VARIATION IN THE ANATOMY AND SPECIFIC GRAVITY OF WOOD WITHIN AND BETWEEN TREES OF RED ALDER (ALNUS RUBRA BONG.)

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ABSTRACT

Six 40-year-old red alders (Alnus rubra Bong.) were harvested from a mixed stand of A. rubra and big-leaf maple (Acer macrophyllum Pursh) in the Oregon Coast Range to evaluate variation in their wood characteristics at two heights. Because the trees had a slight lean (4 to 14°), we sampled along a diametric strip from the lower to upper side of the lean. For a disk from breast height and one from an upper height (5.8 to 6.1 m), we sampled 12–14 designated growth rings on both sides of the pith. For each sample we determined fiber length, vessel diameter, tissue proportion (proportion of a cross section occupied by fibers, vessels, rays, or axial parenchyma), and specific gravity. The variation of these properties between the two heights, between the lower and upper sides of the lean, and along the radius was analyzed among and within trees.

Variations between the two heights and between the lower and upper sides of the lean were minor or not significant for all measured characteristics. In the radial direction, fiber length and vessel diameter increased rapidly during the first 8 to 12 years (from 0.8 to 1.2 mm and 47 to 60 μm, respectively) and then leveled off. From pith to bark, there was no significant change in ray proportion, a small increase in the vessel proportion (from 23 to 28%), and a small decrease in the fiber proportion (from 63 to 57%). Specific gravity was constant radially and with height but varied significantly among trees (from 0.45 to 0.51 for tree means). These results suggest that the wood characteristics of A. rubra are quite uniform within individual trees with the exception of fiber length and vessel diameter, which increase radially in the first several growth rings.

Keywords: Fiber, vessel, ray, specific gravity, radial variation, wood quality.

INTRODUCTION

Red alder (Alnus rubra Bong.) is a common hardwood species of the Pacific Northwest of the United States, whose usage has recently increased greatly. This upsurge in usage of A. rubra for forest products is due to its availability and low cost at a time when the supply of softwoods has been restricted and softwood costs have increased. The hardwood harvest in Oregon and Washington increased by 28% from 1987 to 1991, and more than 76% of the 1991 hardwood harvest was A. rubra (Raettig

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The diffuse-porous wood is used extensively for pallets, furniture, cabinetry, turned products, plywood, and pulp. Its light color allows it to be stained to resemble a variety of other woods. Given the tree's abundance and its wood's value (Atterbury 1978), it is surprising that so little is known about its variability from tree to tree and within a bole. This study was designed to find the patterns of variation in anatomy and specific gravity within and between trees to show whether there are distinct juvenile/mature wood zones as defined by different characteristics.

Most studies on within-plant variation in wood quality focus on radial variation (Zobel and van Buijtenen 1989), and these studies, predominantly in softwoods, usually divide the wood into juvenile- and mature-wood zones. Juvenile wood, the inner portion of the tree stem, is characterized by a progressive change in cell features and wood properties (Panshin and de Zeeuw 1980). It is understood that the terms are convenient labels for zones of wood that actually change gradually, not in a stepwise fashion as the labels would suggest. Because of juvenile wood's poor characteristics (e.g., high longitudinal shrinkage, low strength) for many applications, juvenile wood has been studied extensively (Bendtsen 1978; Thomas 1984; Bendtsen and Senft 1986; Jackson and Megraw 1986; Krahmer 1986; Malone 1986).

The research that has been reported on within-plant variability in Alnus has concerned its wood density. Parker et al. (1978) reported inconsistent trends in wood density from pith to bark in A. rubra. Harrington and DeBell (1980) found that A. rubra lacked a low density, juvenile core. Lowell and Krahmer (1993) reported that although radial position affected longitudinal shrinkage, a slight lean had no effect on wood density in A. rubra. Hernandez and Restrepo (1995) found differences between populations of a Central and South American alder, A. acuminata: some populations had constant, but other populations had increasing, specific gravity from pith to bark.

