models procedure of SAS was run with the following model:

$$\text{Wood characteristic} = \bar{x} + b_1(\text{incrown})$$

where $\bar{x}$ is the mean value, incrown is as previously defined, and b_1 is the regression coefficient indicating the effect of being in the live crown. The error mean squares for this analysis was not entirely correct, because the degrees of freedom used to adjust for tree and disk in the first regression had not been removed from the degrees of freedom for the error mean square. The error mean square was recalculated with the proper degrees of freedom, and the appropriate F values were recalculated.

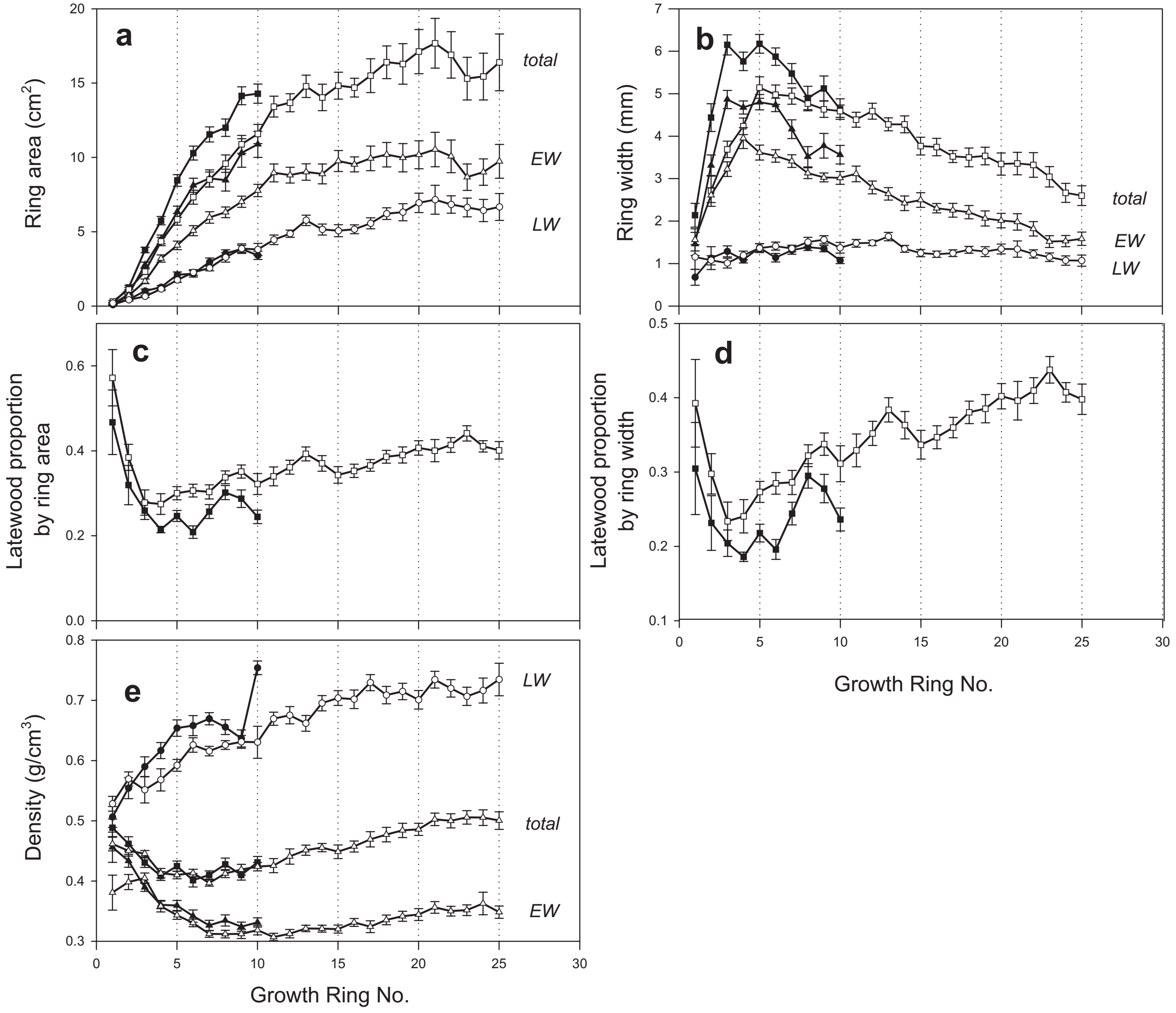
Results

The sampled trees exhibited a wide range of values for the location of the base of the live crown (10–24 nodes) and the lowest green bark (17–27 nodes; Table 1). Trees averaged 20.5 m in height and 20.4 cm in DBH. The ratio of tree height to DBH also varied widely, from 80 to 121 m/m.

