Wood density of young-growth western hemlock: relation to ring age, radial growth, stand density, and site quality

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Abstract: Breast-high stem sections were sampled from 56 western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees growing in 15 plots representing a wide range of tree and site conditions in northwestern Oregon. Growth and wood density traits of individual rings were measured via X-ray densitometry, and relationships of ring density and its components to age and growth rate were analyzed. Ring density was highest (0.49 g/cm³) near the pith, declined to 0.40 g/cm³ at age 10, remained stable to about age 25, and then increased gradually and remained between 0.43 and 0.44 g/cm³ from age 38 to 45 and beyond. A negative influence of rapid growth on whole ring density was greatest at young ages and diminished with time, becoming nonsignificant beyond age 30. Earlywood density, latewood density, and latewood proportion were all negatively related to ring width at young ages, but by age 21–25, latewood proportion was the only component of ring density that remained significantly diminished by increased growth rate. Residual differences in wood density (after age and growth rate were considered) did not appear to be related to either stand density or site class. Overall, young-growth hemlock trees are relatively uniform in wood density and likely to be more so if grown in intensively managed stands.

Résumé : Des sections de tiges ont été prélevées à hauteur de poitrine sur 56 pruches de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) qui croissaient dans 15 places-échantillons représentatives d'une grande variété de conditions tant du point de vue des arbres que des sites dans le nord-ouest de l'Oregon. Les traits de croissance et de poids spécifique du bois de chaque cerne annuel ont été mesurés par densitométrie aux rayons X et les relations du poids spécifique et de ses composantes avec l'âge et le taux de croissance ont été analysées. Le poids spécifique des cernes annuels était le plus élevé (0,49 g/cm³) près de la moelle, diminuait à 0,40 g/cm³ à 10 ans, restait stable jusqu'à environ 25 ans et augmentait ensuite graduellement pour se stabiliser entre 0,43 et 0,44 g/cm³ de 38 à 45 ans et au-delà. L'influence négative de la croissance rapide sur le poids spécifique de l'ensemble du cerne annuel était la plus forte en bas âge et diminuait avec le temps pour devenir non significative après l'âge de 30 ans. Le poids spécifique du bois initial, le poids spécifique du bois final étaient tous négativement reliés à la largeur des cernes annuels en bas âge; mais vers l'âge de 21 à 25 ans la proportion de bois final était la seule composante du poids spécifique des cernes annuels qui continuait à être significativement affectée par l'augmentation du taux de croissance. Les différences résiduelles dans le poids spécifique, après que l'âge et le taux de croissance aient été considérés, ne semblaient pas reliées à la densité du peuplement ni à l'indice de station. Dans l'ensemble, le bois des jeunes tiges de pruche a un poids spécifique relativement uniforme qui devrait être encore plus uniforme dans des peuplements sous aménagement intensif.

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Introduction

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is a major commercial tree species in coastal forests of the northwestern United States and Canada. Its wood is used for construction lumber as well as appearance grades and remanufactured products. Its fiber has very good pulping characteristics and is used to produce a variety of pulp and

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paper products. Among conifers of the Pacific Coast region, only Douglas-fir has generated more interest to date in management and utilization. In the future, the relative importance of western hemlock is likely to increase because its silvical traits (such as shade tolerance) are amenable to a wide range of silvicultural systems, including multi-age methods (Harris and Johnson 1983). Furthermore, the species is resistant to Swiss needle cast, a disease now ravaging plantations of Douglas-fir near the coast in Oregon (Kanaskie et al. 1996; Maguire et al. 2002) and to a lesser extent in Washington (Omdahl 1997). However, relatively little research has been done to characterize the wood properties of young-growth hemlock or to determine and understand the influence of stand conditions and silvicultural practices on such properties.