The location of the juvenile/mature wood boundary depends on the property investigated (e.g., Peszlen 1994 for Populus spp.). Because within-bole properties other than specific gravity have not been reported for A. rubra, it is possible that the patterns of radial variation of anatomical properties are different from those of specific gravity. Moreover, different properties are important for different end-uses of the wood. Therefore, the variation of each property needs to be investigated. The patterns of property variation with height vary by species, and so are currently hard to predict.

The objectives of this study were to determine the extent of variation in the anatomical properties of A. rubra wood among and within trees and to quantify the radial variation of these properties at two heights. These results should be useful to users of Pacific Northwest hardwoods, and also provide clues about the biology of a widespread, yet understudied, native hardwood.

**Materials and Methods**

**Materials**

We randomly selected six 40-year-old trees with similar diameters at breast height (30 to 36 cm) from a mixed stand of Alnus rubra and big-leaf maple (Acer macrophyllum Pursh) in the McDonald-Dunn Forest of Oregon State University, Oregon (123°19'30" W, 44°38'30"N, 200 m elevation). The trees had fairly vertical stems and lacked large scars in the lower bole (0 to 6 m). We recorded their lean angle from vertical and marked its direction on each disk. The lean angles of the lower boles were 5°, 5°, 2°, 5°, 5°, and 14° for trees 1 to 6, respectively, and the trees averaged 20.8 m in height (18.3 to 23.8 m). A 25-cm-thick disk was cut at each of two heights: breast height (1.3 m) and an upper height (5.8 to 6.1 m), which was close to but below the first fork or large branch.
Fig. 1. Preparation technique for *Alnus rubra* samples. (A) Two disks were cut perpendicular to the trunk of the tree; (B) a diametric strip was removed from the lower side to the upper side of the lean; (C) samples from designated growth rings were removed from the diametric strip in order to determine specific gravity and anatomical properties. Two subsamples (blocks) were removed from each sample.

**Sample preparation**

Less than 24 hours after harvest, a 2.5-cm-wide slab was cut along a diameter of each disk from the lower to the upper side of the lean in the tree (Fig. 1). Slabs were kiln-dried and then stored in a room with an equilibrium moisture content of 12%.

Each dried slab was divided at the pith into a lower and an upper side. Then a series of radial samples were sawed from both sides of each disk. The cuts were centered on growth rings 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 23, 26, 30, and 34 at breast height and 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 25, and 30 at the upper height. Ring number from the pith is hereafter referred to as cambial age. We avoided aggregate rays during sample preparation because of their nonuniform distribution (Niskowiak 1978). Samples were 0.51 cm (0.20 in.) in the radial direction, 0.64 cm (0.25 in.) in the tangential direction, and 8.26 cm (3.25 in.) along the grain.

**Measurements**

The specific gravity of each sample was calculated from oven-dry weight and volume of the sample at 12% moisture content. Each sample was subsampled into two blocks, and parts of each of those blocks were macerated and sectioned transversely and radially. Average fiber length and vessel diameter were obtained by measuring 40 individual fibers and vessels from each block, giving 80 measurements/sample (and because there were two radii/designated growth ring, 160 measurements/designated growth ring). The number 80 was derived from a published estimate of variance in fiber lengths in red alder (Berghman 1949). We softened the dried blocks in water, then sectioned them (20 μm thick) in the transverse and radial planes. The transverse sections were stained in aqueous safranin before mounting, but the radial sections were not stained.

To determine fiber length, we macerated
several match-sized sticks/block by boiling them in water for 15 min and then heating them at 85°C for 20 min in a solution of 20 ml 20% nitric acid and 0.5 g sodium chloride. The acid was replaced by water and the fibers were boiled for 10 min more. The water was exchanged several times to remove excess acid; then the fibers were stained in aqueous safranin overnight. Temporary slides of the macerated fibers were made with glycerin as the mounting medium.

We used an image-analysis system for anatomical measurements. The images of the microscope slides were captured through a CCD video camera attached to a stereo-microscope (for fiber lengths) or a compound microscope (for other measurements). Images were processed and analyzed with the public-domain software program NIH Image (Rasband 1992). In this procedure, one first digitizes the microscope image, digitizes a stage micrometer at the same magnification (to get a pixel/µm conversion), then calibrates the screen.