The radial patterns of wood density and growth ring width were generally similar at all heights except the basal disk, so only two heights are shown, the disk from breast height and the disk from node 10 (Fig. 1). Growth ring area increased steadily and was tending to level out in the outer rings from the breast height disk (Fig. 1*a*). From about the fourth growth ring outward, ring width declined because of a decline in the earlywood width (Fig. 1*b*). Latewood proportion (based on either ring area or ring width) declined in the first five or so rings, then increased slowly as growth ring number increased (Figs. 1*c* and 1*d*). Total ring density decreased for the first four or five rings then increased gradually from that point outward (Fig. 1*e*). This pattern resulted from the increase in both latewood width (Fig. 1*d*) and latewood density (Fig. 1*e*) from the pith outward.

The vertical patterns of wood density and growth ring width (Fig. 2) are similar to the radial patterns (Fig. 1) if one compares them by growth ring number, except for the basal disk and in one case, the breast height disk, which have lower density than expected for their cambial ages. There was an increase in ring area (Fig. 2*a*) and a decrease in ring width (Fig. 2*b*) from the top of the tree downward, an increase in latewood proportion from the tip downward (Figs. 2*c* and 2*d*), and an increase in earlywood and total ring densities from about node 10 downward (excepting the base, Fig. 2*e*). In many cases, however, individual trees did not follow the expected pattern.

Fig. 1. Pith to bark variation in (*a*) growth ring area, (*b*) growth ring width, (*c*) latewood proportion by ring area, (*d*) latewood proportion by ring width, and (*e*) density (dry mass/green volume) of the xylem for disks from breast height (open symbols) and 10 nodes from the top of the tree (solid symbols) in 34-year-old *Pseudotsuga menziesii* trees (means ± SE, n = 16–18).



Analyses of the mean values of the last three growth rings showed that the within-tree component of variance (“disk within tree”) accounted for 63–93% of the total variation of wood density and (or) ring width (Table 2).