Although the few studies of wood density (or specific gravity) carried out in young-growth western hemlock are limited in the number of sites sampled, some general pat-

| Attribute | Mean | SD | Min. | Max. | п |
|---------------------------------|--------|-------|-------|--------|----|
| Diameter at breast height (cm) | 36.8 | 17.2 | 13.6 | 84.4 | 56 |
| Total height (m) | 25.8 | 8.1 | 11.4 | 40.1 | 56 |
| Crown ratio | 0.52 | 0.17 | 0.26 | 0.93 | 56 |
| Tree age (year) | 42.4 | 16.8 | 10 | 112 | 56 |
| Site index (m at 50 year) | 34.8 | 3.4 | 30.8 | 41.8 | 23 |
| Trees/ha | 1039.9 | 711.0 | 398.7 | 2861.2 | 23 |
| Basal area (m ² /ha) | 58.4 | 13.1 | 28.8 | 81.3 | 23 |
| Stand density index (trees/ha) | 1090.8 | 229.3 | 637.8 | 1575.6 | 23 |

Table 1. Mean, standard deviation, and range for attributes for 56 sample trees and 23 stands.

terns are apparent. Most general texts and handbooks of wood technology indicate an average density of 0.42 or 0.43 g/cm³ for western hemlock, presumably determined mostly on old-growth samples (Allen 1902; Panshin and deZeeuw 1980; Haygreen and Bowyer 1996; Forest Products Laboratory 1999). Growth rings of the species are distinct, the lower density earlywood usually occupies two-thirds of the annual ring, and the transition to higher density latewood is gradual (Panshin and deZeeuw 1980). Most workers have reported that wood density is highest in the first five rings from the pith (Wellwood and Smith 1962), usually within the first or second ring if individual rings were assessed (Krahmer 1966; Megraw 1986; Jozsa 1998; Fabris 1999). Profiles across the radius indicate that density then declines with age to a low point between 10 and 20 years, followed by an increase. The period during which density is low may be either short and the rate of increase rapid (Jozsa and Middleton 1994; Jozsa 1998) or rather long with a very gradual recovery (Wellwood and Smith 1962; Krahmer 1966; Megraw 1986; Fabris 1999).

Three studies have documented a negative correlation between wood density and growth rate for wood outside what is considered to be the juvenile core (Krahmer 1966; DeBell et al. 1994; Jozsa 1998). Only two studies have provided data suggesting that growth rate has no effect on density of western hemlock wood (Megraw 1985; Watson et al. 2003). Neither of these studies, however, directly examined the relationship between ring width and wood density, either within individual rings or a group of rings known to have the same cambial age. Megraw (1985) found no significant differences in wood density of the outer 25 rings of increment cores extracted from "plus trees" (selected to have exceptionally rapid diameter growth) and "duds" (selected for exceptionally slow growth). Watson et al. (2003) examined the wood density of increment cores from 38-year-old trees growing in a research trial initially established at five different square spacings (0.9-4.6 m). Although the mean diameter of surviving trees (36%-70% had died) differed among some of the spacings, there were no statistically significant differences among the spacings in mean wood density.

Few studies have determined how the components of ring density (earlywood density, latewood density, and latewood percentage) vary by age or growth rate. DeBell et al. (1994), working within a limited age range (rings 20–24), found that earlywood density and latewood percentage were negatively related to growth rate ($R^2 = 0.16$ and 0.48, respectively), but latewood density and latewood width were not correlated

with growth rate. Smith (1980) did not examine wood density directly, but did show that latewood percentage decreased with growth rate in a 20-year-old spacing trial and was less at age 20 than at age 9. Jozsa's (1998) measurements, on the other hand, indicated that latewood percentage increased gradually with age from 15% in rings 6–15 to 48% in rings 71–90 in trees from natural stands. Fabris (1999) found little influence of growth rate and age on either earlywood density or latewood density in a 30-year-old spacing trial. Correlations between latewood percentage were weak during the juvenile period of development, but strengthened after age 20.

Several explanations can be advanced for both major and minor differences among wood density patterns found in these earlier studies, but the limited number of sites (stands or environmental conditions) sampled in each study is likely to be a major contributor.

This paper discusses radial growth and wood density in breast-high sections of young western hemlock trees growing on a wide range of sites and stand conditions in northwestern Oregon. Effects of cambial ring age, growth rate, and the interactions between these factors on ring density and on earlywood and latewood components are elucidated. In addition, wood density traits are examined for trends associated with site class, stand density, and response to thinning or release.

Materials and methods

Study area, field procedures, and data

Trees used for this study were felled as part of a larger research project on industrial forest land in the northern Oregon Coast Range (Marshall et al. 2003; Singleton et al. 2003*a*, 2003*b*). The sampling area extended from Tillamook to the Columbia River (approximately 46° – 47° N) and reached inland to include the eastern foothills of the Oregon Coast Range mountains (123°45′W). The trees were sampled from plots that ranged in elevation from 30 to 300 m, with average precipitation of 200–250 cm, average July maximum temperatures of 21.0–26.5 °C, and average January minimum temperatures of 0–4.5 °C (Jackson and Kimerling 1993).

