

INTRA-ANNUAL CELLULAR CHARACTERISTICS AND THEIR IMPLICATIONS FOR MODELING SOFTWOOD DENSITY¹

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ABSTRACT

A numeric wood density model is presented to investigate the potential and actual influence of intra-annual cell characteristics on wood density. The model was designed for conifers with a distinctive early-latewood transition, and its performance was tested with data from Scots pine trees. The model is a helpful tool to understand how and to what extent cell characteristics influence wood density. Latewood percentage proved to be an excellent predictor for wood density, and the interaction of density with cell characteristics is shown.

Keywords: Wood density, latewood percentage, anatomy, model, *Pinus sylvestris*, earlywood, variability, wood quality.

INTRODUCTION

Wood-density variation both in the radial direction across stems and within annual rings has an important influence on wood quality. Wood density has been used as an indirect measure of various wood properties such as strength, paintability, glueability, and workability (Gilmore et al. 1959; Panshin and de Zeeuw 1980). However, the relationships between density and wood properties are not exact. Since density is primarily a measure of the total amount of cell-wall material per unit volume, it is related to the relative proportions of the different cell types present and to the dimensions of these cells. Differences in cell structure may cause alterations of wood properties with the same wood-density values (Zhang and Zhong 1992). Consequently, it is important to know to what extent single cell

characteristics might affect wood density, both theoretically and experimentally, within the range of natural variability.

Statistical models are widely applied to estimate wood density using anatomical characteristics (e.g., Tsoumis 1964; Leclercq 1980; de Kort 1993a, b; Zhang et al. 1993). Multiple regression and similar techniques, however, are limited by their number of predictors because of various assumptions (e.g., independence, homoscedasticity, normality) or existing intercorrelations between predictors and also being inflexible and restricted to special species and test conditions for which they were developed. A numerical model could be more flexible and generally applicable to different conditions. Reck (1963) developed a numerical density model for softwood to investigate how cell characteristics are related to density as a basis for genetic selections to improve wood properties. Smith (1965) also calculated density using cell parameters from cross sections. Quirk (1984) used Smith's formula in a shrinkage study to estimate wood density of specimens in green and oven-dry conditions.

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Development of the model

The approach used to calculate wood density is based on a theoretical model using geometrical tissue relationships. Softwoods consist mainly of axially aligned tracheids (90% to 95%) with small proportions of parenchyma, ray tissue, and resin canals (Panshin and de Zeeuw 1980). The shape of the cross section of longitudinal tracheids is assumed to be rectangular and uniform; partition walls at their tips are considered, but not the region of ray crossings where the tangential lumen becomes slightly constricted. Ray crossings represent only a very small percentage of the total length of a tracheid. This model is for a normal and very regular piece of wood with abrupt transition from earlywood to latewood. Scots pine (*Pinus sylvestris* L.), a hard pine species, was chosen for the experimental portion of this study because of its abrupt early-latewood transition.

Wood density (DE), as an overall result of the proportions of various tissues, can be generally expressed as:

$$DE = c_1 V_T + c_2 V_R + c_3 V_C \quad (1)$$

where DE is the overall wood density; V_T , V_R , and V_C are volume proportions of tracheids, rays, and resin canals; and c_1 , c_2 , and c_3 are density coefficients for each tissue. A set of cell characteristics was defined. In earlywood, the tangential and radial diameters of the axial tracheids were defined as T_e and R_e , and the average wall thicknesses for both were defined as D because radial and tangential thicknesses were not significantly different. In latewood, the tangential and radial tracheid diameters were defined as T_l and R_l ; and thicknesses of radial and tangential cell wall were defined as D_l and D_r (Fig. 1). The proportion of tangential over radial tracheid diameter Y was defined as a shape factor for earlywood and latewood cells:

$$Y_e = \frac{T_e}{R_e}; \quad Y_l = \frac{T_l}{R_l} \quad (2)$$

The cell-wall proportion of earlywood (C_e) is obtained by dividing cell-wall area ($T_e R_e - (T_e - 2D)(R_e - 2D)$) by the total cell area ($T_e R_e$). Substituting Y_e , the cell-wall proportion becomes:

$$C_e = \frac{2D(R_e + Y_e R_e - 2D)}{Y_e R_e^2} \quad (3)$$

Likewise, for latewood tracheids (C_l) with thickness of the tangential D_l and radial D_r cell wall, the expression for cell-wall proportion becomes:

$$C_l = \frac{2(R_l D_r + Y_l R_l D_l - 2D_l D_r)}{Y_l R_l^2} \quad (4)$$

So far, tracheid length has not been taken into account. A longitudinal tracheid is seen as a long tube with a pointed tip on each end. Tracheid length (L) and tip length (S) are considered. The slanted partition wall at the tracheid tip produces a triangular cross section (Fig. 2). The average tracheid length is defined as $(L-S)$; and the longitudinal and partition walls are assumed to be equal in thickness. The partition end wall proportion for a latewood tracheid is given by the expression:

$$\frac{(R_l - 2D_l)2D_r B}{Y_l R_l^2 (L - S)} \quad (5)$$

where B is unknown and has to be derived by geometrical proportions (Fig. 2):

$$B = S' - 2x \quad (6)$$

where x is calculated from:

$$\frac{x}{D_r} = \frac{S'}{T} \rightarrow x = \frac{D_r S'}{T} \quad (7)$$

Using the Pythagorean theorem, it can be written that:

$$S'^2 = S^2 + T^2 \rightarrow S' = \sqrt{S^2 + T^2} \quad (8)$$

S' is much larger than T , and S' is almost identical with S :

$$S' \gg T \rightarrow S' \cong S \quad (9)$$

Therefore, B can be expressed as:

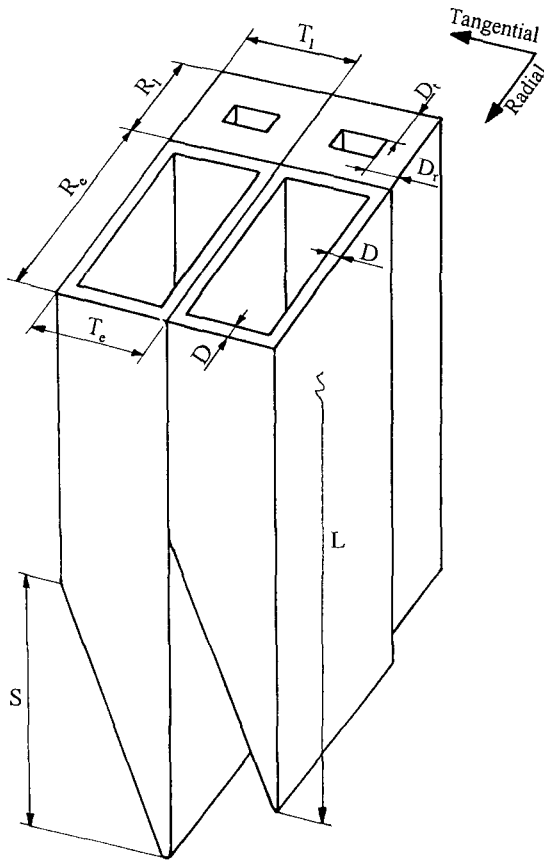


FIG. 1. Cell characteristics used in the wood density model. Earlywood tracheid: T_e tangential diameter, R_e radial diameter, D thickness of radial/tangential cell wall. Latewood tracheid: T_l tangential diameter, R_l radial diameter, D_l thickness of tangential cell wall, D_r thickness of radial cell wall; L tracheid length; S tracheid tip length.

$$B = S - \frac{2D_r S}{T} = \frac{S(T - 2D_r)}{T} \quad (10)$$

Using the above expression for B (Eq. 10) in the cell-wall proportion Eqs. 3 and 4 for complete early- and latewood tracheids, the cell-wall proportion of complete tracheids becomes:

$$C_e = \frac{2D(R_e + Y_e R_e - 2D)}{Y_e R_e^2} + \frac{2DS(R_e - 2D)(T_e - 2D)}{Y_e R_e^2 T_e (L - S)} \quad (11)$$