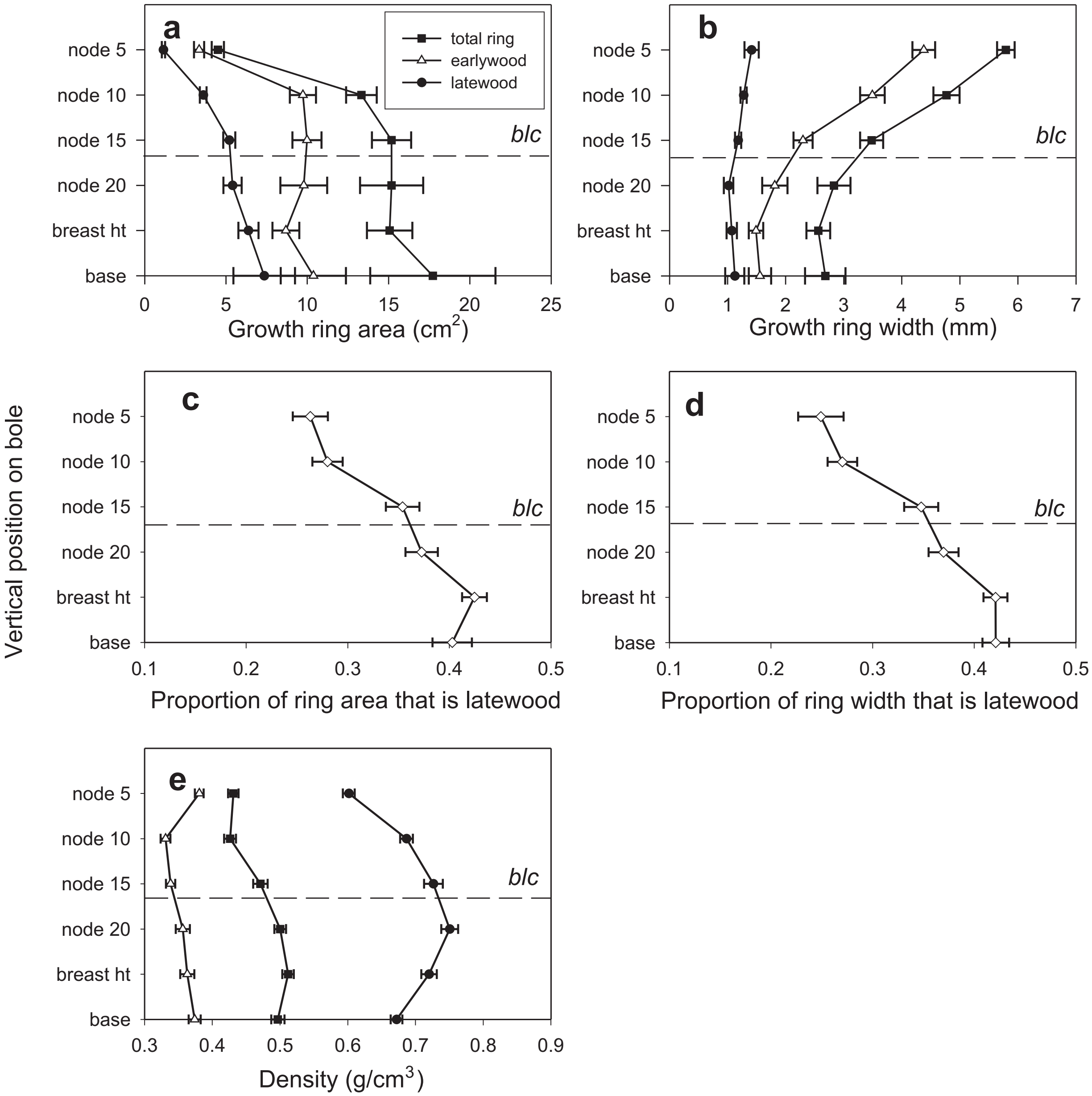
After limiting the data to only disks 15 and 20, 29–78% of the total variation could be accounted for using the first regression (which does not include incrown) (Table 3). Earlywood area was better explained than latewood area (r^2 = 0.638 vs. r^2 = 0.524, respectively), earlywood width was better explained than latewood width (r^2 = 0.690 vs. r^2 = 0.342, respectively), and earlywood density was better explained than latewood density (r^2 = 0.475 vs. r^2 = 0.352, respectively).

Incrown (whether the disk was in or out of the live crown) was not associated with any of the 11 characteristics studied (Table 4). Looking at the total variation, the amount of variation explained by incrown was $(1 - r^2$ (Table 3)) × (r^2 (Table 4)): 1–4% for the ring areas (total, earlywood, and latewood), 2–7% for the ring widths (total, earlywood, and latewood), 6% for latewood proportions (by area and by width), and <1–2% for ring densities (total, earlywood, and latewood). The regression coefficients indicated that, as expected, values of ring area and width were higher within than below the crown.

Discussion

These trees exhibited the same radial patterns of ring width, wood density (Megraw 1986*a*; Jozsa et al. 1989), and ring area (Underwood 1967) as those shown in previous studies. There is a clear trend of decreasing growth ring width, increasing wood density, and increasing latewood proportion from the tree top downward (with the exception of wood density at the lowest two positions), and an increase in ring area. Because the crown is on the upper part of the bole and has a lower cambial age, a comparison of in-crown

Fig. 2. Variation with height in (*a*) growth ring area, (*b*) growth ring width, (*c*) proportion of ring area that is latewood, (*d*) proportion of ring width that is latewood, and (*e*) density (dry mass/green volume) of the xylem, for the mean of the outer three growth rings in 34-year-old *Pseudotsuga menziesii* trees (means ± SE, n = 16–18). The broken line shows the mean base of live crown (blc).



to below-crown wood should always give the pattern that the wood higher up has more juvenile properties (Fig. 2). The question of the current research is whether crown position per se influences the rate of transition from the juvenile to the mature wood.