Fifty-six trees used in the current study were selected from 23 stands to represent the full range of diameters, crown ratios, site indices, and stand density conditions that were sampled in the larger project. Trees of the oldest ages were favored in the selection so as to provide wood samples with the widest range of cambial ages. The sampling scheme consisted of collecting a cross-sectional disk at breast height

Table 2. Mean wood density and ring width statistics for rings along short and long radii in breast-high samples of young-growth western hemlock (n = 4096).

| Variable | Mean | SD | Min. | Max. |
|--|-------|-------|-------|-------|
| Ring density (g/cm ³) | 0.410 | 0.060 | 0.203 | 0.724 |
| Earlywood density (g/cm ³) | 0.361 | 0.056 | 0.156 | 0.695 |
| Latewood density (g/cm ³) | 0.530 | 0.055 | 0.191 | 0.765 |
| Ring width (cm) | 0.453 | 0.280 | 0.020 | 1.420 |
| Earlywood width (cm) | 0.332 | 0.240 | 0.015 | 1.255 |
| Latewood width (cm) | 0.121 | 0.101 | 0.005 | 1.076 |
| Latewood proportion | 0.301 | 0.159 | 0.013 | 0.936 |

(1.37 m above ground) from each tree. Table 1 summarizes tree- and stand-level characteristics of the 56 study trees and 23 stands from which they were sampled. Trees per hectare and site index were based on stand inventory data provided by the industrial owner. Site indices were computed using curves prepared by J.W. Flewelling (Bonnor et al. 1995) for western hemlock.

Laboratory procedures

Care and preparation of samples

The disks were transported from the field to the Forest Research Laboratory at Oregon State University in Corvallis within 4 days after cutting, then stored at 5 °C to curtail drying and fungal growth. After all the samples were collected, the disks were placed on pallets and air-dried using fans.

Radial samples were sawn from each disk for X-ray density analysis. These were obtained from one bark-to-bark strip (7 mm wide (cross-sectional) \times 1.6 mm thick (longitudinal)) through the pith such that it included a short and a long radius, the two of which summed to the average sample diameter. This approach facilitated consistent, accurate estimates of annual radial or diameter increment (Reukema 1971).

Extraction and X-ray procedures

The radial samples were extracted by being boiled in an 800-mL beaker in a series of 95% ethyl alcohol-toluene solutions (Singleton et al. 2003a). Samples were then spread on blotter paper, weighted to prevent out-of-plane warping, and allowed to air-dry. The air-dried samples were placed in the humidity-controlled X-ray room so they could equilibrate to its moisture content. After equilibration, the samples were run through a direct-scanning X-ray wood densitometer (Gartner et al. 2002) to determine their density and the variation within and between growth rings. Data were collected every 200 µm along the scan, then deconvoluted using standard methods (Liu et al. 1988) to give estimates of density backcalculated to dry mass per green volume (g/cm^3) . The mass attenuation coefficient needed to convert manipulated values to basic densities was calculated from a subset of eight samples. The positional data were then analyzed using Dendroscan software (Varem-Sanders and Campbell 1996) to find the boundaries between growth rings and between earlywood and latewood, and to summarize density components for each sample. The earlywood-latewood boundaries were determined by Dendroscan as the location of the average of the maximum and minimum density values within each annual ring. The final values for each growth ring in each sample were whole ring density, earlywood density, latewood density, whole ring width, earlywood width, latewood width, and latewood percentage.

Data summary and analyses

The primary variables used in the analyses were ring density, radial growth, and their components. These were defined as follows: ring density (basic density of entire annual ring, g/cm³); earlywood density (density of earlywood portion of annual ring, g/cm³); latewood density (density of latewood portion of annual ring, g/cm³); ring width (thickness of entire annual ring, cm); earlywood width (thickness of earlywood portion of annual ring, cm); latewood width (thickness of latewood portion of annual ring, cm); latewood proportion (proportion of annual ring that is latewood).

Means and various measures of variation for each component of ring width and density were calculated and plotted over number of rings from the pith (hereafter referred to as age profile plottings) to determine how such values changed with tree age. We limited evaluation of such trends to age 50, because beyond that age we had only a small sample of trees (all statistics up to age 50 were based on 10 or more trees).