Anatomical characteristics were determined on digitized images of the macerated wood (fiber lengths) or transverse sections (vessel diameters) using the image analysis system described above. For fiber lengths, we used a mouse to designate each end of the fiber, ensuring that only entire fibers were measured. Measurements on the transverse sections were made in the tangential direction.

The proportion of tissue in different cell types was estimated for two sections (almost duplicates of one another) from each block (so four sections/sample) of about 10–45 mm² each, depending on ring width. Vessels were distinguished from fibers and axial parenchyma by defining 620 µm² as the smallest vessel lumen area, based on preliminary measurements. The axial parenchyma cells of each cross section, and then the vessels, were “painted” on the computer screen by the computer operator, and their area relative to the whole section was then assessed by the program. Ray proportion was measured by the same method, but on radial sections. The fiber proportion was obtained by subtracting proportional areas of vessel, ray, and axial parenchyma from unity (100%).

**Analysis of variance**

An analysis of variance (ANOVA) was performed to evaluate the variation in wood properties among trees (tree effect), between the two heights (height effect), and between the lower and upper sides of the lean (lean effect), with an SAS general linear model (SAS Institute 1988). In order to control for the differential effect of cambial age between the two heights, we used samples from twelve cambial ages at each height: 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, and 30 at both heights, and in addition, 26 at breast height and 25 at the upper height.

**Regression analysis**

We used regression analyses to describe the radial profiles of each wood property as a function of cambial age at each height. If preliminary analyses showed that the tree effect and its interaction with age and the variable were not significant (P < 0.05), regressions were based on pooled data from the six trees. Otherwise, regressions were calculated separately for each tree.

We used simple linear regressions when the relationship between a wood property and cambial age followed a linear pattern. We used a piecewise linear regression (also called a segmented regression; Neter et al. 1985) to fit together two or more linear regressions to detect demarcation ages between juvenile and mature wood (Bendtsen and Senft 1986; Quanci 1988; Abdel-Gadir and Krahmer 1993). For a two-segmented piecewise linear regression, we used the formula $Y = \beta_0 + \beta_1 X$ for the juvenile wood segment, and $Y = (\beta_0 + \beta_1 + \beta_2) + (\beta_3 + \beta_4) X$ for the mature wood segment. A regression was run independently for a range of demarcation ages for each feature (fiber length, vessel diameter, the three tissue proportions, specific gravity); then the regression function with the strongest determination coefficient (or minimum mean squared error)
Table 1. Mean characteristic values of six Alnus rubra trees at two heights and for the two sides of the lean. Axial parenchyma represented 1-5% of the volume, and is not shown in the table.

<table>
<thead>
<tr>
<th>Height</th>
<th>Side of the lean</th>
<th>Sample size (mm)</th>
<th>Ring width (mm)</th>
<th>Fiber length (µm)</th>
<th>Vessel diameter (%)</th>
<th>Fiber proportion (%)</th>
<th>Vessel proportion (%)</th>
<th>Ray proportion</th>
<th>Specific gravity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper height</td>
<td>Both</td>
<td>144</td>
<td>3.1</td>
<td>1.1</td>
<td>57</td>
<td>61</td>
<td>24</td>
<td>13</td>
<td>0.48</td>
</tr>
<tr>
<td>Breast height</td>
<td>Both</td>
<td>144</td>
<td>3.3</td>
<td>1.1</td>
<td>61</td>
<td>59</td>
<td>27</td>
<td>14</td>
<td>0.46</td>
</tr>
<tr>
<td>Both</td>
<td>Lower side</td>
<td>144</td>
<td>3.2</td>
<td>1.1</td>
<td>58</td>
<td>60</td>
<td>25</td>
<td>14</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>Upper side</td>
<td>144</td>
<td>3.4</td>
<td>1.1</td>
<td>60</td>
<td>60</td>
<td>25</td>
<td>14</td>
<td>0.47</td>
</tr>
<tr>
<td>Upper height</td>
<td>Lower side</td>
<td>72</td>
<td>3.0</td>
<td>1.1</td>
<td>56</td>
<td>61</td>
<td>23</td>
<td>13</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Upper side</td>
<td>72</td>
<td>3.2</td>
<td>1.1</td>
<td>58</td>
<td>61</td>
<td>24</td>
<td>13</td>
<td>0.48</td>
</tr>
<tr>
<td>Breast height</td>
<td>Lower side</td>
<td>72</td>
<td>3.2</td>
<td>1.1</td>
<td>60</td>
<td>59</td>
<td>27</td>
<td>14</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>Upper side</td>
<td>72</td>
<td>3.4</td>
<td>1.1</td>
<td>62</td>
<td>59</td>
<td>28</td>
<td>14</td>
<td>0.46</td>
</tr>
<tr>
<td>Tree mean</td>
<td></td>
<td>288</td>
<td>3.2</td>
<td>1.1</td>
<td>59</td>
<td>60</td>
<td>26</td>
<td>14</td>
<td>0.47</td>
</tr>
</tbody>
</table>