Whether a disk was in the live crown had no statistically significant effect on any of characteristics studied in these Douglas-fir trees: growth ring area (total, earlywood, and latewood), growth ring width (total, earlywood, and latewood), growth ring proportion (by either ring width or ring area), or growth ring density (total, earlywood, and latewood). Spacing trials support the conclusion with Douglas-fir that position of the crown has little influence on wood density. Fabris (2000) found no effect of initial spacing on wood density values (total, earlywood, and latewood) or on latewood proportion, in spite of significant effects on ring widths (total, earlywood, and latewood). His study averaged values for the whole core of the 50-year-old trees for the breast-height disk. Robbins (2000) compared wood density in Douglas-fir trees along a continuum of extremes in stand density, from 309 to 18 730 trees/ha. Whereas initial tree spacing had the large expected negative effect on height to the live crown and positive effect on diameter growth, it had little effect on wood density. At one of the two sites, earlywood density of growth rings 14–16 at breast height increased slightly with increased spacing (r^2 = 0.28, p = 0.0038) and latewood density decreased very slightly with increased spacing (r^2 = 0.14, p = 0.0480). The latter relationship was no longer significant when the smallest four trees (of 28 total) were removed. At the second site the relation-

Table 2. Variance components and proportion of total variance of wood characteristics using the mean values per ring of the outer three growth rings of disks 5, 10, 15, 20, breast height, and base in 34-year-old *Pseudotsuga menziesii* trees.

	Treatment		Tree within treatment		Disk within tree	
Wood characteristic	Variance component	% of total	Variance component	% of total	Variance component	% of total
Ring area	14.578	18	6.964	8	63.461	74
Earlywood area	7.308	24	4.241	13	19.639	63
Latewood area	1.225	8	0.050	0	15.137	92
Latewood area proportion	0.001 156	14	0.000 034	0	0.007 064	86
Ring width	0.359 6	14	0.145 7	6	2.101 6	81
Earlywood width	0.233 0	13	0.024 4	1	1.566 9	86
Latewood width	0.009 59	5	0.031 69	16	0.151 99	79
Latewood width proportion	0.000 765	9	0.000 09	1	0.007 74	90
Ring density	0.000 269	10	0.000 04	1	0.002 424	89
Earlywood density	0.000 097	7	0.000 292	20	0.001 096	74
Latewood density	0.000 351	7	0.0	0	0.004 959	93

Table 3. Dependent variables used to estimate wood characteristics and the resulting r^2 in 34-year-old *Pseudotsuga menziesii* trees.

Wood characteristic	Significant variables	r^2
Ring area	Disk 10 value	0.693
Earlywood area	Disk 10 value	0.638
Latewood area	Disk 10 value, BH value	0.524
Latewood area proportion	Disk 10 value	0.316
Ring width	Disk 10 value, nodes to BH	0.776
Earlywood width	Disk 10 value, nodes to BH	0.690
Latewood width	Disk 10 value, BH value	0.342
Latewood width proportion	Disk 10 value	0.293
Ring density	BH value, nodes to BH, disk 10 value	0.440
Earlywood density	BH value, nodes to BH, disk 10 value	0.475
Latewood density	Nodes to BH, nodes to disk 10	0.352

Note: Those variables that were significant in stepwise regression using the value of the wood characteristic at ring 10, the value at breast height, number of nodes to ring 10, and number of nodes to breast height.

Table 4. *F* value, significance, and correlation coefficient from models of the importance of disk position relative to crown position (disk within crown or below it) on the wood characteristics, using the residuals from the regression analyses.