Simple linear regressions were run to test the relationship of ring density, earlywood density, latewood density, and latewood proportion to ring width within individual rings (i) for each ring age from 1 to 40 years and (ii) for means of 5-year age groupings up to age 40. Quadratic equations for the latter means were also examined. Trait values for each age ring along the short and long radii were averaged for each sample tree before the regressions were run. These analyses were based on data from 25 or more trees.

To assess effects of site index and stand density on wood density, we compared age profile plottings for contrasting high and low site index classes and stand density classes. Data from trees at the extreme ends of the site and stand density classes were used for comparison: trees with the nine lowest and nine highest site index values (thus, 18 trees) were chosen for examining the relationship of site (or productivity) classes to wood density; and trees from plots with the seven lowest and eight highest stand densities (thus, 15 trees) were selected to assess the relationship between stand density and wood density. These selections constituted the most reasonable break-off points for contrasting comparisons. Visual examination and interpretation of the plottings was followed by multiple regression analyses (by 5-year age-classes) of ring density as a function of ring width plus indicator variables for site class or density classes. In addition, we screened age profile plots of ring width to identify trees that had grown slowly for several years before having a dramatic increase in growth rate, thus implying that the tree had experienced a sudden release from competition. Wood density - ring width relationships for "suddenly released" trees were compared with those determined for all trees.



Fig. 1. (*a*) Means and (*b*) coefficients of variation of ring width (rw), earlywood width (eww), latewood width (lww), and latewood proportion (lwpr) as related to ring number from pith (breast-high age) in western hemlock stem samples.

Results and discussion

General characterization of wood density of younggrowth hemlock samples

Mean ring density for rings along the short and long radii of all breast-high samples (n = 4096) in our study was 0.41 g/cm^3 (Table 2), with a coefficient of variation of 15%. This average density is similar to the most commonly published value (0.42 g/cm³) for western hemlock wood, and well within the range of mean ring densities observed in other studies of young western hemlock trees (Krahmer 1966; Megraw 1985; Jozsa 1998; Fabris 1999). Mean earlywood density averaged 0.36 g/cm³, and its range and coefficient variation (CV = 16%) were similar to that for whole rings. Mean latewood density averaged 0.53 g/cm³, but its CV was markedly lower (10%) than either whole ring or earlywood density. Latewood proportion averaged 0.30, and was much more variable than wood density values (CV = 54%). A wide range of values was obtained as intended for mean ring growth and the earlywood and latewood components thereof. The samples, therefore, were representative of and seemed adequate for refining and extending knowledge of wood density patterns in the young-growth western hemlock resource.

Relation of growth and wood density to breast-high age (ring number from pith)

Radial growth and its components

The pattern of mean ring width as related to breast-high age (Fig. 1*a*) was typical of that expected in young western hemlock trees on good sites in the Pacific Northwest (cf. Barnes 1962; Smith 1976). Ring width increased from 0.35 to 0.59 cm during the first decade of growth as the tree crowns expanded in width and length. After attaining a peak at age 7, ring growth more or less remained on a high plateau until the latter part of the second decade. Growth then began a gradual decline, eventually decreasing to a mean value of 0.21 cm at age 50. We assume that the decline is due in part to increasing competition from other trees in the stand. This decline is common to minimally managed stands of all species, and may be more pronounced in stands of tolerant species such as hemlock because competition-related mortality (i.e., natural or self-thinning) occurs more slowly

Fig. 2. (*a*) Means and (*b*) coefficients of variation of ring density (rd), earlywood density (ewd), and latewood density (lwd) as related to ring number from pith (breast-high age) in western hemlock stem samples.



than in stands of less-tolerant species. In a few trees, ring growth began to increase sharply at various ages after the initial decline, presumably because of the harvest or death of surrounding trees (see "Effects of stand density, site class, and 'release'on ring density" below). The plateau of high growth rate could no doubt be extended considerably through judicious early thinning, and growth rates could be markedly improved at older ages via later thinnings.

Age trends in the coefficient of variation for ring width (Fig. 1*b*) tended to be a mirror image of trends in ring width (Fig. 1*a*): 55% at breast-high age 1, declining to 44% by age 5, remaining between 44 and 50% to age 20, gradually increasing to an average of 59% from age 21 through about age 30, remaining steady at about 59% for the next 15 years, and then, fluctuating greatly year to year, increasing greatly between ages 45 and 50, but with a somewhat lower average level.