RESULTS

Analysis of variance (ANOVA)

The mean values of wood properties from each height and each side of the lean are shown in Table 1. The results of the analysis of variance for each wood property are shown in Table 2. Axial parenchyma proportion is not reported here because it represented a small proportion of the volume (<5% for individual measurements, generally 0.5-1.8%) and showed no significant trends.

Differences between trees.—Vessel diameter and specific gravity varied significantly among trees, but there were no other significant variations among trees (Table 2). Mean vessel diameter varied from 43 to 71 µm among the six trees and mean specific gravity varied from 0.45 to 0.51 among trees (mean of both heights, both sides of disks, and all growth rings at each height). Based on the least significant difference (Steel and Torrie 1980), the trees were classified into three homogeneous categories of vessel diameter: (A) trees 4 and 6 had the smallest vessel diameter; (B) trees 1, 2, and 3 had the largest; and (C) tree 5 had a vessel diameter between (A) and (B). By the same method, the trees were classified into four homogeneous categories for specific gravity: (A) tree 2 had specific gravity of 0.45; (B) trees 1, 3, and 4 had specific gravity between 0.46 to 0.47; (C) tree 5 had specific gravity of 0.48; and (D) tree 6 had specific gravity of 0.51.

Effects of height and lean.—The only significant differences between the two heights were vessel diameter and vessel proportion (Table 2, Figs. 2 and 3). Specific gravity was slightly higher at the upper than lower height at P = 0.06 (Table 2, Fig. 4). There were no

Table 2. Analysis of variance (P-values) of wood characteristics within and between Alnus rubra trees as a function of height in the tree (upper vs. breast height), the upper vs. the lower side of the lean, and the interaction of the two. DF is degrees of freedom.

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>DF</th>
<th>Ring width</th>
<th>Fiber length</th>
<th>Vessel diameter</th>
<th>Fiber proportion</th>
<th>Vessel proportion</th>
<th>Ray proportion</th>
<th>Specific gravity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree</td>
<td>5</td>
<td>0.57</td>
<td>0.15</td>
<td>0.001**</td>
<td>0.51</td>
<td>0.14</td>
<td>0.64</td>
<td>0.009**</td>
</tr>
<tr>
<td>Height (tree)</td>
<td>1</td>
<td>0.23</td>
<td>0.11</td>
<td>0.04*</td>
<td>0.13</td>
<td>0.025*</td>
<td>0.22</td>
<td>0.06</td>
</tr>
<tr>
<td>Lean (tree)</td>
<td>1</td>
<td>0.20</td>
<td>0.16</td>
<td>0.15</td>
<td>0.53</td>
<td>0.55</td>
<td>0.95</td>
<td>0.41</td>
</tr>
<tr>
<td>Height × lean (tree)</td>
<td>5</td>
<td>0.97</td>
<td>0.24</td>
<td>0.94</td>
<td>0.62</td>
<td>0.75</td>
<td>0.36</td>
<td>0.64</td>
</tr>
</tbody>
</table>

* P < 0.05.
** P < 0.01.
significant differences between the lower and upper sides of the lean, nor were there any significant interactions between height and lean for any of the measured characteristics (Table 2).

**Analysis of radial profiles**

Preliminary analyses (Lei 1995) indicated that the data for each height from the six trees should be pooled for the regression analyses for most properties except vessel diameter and specific gravity. The radial profiles of vessel diameter and specific gravity were analyzed separately for each tree.