Wood characteristic	Coefficient	F	p	r^2
Ring area (cm^2)	1.719	1.5313	0.2252	0.0470
Earlywood area (cm^2)	1.475	1.8043	0.1889	0.0550
Latewood area (cm^2)	0.325	0.3456	0.5610	0.0114
Latewood area proportion	–0.035	2.9951	0.0935	0.0881
Ring width (mm)	0.318	2.9938	0.0942	0.0936
Earlywood width (mm)	0.290	3.0972	0.0889	0.0965
Latewood width (mm)	0.173	3.3461	0.0779	0.1034
Latewood width proportion	–0.034	2.7779	0.1060	0.0847
Ring density (g/cm^3)	–0.006	0.2466	0.6233	0.0087
Earlywood density (g/cm^3)	0.008	0.5544	0.4627	0.0198
Latewood density (g/cm^3)	0.002	1.0789	0.3070	0.0336

Note: A positive coefficient means that the value is higher in the crown than below the crown.

ships were not significant at $p < 0.05$. Cown (1973) found no evidence that severe or moderate live-branch pruning accelerated the transition to mature wood in young radiata pines: severe pruning caused an increase in wood density (through a decrease in earlywood width) but had no effect on tracheid length. In contrast to the findings in the current study and the radiata pine study but consistent with Larson's (1963) hypotheses, several researchers have presented evidence in Douglas-fir that live-branch pruning can accelerate the transition to mature wood (Polge et al. 1973; DiLucca 1989; Jozsa 1995). Polge's study compared eight pruned to eight unpruned trees, but the other studies were not as well replicated; DiLucca's study was in only two trees, and Jozsa's strongest data were from 11 pruned trees versus 1 unpruned control.

Typically growth rings are wider within the crown than below the crown (reviewed in Larson 1963; Underwood 1967; Megraw 1986*a*). This pattern was seen in these data, but their magnitude was very low; about 2–7% of the total variation in growth ring width was attributable to whether the disk came from within the crown. Fabris (2000) found significant effects of tree spacing on ring widths at breast height, with wider spaced trees having prolonged periods of production of wide earlywood bands.

In the current study, growth ring width decreased with cambial age, whereas growth ring area increased. Ring width has many useful applications for an ecologist, forester, and wood scientist (for example, detecting the timing and magnitude of disturbance on the stand and tree level, gauging how steady is a tree and stand's growth, and explaining the change in wood density from pith to bark by percent latewood and latewood density). However, from the point of view of wood production, the growth ring area tells more.

These data show that even though the ring widths are decreasing after about the first four or five growth rings, the actual volume of wood added at a given height continues to climb much longer. However, the data from the current experiment shows no effect of crown base on the shape of either the ring width or ring area curves. Either measure gives about the same result for the proportion of latewood.

Most studies on Douglas-fir suggest that one can remove the lower third of the crown without much impact on diameter growth (reviewed in O'Hara 1991). Moreover, one-third of the live branches have many missing rings (Reukema 1959; Robbins 2000), suggesting that they have insufficient photosynthate to build their own structure and probably, therefore, do not contribute to bole structure (reviewed in Sprugel et al. 1991). Therefore, a first alternative to the base-of-crown theory is that the better indicator of change in wood is the location of two-thirds the length of the live crown (here, measured in nodes), which may be a good estimate of the base of the "functional" live crown. This point may have provided a better indicator of the vertical transition point from production of juvenile to mature wood. A second alternative indicator of the transition point may be the lowest position on the bole on which there is green bark (phelloderm), because the phelloderm, and not the foliage, could be the source of the signal for continued production of juvenile wood (Gartner 1996). The phelloderm is only millimetres away from the cambium and is often found only along the upper 10–40 years of the Douglas-fir stem (mean of 22–26 years in different sites; Gartner 1996). Therefore, we did all the same analyses presented in this paper using these two criteria (separately) for the vertical indicator of transition point. The analyses were complicated by the data distribution: we had only one bole position to examine and, therefore, fewer disks to compare. However, analysis of the data with these indicator variables (height of 67% of live crown, or base of green bark) also showed no effects on any measured or calculated wood characteristic.

The current research has implications for management and modeling of Douglas-fir stands. It suggests that live-branch pruning should have no practical effect on the transition age from juvenile to mature wood and that tree spacing should not affect the age of transition from juvenile to mature wood. It is possible that small effects have been masked by the small sample size in this study, and it is also possible that a study of a larger range of sites will find contradictory information; however, the current study suggests that if any differences do exist in wood density because of the location of the crown, they are very small and most likely not of practical significance for wood value. Other effects of crown position (such as branch size, volume growth, and the radial growth rates within the juvenile-wood vs. mature-wood zones) are probably much more important determinants of Douglas-fir wood quality and value.

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