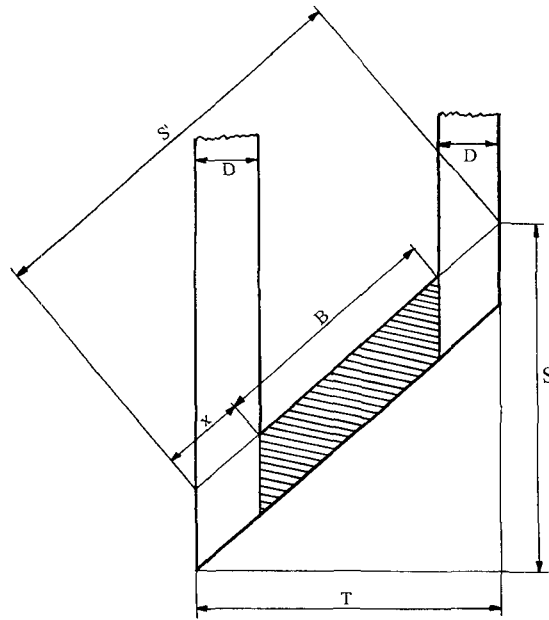


FIG. 2. Partition end wall proportion for a tracheid. S tracheid tip length, T tangential diameter, D (radial) wall thickness, B partition wall length, S' diagonal tip length.

and

$$C_l = \frac{2(R_l D_r + Y_l R_l D_l - 2D_l D_r)}{Y_l R_l^2} + \frac{2D_r S(R_l - 2D_l)(T_l - 2D_r)}{Y_l R_l^2 (L - S)} \quad (12)$$

Earlywood and latewood have to be weighted by latewood proportion, P , resulting in:

$$C = (1 - P)C_e + PC_l \quad (13)$$

Actual wood density can be obtained by multiplication of Eq. (13) with known values of cell-wall density (c_i). Uniseriate (R_u) and fusiform (R_f) wood rays with density factor c_2 , as well as resin canal proportion (A_r), are considered. Epithelial cells are very thin-walled parenchyma cells that surround longitudinal resin canals. Therefore, the cavity of resin canals is seen as an intercellular space, and their proportion A_r is subtracted from the equation. Total wood ray area was measured, and a factor p was used to calculate actual cell-wall area

TABLE 1. Basic wood anatomy data from 8 Scots pine trees.

Anatomical feature	Code	Mean μm	Coefficient of variation %	Percentile values	
				5% (μm)	95% (μm)
Earlywood tracheids					
Tangential diameter	T_e	36.23	8.4	30.59	41.06
Radial diameter	R_e	44.66	7.2	39.31	50.01
Thickness of radial/tangential cell walls	D	2.59	9.6	4.45	6.01
Latewood tracheids					
Tangential diameter	T_l	34.33	8.6	29.35	39.36
Radial diameter	R_l	26.28	9.7	21.93	29.98
Thickness of tangential cell wall	D_t	6.63	14.6	4.95	8.20
Thickness of radial cell wall	D_r	7.98	14.2	6.09	9.84
Tracheid length	L	3,120	15.0	2,352	3,858

for a ray. The value for P was determined with 0.65 for uniseriate and also for fusiform rays.

$$DE = c_1(C - (R_u + R_f)) + c_2p(R_u + R_f) - A_r \quad (14)$$

Wood ray cells are reported to be 35% higher in lignin content than earlywood tracheid secondary walls (Saka and Thomas 1982). Although lignin is supposed to be lower in density (1.40 g/cm^3 , Roelofsen 1959), it is assumed that c_2 is not different from c_1 ; thus a uniform wall density of 1.52 g/cm^3 was used (Kellogg and Wangaard 1969). A final adjustment is necessary because anatomical features were measured on fully swollen thin sections. According to Kollmann and Côté (1968), DE has to be reduced by using fiber saturation moisture ($m = 0.28$) and a volumetric swelling coefficient α_v , which is 13% for *Pinus*:

$$DE_0(\text{kg/m}^3) = \frac{1520(C - 0.35(R_u + R_f) - A_r)(1 + \alpha_v)}{1 + m} \quad (15)$$

EXPERIMENTAL DATA COLLECTION

Approximately 260 cubes (2 cm by 2 cm by 2 cm) were cut from sapwood at the lower part of the trunk from eight, 80- to 100-year-old Scots pine trees (*Pinus sylvestris* L.) grown in Upper Austria. The trees were from similar site conditions. To obtain a homogeneous da-

taset, all samples were free of knots, grain-defects, high resin content, and heartwood. Thin transverse and longitudinal sections were cut with a sliding microtome, stained with safranin, and mounted with glycol on microslides. From these sections all anatomical characteristics were measured using a digitizer tablet connected to a Video Image System. An average of 45 measurements were taken from each section for each anatomical characteristic. Latewood percentage was determined on cross sections using Mork's criterion (Denne 1989). Tracheid length was measured after Ladell (1959), and oven-dry wood density was measured volumetrically/gravimetrically according to DIN Standard 52182. Table 1 shows the basic statistics of cell characteristics that will be used in the wood-density model. Mean axial resin canal percentage (A_r) was 0.42%, uniseriate rays (R_u) 1.8%, and fusiform rays (R_f) 1.4%. The percentage of latewood (P) was 33%, and tracheid tip length (S) was $470 \mu\text{m}$.