**Fiber length.**—Fiber length increased markedly with cambial age at both heights, and fibers at breast height were initially longer than those at the upper height (Fig. 5). The demarcation age between juvenile and mature wood was 10 years at breast height and 8 years at the upper height (Table 3).

**Vessel diameter.**—The mean vessel diameter at both heights increased with increasing cambial age, and the initial vessel diameter at breast height was larger than at the upper height (Fig. 2). Because the large variation in vessel diameter among trees prevented us from pooling the data from the six trees for the regression analysis, a piecewise linear regression analysis was conducted for each tree for each height separately. The regression results show that vessel diameter at breast height had a demarcation age of 8 to 12 years depending on the tree (Table 4). At the upper height, the demarcation age for vessel diamete-
Breast height

Upper height

Cambial Age (yrs)

FIG. 4. Specific gravity (x ± s.e., n = 6 trees) as a function of cambial age at breast height (1.3 m) and an upper height (5.6 to 6.1 m). Data from the lower and upper sides of each disk are pooled, so each value/tree represents two measurements.

Vessel proportion also followed a three-segment radial trend (Fig. 2), but the trend was the reverse of that for fiber proportion. Piecewise regression analysis showed the same demarcation points for vessel proportion at breast height as for fiber proportion at breast height: 8 and 16 years (Table 5). At the upper height, a simple linear regression fit the data (Table 5). Ray proportion changed little at either height and varied from 13 to 16% with cambial age (Fig. 3). Axial parenchyma proportion showed no significant radial trends and had a relatively low value (generally <2%, data not shown).

Specific gravity.—Specific gravity did not vary significantly with cambial age (Fig. 4).

DISCUSSION

Variation among trees

The degree of variation among trees was not the same for different wood characteristics. Vessel diameter and specific gravity varied considerably among trees, whereas fiber length and fiber, vessel, and ray proportion varied little among trees.

The inter-tree variation in vessel diameter was probably due to genetic factors. It does not seem to be associated with growth rate because there is no significant difference in growth-ring width among trees (data not shown). A large variation in specific gravity among trees is not uncommon for diffuse-po-

TABLE 3. Piecewise regression analyses, at two heights, of fiber length vs. cambial age of Alnus rubra. $X'$ is the best-fit demarcation age that fits both the juvenile ($Y = \beta_0 + \beta_1X$) and the mature wood segment ($Y = (\beta_0 + \beta_1X') + (\beta_2 + \beta_3X)$). MSE is the mean squared error ($P < 0.01$).

<table>
<thead>
<tr>
<th>Regression parameter</th>
<th>Fiber length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Breast height</td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>0.806</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>0.0298</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>0.2726</td>
</tr>
<tr>
<td>$\beta_3$</td>
<td>-0.0255</td>
</tr>
<tr>
<td>$X'$</td>
<td>10</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.73</td>
</tr>
<tr>
<td>MSE</td>
<td>0.0011</td>
</tr>
</tbody>
</table>

Vessel proportion also followed a three-segment radial trend (Fig. 2), but the trend was the reverse of that for fiber proportion. Piecewise regression analysis showed the same demarcation points for vessel proportion at breast height as for fiber proportion at breast height: 8 and 16 years (Table 5). At the upper height, a simple linear regression fit the data (Table 5). Ray proportion changed little at either height and varied from 13 to 16% with cambial age (Fig. 3). Axial parenchyma proportion showed no significant radial trends and had a relatively low value (generally <2%, data not shown).