Earlywood width showed a pattern more or less parallel to that of whole ring width, and ranged from a high of 0.45 cm at breast-high age 7 to a low of 0.14 cm at age 50 (Fig. 1*a*). The age trend in the coefficient of variation for earlywood

width exhibited a pattern similar to that for ring width, but averaged about 10 percentage points higher (Fig. 1*b*). In contrast to ring width and earlywood width, latewood width was much more constant over time. It showed only a very slight increase from 0.11 cm at breast-high age 1 to 0.14 cm at ages 12–14, followed by nearly constant widths averaging 0.12 cm until about age 45, at which point it declined to 0.07 cm at age 50 (Fig. 1*a*). Although latewood width itself was rather constant over time, its coefficients of variation were markedly higher than those for ring width and earlywood width up to breast-high age 45 and fluctuated much more from year to year (Fig. 1*b*). From age 46 to 50, variation in late wood width was, on average, similar to that for ring width and earlywood width.

Latewood proportion started fairly high (33%), declined during the first 5–7 years to a mean low of 25%, and then remained constant or showed slight increases (25%-29%)through breast-high age 20 (Fig. 1*a*). It then began to increase gradually to an average of 40% at age 40 and beyond. From age 44 to 50, however, year-to-year fluctuations increased. Jozsa's (1998) results, based on 166 trees from five sites in coastal British Columbia, indicated that latewood percentage was lowest (15%) in rings 6–15 (he didn't show data for rings 1–5 and thus did not report any initial decline) and gradually increased to about 45% for ages 36–50 years. Coefficients of variation for latewood proportion averaged about 48% until about age 20, gradually declined to 37% by age 30, after which they became more erratic from year to year (though averaging 35%) through age 50 (Fig. 1*b*).

Ring density and its components

Mean ring density was highest (0.49 g/cm³) at breast-high age 1, declined rapidly to about 0.40 g/cm³ at age 10, and remained fairly constant at about 0.39 g/cm³ to age 28 (Fig. 2a). It then began to increase gradually and remained between 0.43 and 0.44 g/cm³ from age 38 to 44 years. At age 45 and beyond, density varied from year to year, averaging 0.43 g/cm³, and showed no obvious trend with age. This profile is consistent with the general pattern reported by Krahmer (1966), Megraw (1986), and Fabris (1999). The patterns reported by Wellwood and Smith (1962), Jozsa and Middleton (1994), and Jozsa (1998) were also similar, though their samples did not have the long period during which low density wood was produced. In their samples, density began to increase more quickly after reaching the low point. The high density values observed near the pith may result in part from large amounts of compression wood associated with the drooping leader characteristic of both eastern and western hemlock trees (Mergen 1958; Krahmer 1966), but it extends beyond the rings directly involved in the droop and thus must be influenced by additional factors. Coefficients of variation for ring density (Fig. 2b) were much lower than those for ring width. They were slightly greater from breast-high age 1 to age 17 (11%-15%) than from age 18 to 37 (9%-11%). Beyond 37 years, variation increased for 3 years (averaging 13%), but later declined and remained between 8 and 12% through age 50.

Earlywood density followed a pattern parallel to that of whole ring density: a high of 0.46 g/cm³ at breast-high age 1, a rapid decline to 0.36 g/cm³ at age 8, a broad period of low density (0.34–0.35 g/cm³) from age 10 to 29, and a very gradual increase to 0.37 g/cm3 at about age 39, followed by year-to-year variation about a fairly constant average density of 0.36 g/cm³ to age 50 (Fig. 2a). Trends in the coefficient of variation for earlywood density were similar to those for variation in ring density, but tended to be slightly higher at most ages (Fig. 2b). Latewood density showed the same basic pattern, but the amplitude of trends was markedly less. The initial high density was 0.55 g/cm³ and the low was 0.51 g/cm^3 at breast-high age 12 (Fig. 2a). It therefore appears that the high levels of overall ring density near the pith are more closely related to increased density in the earlywood portion of the ring and, to a lesser extent, to a higher proportion of latewood (Fig. 1a) than to greater density in the latewood portion of the ring. Most other workers did not report age profiles for earlywood and latewood densities in their papers. Fabris' thesis (1999) depicted and discussed age trends in these components of density, but trends were weak. He found no increase with time in earlywood density after an initial decline, and observed little variation in latewood density with age. The lack of strong trends in Fabris' study is most likely related to the nature of his sample (mostly suppressed trees). Coefficients of variation for latewood density were lower than those for ring density and earlywood density, and showed little trend with age except for being somewhat higher and more erratic from year to year after age 30 (Fig. 2b).