RESULTS AND DISCUSSION

Evaluation of the wood density model

Oven-dry wood density was estimated using the anatomical measurements (Table 1) in Eq. (15). Entering mean values from the measurements, a mean wood density of 481 kg/m^3 was calculated; this value is near the actual measured oven-dry wood density (482 kg/m^3). Sell (1989) reported a mean density of 490 kg/m^3 for Scots pine grown in Europe. Calculated

TABLE 2. Comparison of measured and modeled wood density for individual Scots pine trees.

Tree	n	DE ₀ measured	DE ₀ modeled	r	P
1	28	429	406	0.68	**
2	71	479	477	0.83	***
3	20	504	518	0.94	***
4	21	544	538	0.83	***
5	26	461	471	0.84	***
6	32	491	477	0.77	***
7	40	482	482	0.86	***
8	19	528	520	0.64	**
Total	257	482	481	0.85	***

Note: n: number of specimens, DE in kg/m³; P: *** $P < 0.001$, ** $P < 0.01$.

wood-density values for all samples were correlated with their measured wood densities. Figure 3 shows the plot with Pearson's correlation coefficient of $r = 0.85$ ($P < 0.001$). Wood-density values were calculated using the density model for each of the eight trees separately. Table 2 shows a comparison between measured and modeled average wood density and Pearson's correlation coefficients for samples from each tree. The wood-density model also allows one to calculate earlywood and latewood density by using either C_e (Eq. 11) and C_l (Eq. 12) instead of C in Eq. (15), resulting in 284 kg/m³ and 855 kg/m³, respectively. The latewood/earlywood density ratio is consequently 3.0, which is within the range reported by Trendelenburg and Mayer-Wegelein (1955).

Partial differentiation of the wood density model

The wood density model was mathematically differentiated for all anatomical characteristics. This allows an evaluation of how individual anatomical parameters mathematically change wood density. The following are examples of partial differential equations for thickness of earlywood walls and tangential latewood walls:

$$\frac{\partial DE_0}{\partial D} = 1.52(1 - P).$$

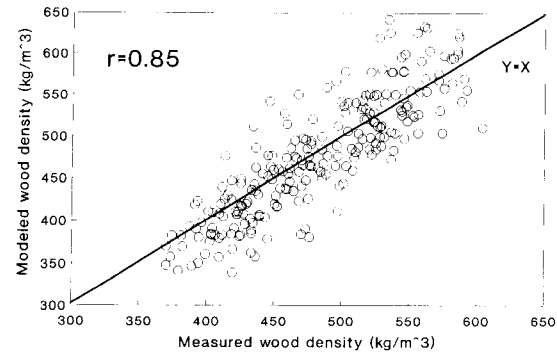


FIG. 3. Comparison of measured and modeled wood density values.

$$\left[\frac{2R_e + 2Y_e R_e - 8D}{Y_e R_e^2} + \frac{2S(R_e T_e - 4D T_e - 4D R_e + 12D^2)}{Y_e R_e^2 T_e (L - S)} \right] \quad (16)$$

$$\frac{\partial DE_0}{\partial D_t} = 1.52P \left[\frac{2(Y_l R_l - 2D_l)}{Y_l R_l^2} + \frac{2D_l S(2T_l + 4D_l)}{T_l Y_l R_l^2 (L - S)} \right] \quad (17)$$

Mean values from Table 1 were used in these partial differentiation equations to calculate the differential change rate of density for each cell parameter (Fig. 4). Earlywood wall thickness (D), either from radial or tangential cell walls, alters wood density most with 28 kg/m³ per changing wall thickness unit, followed by radially measured wall thickness of the latewood tracheids with 19 kg/m³. Radial diameters of earlywood and latewood tracheids (R_e , R_l) rank immediately below wall thicknesses. A change in tangential diameter (T_e , T_l) has almost zero effect, and tracheid length has by far the weakest differential density rate.