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TABLE 4. Linear piecewise regression analyses for vessel diameter of Alnus rubra trees at two heights. \( Y' \) is the demarcation age that fits both the juvenile wood segment \( (Y = \beta_0 + \beta_1 X) \) and the mature wood segment \( (Y = (\beta_0 + \beta_2 + \beta_3) + (\beta_4 + \beta_5) X) \). A dash signifies that the two-piece regression was inappropriate. MSE is the mean squared error \( (P < 0.01) \).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Tree 1</th>
<th>Tree 2</th>
<th>Tree 3</th>
<th>Tree 4</th>
<th>Tree 5</th>
<th>Tree 6</th>
<th>Tree 1</th>
<th>Tree 2</th>
<th>Tree 3</th>
<th>Tree 4</th>
<th>Tree 5</th>
<th>Tree 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta_0 )</td>
<td>43.75</td>
<td>56.55</td>
<td>48.2</td>
<td>45.12</td>
<td>38.33</td>
<td>18.2</td>
<td>43.21</td>
<td>53.7</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>( \beta_1 )</td>
<td>1.79</td>
<td>2.25</td>
<td>1.55</td>
<td>1.98</td>
<td>3.875</td>
<td>3.73</td>
<td>1.93</td>
<td>3.1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>3.33</td>
</tr>
<tr>
<td>( \beta_2 )</td>
<td>16.86</td>
<td>11.8</td>
<td>7.16</td>
<td>8.97</td>
<td>24.78</td>
<td>18.07</td>
<td>22.98</td>
<td>10.4</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>19.21</td>
</tr>
<tr>
<td>( \beta_3 )</td>
<td>-1.41</td>
<td>-1.88</td>
<td>-0.99</td>
<td>-1.21</td>
<td>-3.60</td>
<td>-3.23</td>
<td>-1.86</td>
<td>-2.7</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>-3.02</td>
</tr>
<tr>
<td>( X' )</td>
<td>10</td>
<td>10</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td>8</td>
<td>12</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>( R^2 )</td>
<td>0.91</td>
<td>0.84</td>
<td>0.84</td>
<td>0.76</td>
<td>0.78</td>
<td>0.88</td>
<td>0.96</td>
<td>0.83</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.91</td>
</tr>
<tr>
<td>MSE</td>
<td>6.50</td>
<td>7.35</td>
<td>10.7</td>
<td>19.2</td>
<td>8 12</td>
<td>8</td>
<td>19.2</td>
<td>7.77</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>5.31</td>
</tr>
</tbody>
</table>

Vessel diameter was larger at breast height than at upper height. Vessel proportion in the juvenile wood zone was larger at breast height than upper height (Fig. 3). The within-tree variation of these vessel diameters and vessel proportions may not have a significant effect on the use of wood, but may have a large influence on water transport to the crown.

For most diffuse-porous species, specific gravity does not change with height (Olkonon et al. 1972), but some diffuse-porous species have higher values higher on the bole than at breast height (Fukazawa 1984). In this study, slightly higher fiber proportion but lower vessel proportion at the upper height may explain the trend toward higher specific gravity at the upper height.

We found only minor variations in wood properties with height. This was the most common pattern in hardwoods according to the synthesis by Zobel and van Buijtenen.

TABLE 5. Linear piecewise regression analyses of fiber and vessel proportion versus cambial age in Alnus rubra. The regression model is a three-segment function* at breast height and a simple linear function** at the upper height.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Fiber proportion (%)</th>
<th>Vessel proportion (%)</th>
<th>Fiber proportion (%)</th>
<th>Vessel proportion (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta_0 )</td>
<td>63.23</td>
<td>20.141</td>
<td>63.96</td>
<td>20.53</td>
</tr>
<tr>
<td>( \beta_1 )</td>
<td>-0.771</td>
<td>0.975</td>
<td>-0.229</td>
<td>0.221</td>
</tr>
<tr>
<td>( \beta_2 )</td>
<td>-8.350</td>
<td>9.419</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>( \beta_3 )</td>
<td>11.848</td>
<td>-11.805</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>( \beta_4 )</td>
<td>1.070</td>
<td>-1.248</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>( \beta_5 )</td>
<td>-0.6716</td>
<td>0.654</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>( X' )</td>
<td>8</td>
<td>8</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>( X'' )</td>
<td>16</td>
<td>16</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>( R^2 )</td>
<td>0.23</td>
<td>0.21</td>
<td>0.15</td>
<td>0.18</td>
</tr>
<tr>
<td>MSE</td>
<td>12.78</td>
<td>16.59</td>
<td>17.06</td>
<td>13.21</td>
</tr>
</tbody>
</table>

* When age \( \leq X' \), \( Y = \beta_0 + \beta_1 X \); when \( X' < age < X'' \), \( Y = (\beta_0 + \beta_2 + \beta_3) + (\beta_4 + \beta_5) X \); when age \( \geq X'' \), \( Y = (\beta_0 + \beta_1 + \beta_2 + \beta_3) + (\beta_4 + \beta_5 + \beta_6) X \).