Relation of wood density to ring width or growth rate

Plottings and linear regression analyses of relationships of whole ring wood density and its components to ring width at individual ages (i.e., by 1-year age-classes) indicated significant relationships between growth rate and all density variables in early years, with a gradual decline in the strength of the relationships as breast-high age increased. Trends between some components and ring width became nonsignificant, whereas the relationships of whole ring density and latewood proportion to ring width remained significant through at least breast-high age 30 and 40, respectively. Analyses based on means of 5-year age-classes revealed similar trends. Thus, in the interest of brevity and simplicity, the discussion and associated graphs (Fig. 3) and statistical parameters (Table 3) presented here are based on the analyses of 5-year age-classes.

Because plotted data points for a few relationships suggested the possibility of curvilinear trends, we also examined quadratic equations. The quadratic term was statistically significant in only about 25% of the equations. For most of the significant quadratic relationships, there was little change from the general trends observed in the simple linear equations. In nearly all cases where substantial changes were noted, the resulting trends (curves) did not seem biologically reasonable, nor were they supported by the data (i.e., the statistical relationships had been heavily influenced by only one or two points). We therefore report and discuss only simple linear relationships in this section.

Wood density was reduced as radial growth rate increased (Fig. 3; Table 3). The reduction was greatest at early ages (when, in general, growth was increasing and density was decreasing). At breast-high ages 1-5 years, growth rate accounted for 37% of the variation in ring density. The reduction in wood density associated with increased growth decreased over time: it was 29% at 6-10 years, 20% at 11-15 years, and between 9% and 13% through age 30, after which ring width and wood density were not significantly related. Slopes also declined over time from -0.15 at ages 1-5 years to -0.10 at 6-10 years, -0.09 at 11-15 years, -0.05 or -0.06 at 16-20, 21-25, and 26-30 years. Although it should be recognized that the trend of decreasing values for p level and R^2 with age (Table 3) may be influenced to some degree by the decreasing numbers of samples, particularly at the later ages, the general tendency was strong even during the first 25 years when sample numbers remained similar. These can be observed in slopes depicted in Fig. 3.

The reduction in wood density was mediated through changes over time in the effect of growth rate on the components of wood density. Earlywood density decreased with increased radial growth at early ages. Up to about breast-high age 15, the slope of the relationship between growth rate and earlywood density was nearly parallel to that between growth rate and ring density. Growth rate at later ages had no significant effect on earlywood density. Latewood density decreased with increased growth rate in a consistent manner



Fig. 3. Ring density (rd), earlywood density (ewd), and latewood density (lwd), and latewood proportion (lwpr) as related to ring width by 5-year age-classes in breast-high stem samples of young-growth western hemlock.

up to about age 20, and thereafter was not significantly affected. Latewood proportion, however, was consistently and significantly reduced with increased growth rate for all ageclasses; and growth rate accounted for 15%–24% of the variation in latewood proportion. The reason for this relationship was that earlywood width, on average, increased proportionately more as ring width increased than did latewood width.

The net effect of such component changes was a decrease in the relative reduction in wood density associated with increased growth as trees became older (and taller, with greater distances between diameter at breast height and lowest live limbs). In other words, wood produced at a wide range of growth rates became more similar with increased age. This suggests that growth of trees more than 30 years old might be enhanced by silvicultural practices, with minimal reduction in wood density.

Effects of stand density, site class, and "release" on ring density

Plottings of ring density over ring number for highly contrasting site or stand density classes suggested that some differences in ring density at some ages may be associated with site productivity or stand density. After an initial decline, ring density was, on average, lower on high sites than on

Table 3. Statistics for regressions of ring density (rd), earlywood density (ewd), latewood density (lwd), and latewood proportion (lwpr) on ring width by 5-year age-classes.