Calculations from partial differentials of the wood-density equation showed that earlywood wall thickness theoretically has high potential to influence wood density. Goggans (1964) published detailed analysis on genetic relationships of anatomy with wood properties.

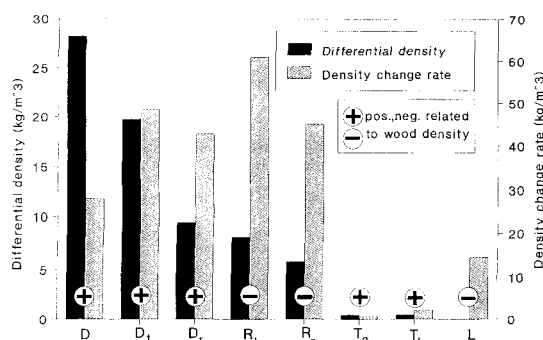


FIG. 4. Partial differential rates of cell characteristics compared with density change rates within their 5-95 percentile variability. Signs tell the relationship with wood density. Earlywood tracheid: T_e tangential diameter, R_e radial diameter, D thickness of radial/tangential cell wall. Latewood tracheid: T_l tangential diameter, R_l radial diameter, D_t thickness of tangential cell wall, D_r thickness of radial cell wall; L tracheid length; S tracheid tip length.

Among all earlywood and latewood cell characteristics, double wall thickness of earlywood was phenotypically most correlated with wood density. During the major part of the season, the variation of radial diameter of tracheids does not coincide with changes in thickness of their secondary wall (Wodzicki 1971). Larson (1973) reported that radial tracheid diameter is regulated by growth hormones produced by the elongating needles. Wall thickness is related to the available photosynthate after the needles have matured. With proper manipulation of experimental conditions, it is even possible to produce tracheids with almost any combination of wall thickness and cell radial diameter (Wilson and Howard 1968). Thus, among all cellular characteristics, manipulation of earlywood wall thickness would have the most effect upon wood density. Heritability is very low for earlywood wall thickness (Goggans 1964). This indicates that there is no potential for genetic selection of earlywood wall thickness to improve wood properties. The variability, therefore, is governed mainly by environmental conditions.

Cell characteristic variation

The previous calculations do not consider the ranges of natural variability for each cell

characteristic. Table 1 shows the coefficient of variation and values for 5 and 95 percentiles. Coefficients of variation range from 7% to 10% for most cell characteristics, but are larger for wall thicknesses in latewood and tracheid length. The radial diameter of latewood tracheids (R_l is negatively related to density in the model (see signs in Fig. 4), whereas measured values of R_l and wood density are correlated positively ($r = 0.39$, $P < 0.001$). R_l must be somehow intercorrelated with other anatomical factors that influence wood density. Thickness of tangential latewood tracheid walls (D_t) is correlated with measured wood density positively ($r = 0.51$, $P < 0.001$), but D_t is also correlated positively with R_l ($r = 0.56$, $P < 0.001$). Therefore, the partial correlation between R_l and modeled wood density was calculated by taking D_t as well as D_r , P , R_e , T_e , T_l , L and ring width as partial variables. The partial correlation coefficient was hereafter clearly negative ($r_p = -0.70$, $P < 0.001$). Such a negative correlation between radial tracheid diameter and wood density has been mentioned by several authors (Goggans 1964; van Buijtenen 1964).

The relationship between tracheid length and wood density has been reported to be positive in some studies while others report no relationship (Zobel and van Buijtenen 1989), but most authors have found a negative relationship (Jackson and Strickland 1962; Matziris and Zobel 1973; Zobel and van Buijtenen 1989). A negative correlation coefficient ($r = -0.31$, $P < 0.001$) was found in our data as well. The wood-density model shows that the tracheid length wood-density relationship is basically negative (Fig. 4), but again statistical correlations might differ because of various interrelationships with other wood parameters.

Wood density change within 5-95 percentile variation for all cell characteristics was calculated. The results do not coincide with differential density changes (Fig. 4). Radial diameter of latewood tracheids (R_l) ranks before wall thickness of tangential latewood tracheids (D_t) and radial diameter of earlywood (R_e). Taking natural variability of cell characteris-

tics into account, radial diameter and thicknesses of latewood tracheid walls have the most influence on wood density. Authors report that latewood wall thickness correlates highest with wood density (Quirk 1984; Zobel and van Buijtenen 1989). There is again no observed relationship of tangential diameter with wood density (Zobel and van Buijtenen 1989).