** \( Y = \beta_0 + \beta_1 X \).

— Not applicable to simple linear functions.
(1989). Although variations in some wood properties between the two heights were statistically significant, these variations can be ignored because they are relatively small compared to the variation among trees and in the radial direction. Breast height sampling should be adequate to predict upper-height values, especially when samples are taken from mature wood.

**Lean effect**

In agreement with Leney et al. (1978), we found no tension wood in the sample trees (as judged by the absence of gelatinous fibers on the upper side of the lean). In agreement with Lowell and Krahmer (1993), we also found no effect of lean on specific gravity in this species. Wilson and Gartner (1996) looked for the presence of tension wood in the upper side of leaning A. rubra stems. At stem angles of 0 to 9° from the vertical, none of the seven samples had tension wood; at angles of 9 to 26°, four of the 18 samples had tension wood; and at angles greater than 26°, all five of the samples had tension wood. Furthermore, only about 10% of trees in natural stands leaned enough to have tension wood. Only one tree (tree 6) in the current experiment had a lean greater than 5° (14°); thus it is not surprising that no tension wood was found in the current study.

**Radial variation**

The patterns of radial variation are not the same for all wood characteristics. The radial pattern of variation for fiber length shows a marked transition from juvenile to mature wood at both heights. A similar conclusion was drawn in studies of other hardwoods (Dinwoodie 1961; Bendtsen 1978; Bendtsen and Senft 1986; Zobel and van Buijtenen 1989; Peszlen 1994).

The increase in vessel diameter with cambial age reported here agrees with many studies of hardwoods (Fukazawa and Ohtani 1982; McKimm and Ilic 1987; Butterfield et al. 1993; Peszlen 1994). Based on these and other studies on fiber length and vessel diameter, it appears that fiber length and vessel diameter are the two anatomical features that show a juvenile-mature pattern of variation in most hardwoods. In this study, the boundary between juvenile and mature wood as defined by fiber length and vessel diameter was roughly 10 years of cambial age.

According to the radial profiles of tissue proportion, however, no definite pattern of radial variation or juvenile/mature wood zone could be defined in A. rubra. Why fiber and vessel proportions in A. rubra followed a three-segment radial variation was not understood.

*A. rubra* showed tree-to-tree differences in specific gravity, but within a tree the wood was quite uniform. This uniformity across the radius and with height suggests that the wood should not be affected by differences in size and age that exist in a typical log load, and it should prove advantageous for use in composites, pulp, and solid-wood products. Moreover, extreme differences in radial growth rate (ranging from 2.0 to 9.3 mm/year) did not affect specific gravity in 7-year-old *A. rubra* (Lei et al., in press). These data taken together suggest that stand management of *A. rubra* to increase growth rate will not produce an undesirable, low-density, juvenile core. The juvenile wood had, on average, a modulus of elasticity about 7.5% lower and a modulus of rupture 5% lower than the mature wood (both tested in bending at 12% moisture content); this suggests only modest differences in mechanical properties between different zones of the wood (Lei 1995). In contrast, however, see Evans (1996), who found larger differences in modulus of elasticity for green specimens from the same trees.

**Conclusions**

The magnitude of variation in wood properties within *A. rubra* trees is very little, and probably negligible for most wood uses. There was no significant variation as a function of natural lean in this study, and the only significant variation with height was in vessel
diameter and vessel proportion. Radial variation was small, although it was significant for fiber length, vessel diameter, and proportions of fiber and vessel. The age of demarcation between juvenile and mature wood is either 8 or 12 years as defined by fiber length or vessel diameter, respectively.

There was significant variation in several characteristics between trees (specific gravity, vessel diameter), although the magnitudes of these differences were not large. Nonetheless, to better understand wood quality and its variation in *A. rubra*, we need more information on different populations as well as information on this species growing in a range of silvicultural conditions.

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