| Ring group | Variable | Slope (rw) ^a | р | R^2 | п |
|------------|----------|-------------------------|----------|-------|----|
| 1–5 | rd | -0.147 | < 0.0001 | 0.367 | 55 |
| 1-5 | ewd | -0.136 | < 0.0001 | 0.349 | 55 |
| 1–5 | lwd | -0.069 | 0.0048 | 0.141 | 55 |
| 1–5 | lwpr | -0.223 | 0.0004 | 0.212 | 55 |
| 6-10 | rd | -0.103 | < 0.0001 | 0.289 | 56 |
| 6-10 | ewd | -0.088 | 0.0002 | 0.230 | 56 |
| 6-10 | lwd | -0.070 | < 0.0001 | 0.281 | 56 |
| 6-10 | lwpr | -0.139 | 0.0029 | 0.152 | 56 |
| 11–15 | rd | -0.087 | 0.0005 | 0.201 | 56 |
| 11–15 | ewd | -0.061 | 0.0050 | 0.136 | 56 |
| 11–15 | lwd | -0.055 | 0.0066 | 0.129 | 56 |
| 11–15 | lwpr | -0.170 | 0.0013 | 0.175 | 56 |
| 16–20 | rd | -0.048 | 0.0360 | 0.085 | 52 |
| 16–20 | ewd | -0.010 | 0.5988 | 0.006 | 52 |
| 16–20 | lwd | -0.043 | 0.0289 | 0.092 | 52 |
| 16–20 | lwpr | -0.157 | 0.0032 | 0.161 | 52 |
| 21–25 | rd | -0.059 | 0.0100 | 0.130 | 50 |
| 21–25 | ewd | -0.006 | 0.7470 | 0.002 | 50 |
| 21–25 | lwd | -0.027 | 0.2120 | 0.032 | 50 |
| 21–25 | lwpr | -0.237 | 0.0004 | 0.235 | 50 |
| 26–30 | rd | -0.065 | 0.0452 | 0.090 | 45 |
| 26-30 | ewd | -0.021 | 0.4035 | 0.016 | 45 |
| 26-30 | lwd | -0.011 | 0.6880 | 0.004 | 45 |
| 26-30 | lwpr | -0.243 | 0.0007 | 0.235 | 45 |
| 31–35 | rd | -0.050 | 0.1706 | 0.058 | 34 |
| 31–35 | ewd | -0.013 | 0.7065 | 0.005 | 34 |
| 31–35 | lwd | -0.013 | 0.7334 | 0.004 | 34 |
| 31–35 | lwpr | -0.191 | 0.0153 | 0.170 | 34 |
| 36–40 | rd | -0.077 | 0.1286 | 0.087 | 28 |
| 36–40 | ewd | -0.009 | 0.8475 | 0.001 | 28 |
| 36–40 | lwd | -0.038 | 0.4715 | 0.020 | 28 |
| 36–40 | lwpr | -0.269 | 0.0181 | 0.197 | 28 |

^arw, ring width.

low sites (0.36 vs. 0.40 g/cm³) until about breast-high age 25, after which density tended to be greater on high sites. In addition, the age profile plottings also suggested that ring density might be somewhat greater in trees grown in stands with the highest density than in stands with the lowest density (0.38 vs. 0.35 g/cm³). Parallel age profile plottings for ring width, however, revealed trends nearly opposite those for ring density — that is, at younger ages, ring width was wider on high sites than on low sites and in plots with low stand density than in those with high stand density. These trends reversed as stands became older. Intertree competition increased more rapidly with higher growth rates and, consequently, ring width decreased more rapidly in stands on high sites or with low stand density.

Based on our findings and those of others regarding the negative relationship between ring width and wood density, we suspected that such differences in ring density as existed between site or stocking classes were likely associated with trends in ring width. Plottings of ring density over ring width for contrasting site or stand density classes by 5-year age groups (similar to those in Fig. 3, but not shown) revealed no differences in the overall trend that was associated with site or stand density class. In addition, multiple regression analyses (by 5-year age-classes) of ring density as a function of ring width with indicator variables for site or stand density classes demonstrated an absence of any effect of the latter variables (p levels were not even close to significant). It therefore appears that within the broad range of conditions represented in our data set (further subsampled to provide the extreme contrasts), ring density was little affected by either site class or stand density class per se; and that apparent differences in wood density at some ages can be attributed to expected patterns in, and relationships to, growth rate (ring width).