Variation of latewood percentage

In the wood-density model, latewood proportion is an important parameter for predicting wood density. Latewood percentage has a CV of 30% and ranges from 19% to 50% within 5 and 95 percentile variation. As latewood percentage varies, cell characteristics change in their potential to influence wood density. Figure 5 depicts how a changing latewood percentage alters the relationships. A vertical profile through average latewood percentage of 33% would give the order of density change rates (5–95 percentiles) in Fig. 4. Decreasing latewood percentages obviously provide more power for earlywood parameters. Heritabilities of latewood percentage vary greatly (Goggans 1964) and might be influenced by environmental factors and by a strong genetic control (Zobel and van Buijtenen 1989). Latewood percentage has generally a high correlation to wood density of conifers (Yao 1970; Wimmer 1991; de Kort 1993b). Using data from our trees, the overall correlation coefficient between latewood percentage and measured wood density was $r = 0.82$ ($P < 0.001$), which actually comes close to the correlation between the model and measured wood density. De Kort (1993b), as well as Abdel-Gadir et al. (1993), obtained a wood density-latewood percentage correlation of $r = 0.93$ for Douglas-fir. No known single tree ring parameter correlates higher with wood density. With the knowledge of latewood percentage, one can estimate wood density efficiently, which should be valid at least for softwood species with abrupt early-latewood transition (Zobel and van Buijtenen 1989). Therefore, the purpose of this wood density model is not just to accurately predict wood density, but to analyze

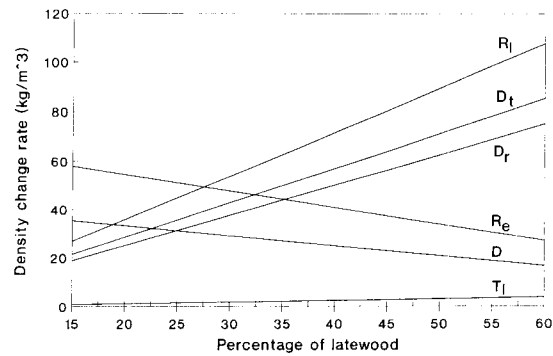


FIG. 5. Influence of latewood percentage on rate of wood density change caused by cell characteristics. Earlywood tracheid: R_e radial diameter, D thickness of radial/tangential cell wall. Latewood tracheid: T_l tangential diameter, R_l radial diameter, D_r thickness of radial cell wall, D_t thickness of tangential cell wall.

the influence of individual cell characteristics on total wood density.

CONCLUSIONS

The wood-density model presented in this study is a useful tool for investigating relationships between single cell characteristics and wood density. The wood-density model is not recommended for compression wood or extractive-rich wood, because it is based on normal anatomical structure. This model demonstrates how changes of single cell characteristics like tracheid length or radial diameter of tracheids might have an effect on wood density independent of other anatomical parameters. This ability to relate individual characteristics to wood density helps to better define the complex and often counteracting relationships of anatomical characteristics. In a normal range of latewood percentage, earlywood wall thickness, either radial or tangential, has high potential to alter wood density. However, taking natural variability into account, radial diameter and wall thickness of latewood tracheids have the most influence on wood density. This model is a didactic tool to get a better understanding of wood properties in relation to their physiological, ecological, and genetic properties.

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REFERENCES

- ABDEL-GADIR, A. Y., R. L. KRAHMER, AND M. D. McKIMMY. 1993. Relationships between intra-ring variables in mature Douglas-fir trees from provenance plantations. *Wood Fiber Sci.* 25(2):182-191.
- DE KORT, I. 1993a. Wood production and latewood percentage of Douglas-fir from different stands and vitality classes. *Can. J. For. Res.* 23:1480-1486.
- . 1993b. Relationships between sapwood amount, latewood percentage, moisture content, and crown vitality of Douglas fir, *Pseudotsuga menziesii*. *IAWA J.* 14(4):413-427.
- DENNE, M. P. 1989. Definition of latewood according to Mork (1928). *IAWA Bull. n.s.* 10(1):59-62.
- GILMORE, A. R., G. E. METCALF, AND W. R. BOGGESS. 1959. Specific gravity of shortleaf pine and loblolly pine in southern Illinois. *J. Forestry* 59:894-896.
- GOGGANS, J. F. 1964. Correlation and heritability of certain wood properties in loblolly pine (*Pinus taeda* L.). *Tappi* 47(6):318-322.
- JACKSON, L. W., AND R. E. STRICKLAND. 1962. Geographic variation in tracheid length and wood density of loblolly pine. *Georgia Res. Council* 8:1-4.
- KELLOGG, R. M., AND F. F. WANGAARD. 1969. Variation in the cell-wall density of wood. *Wood Fiber* 1(3):180-204.
- KOLLMANN, F. F. P., AND W. A. CÔTÉ, JR. 1968. Principles of wood science and technology. Vol. 1. Solid wood. Springer-Verlag, New York, NY.
- LADELL, J. T. 1959. A new method of measuring tracheid length. *Forestry* 32:124-125.
- LARSON, P. R. 1973. The physiological basis for wood specific gravity in conifers. IUFRO Div 5 Meeting, Brisbane, Australia 2:672-680.
- LECLERQ, A. 1980. Relationships between beechwood anatomy and its physico-mechanical properties. *IAWA Bull.n.s.* 1(1-2):65-71.
- MATZIRIS, D. I., AND B. J. ZOBEL. 1973. Inheritance and correlation of juvenile characteristics in loblolly pine (*P. taeda*). *Silvae Genet.* 22:104-106.
- PANSHIN, A. J., AND C. DE ZEEUW. 1980. Textbook of wood technology. 4th ed. McGraw-Hill Book Company, New York, NY.
- QUIRK, T. 1984. Shrinkage and related properties of Douglas-fir cell walls. *Wood Fiber Sci.* 16(1):115-133.
- RECK, S. 1963. Die Variation und Kovariation einiger anatomischer Holzmerkmale und ihre Beziehung zur Raumdichte bei Fichtenholz. Ph.D. thesis, University of Hamburg, Germany.
- ROELOFSEN, P. A. 1959. The plant cell wall. Gebrueder Borntraeger, Berlin, Germany.
- SAKA, S., AND R. J. THOMAS. 1982. A study of lignification on loblolly pine tracheids by the SEM-EDXA technique. *Wood Sci. Technol.* 16:1-18.
- SELL, J. 1989. Eigenschaften und Kenngrößen von Holzarten. Bauverlag, Zurich, Switzerland.
- SMITH, D. M. 1965. Rapid measurement of tracheid cross-sectional dimensions of conifers. *Forest Prod. J.* 15(8):325-334.
- TRENDELENBURG, R., AND H. MAYER-WEGELIN. 1955. Das Holz als Rohstoff. 2th ed. Carl Hauser Verlag, Muenchen, Germany.
- TSOUMIS, G. 1964. Microscopic measurement of the amount of cell wall substance in wood and its relationship to specific gravity. *Tappi* 47(11):675-677.
- VAN BUIJTENEN, J. P. 1964. Anatomical features influencing wood specific gravity of slash pines and the implications for the development of a high-quality pulpwood. *Tappi* 47:401-404.
- WILSON, B. F., AND R. A. HOWARD. 1968. A computer model for cambial activity. *Forest Sci.* 14(1):77-90.
- WIMMER, R. 1991. Beziehungen zwischen Jahrringparametern und Rohdichte bei Kiefernholz. *Holzforsch. Holzverwert.* 43(4):79-82.
- WODZICKI, T. J. 1971. Mechanism of xylem differentiation in *Pinus sylvestris* L. *J. Exp. Bot.* 22(72):670-687.
- YAO, J. 1970. Influence of growth rate on specific gravity and other selected properties on loblolly pine. *Wood Sci. Technol.* 4:163-175.
- ZHANG, S. Y., AND Y. ZHONG. 1992. Structure-property relationship of wood in East-Liaoning oak. *Wood Sci. Technol.* 26:139-149.
- , R. EYENO, G. NEPVEU, F. MOTHE, AND J.-F. DHOTE. 1993. Modelling wood density in European oak (*Quercus petraea* and *Quercus robur*) and simulating the silvicultural influence. *Can. J. For. Res.* 23:2587-2593.
- ZOBEL, B. J., AND J. P. VAN BUIJTENEN. 1989. Wood variation-Its causes and control. Springer Series in Wood Science, Springer-Verlag, New York, NY.