Although stand density differences in a general sense had no effect on ring density beyond that associated with growth rate, we wondered about effects of a very rapid increase in growth rate. Perhaps "release" of a very slow-growing, suppressed tree in an overly dense stand might cause a greaterthan-expected decline in wood density. Age profile plottings of growth and ring density for individual trees showed that 15 of the 56 trees had substantial increases in ring width after having grown much more slowly than the average tree in our sample. The wood density change that accompanied the dramatic increase in radial growth was, in general, similar to what would be expected based on the ring density versus ring width relationships at the same age. In a few cases, the change — that is, the reduction in wood density — was greater than would be expected, but in all such cases the starting ring density was very high (>0.50 g/cm³) and the ending density was equal to that expected for the growth rate. In one case, a dramatic growth increase had no effect at all on wood density, but the tree in question was about 40 years old at the time, an age at which effects of growth on wood density were no longer significant (Table 3). We therefore conclude that sudden and extreme increases in radial growth caused by release will have no major deleterious effects on wood density, and that the likelihood of exceptional decreases in wood density is less at older than younger ages.

Evidence of juvenile-mature transition

Juvenile wood is the wood first formed near the pith at any height in the tree. It is laid down when the tree (or that height segment of the tree) is young, and its properties differ from those of mature wood. The amount and proportion of juvenile wood is an important consideration in the evaluation of suitability of young-growth trees for various end uses. For this reason, wood scientists have spent much effort in determining the transition point or zone from juvenile to mature wood for various species. Such determination is difficult because the individual wood properties (such as density, fiber length, and microfibril angle) may exhibit different trajectories as they change with age or distance from the pith. In addition, the zone may be indistinct and gradual in species such as spruce and cypress, but rather distinct in most hard pines and Douglas-fir (Di Lucca 1989).

Few attempts have been made to define the juvenile-mature transition for western hemlock. Fabris (1999) used segmented regression models to define the transition point, and determined a mean age of 21.5 years for western hemlock in his study. He also found that transition age decreased with crown class from dominant trees to suppressed trees. Jozsa (1998)

considered the juvenile zone as having a wood density ≤ 0.43 g/cm³ and used this rule of thumb to estimate amounts of juvenile and mature wood in his tree samples. If we apply that criterion to density–age trajectories for western hemlock trees on the sites he sampled, the transition point at breast height would range from 20 to 40 years on various sites; and if we apply it to his mean trajectory for "vigorous" young-growth hemlock (Jozsa and Middleton 1994), the transition age would be 32 years. As well, if we apply Jozsa's (1998) criterion — >0.43 g/cm³ — to the mean density–age trajectory for trees in our study (Fig. 2*a*), we would also place the end of the juvenile period at about 30 years. It is clear, however, that the juvenile-mature transition for western hemlock is indistinct and the change very gradual, insomuch as it can be characterized by wood density.

Summary and implications

Wood density in breast-high sections of young-growth hemlock was influenced by age and growth rate. These findings confirm, refine, and extend those of previous reports of other workers. Density was highest near the pith, declined rapidly during the first decade, remained stable until about age 25, increased gradually until age 40, and thereafter remained more or less level to age 50. Although the duration of the period of low density and the rate of recovery differ among previous studies, we suspect such differences are related to stand density and the associated development of inter-tree competition as it affects tree growth. If so, we would expect slower, more gradual increases in wood density in managed stands where growing stock (hence, competition) is maintained by thinning at levels favorable for growth. Although such practice would result in lower wood density on average, it would also lead to more uniform wood from pith to bark, thereby lessening any problems associated with an abrupt transition from juvenile to mature wood.

Wood density was negatively related to radial growth rate as indicated by ring width. The influence of rapid growth on wood density was most pronounced at young ages and diminished with time, becoming nonsignificant beyond age 30. (The same is true of the influence of age itself on wood density.) We found that this pattern was associated with changes over time in the relative influence of growth rate on three components of ring density: earlywood density, latewood density, and latewood proportion. At young ages, all three components were negatively related to ring width, whereas by age 21-25, latewood proportion was the only component of ring density that remained significantly diminished by increased radial growth rate. Thus, any penalty (i.e., reduced wood density) associated with thinnings that enhance radial growth of residual trees would likely lessen as trees became older.

Once age and growth rate were taken into account, we were unable to relate any residual differences in wood density to either site or stand density classes, even when comparing trees in the most contrasting conditions of site class and stand density. The possibility remains, however, that such differences might exist for trees or sites that are distinct geographically or environmentally from those in our data set. Overall, it seems that young-growth western hemlock is rather uniform with respect to wood density and will likely be more so in intensively managed stands.

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