DETERMINING JUVENILE-MATURE WOOD TRANSITION IN SCOTS PINE USING LATEWOOD DENSITY

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ABSTRACT

Segmented regression models are applied successfully to estimate the cambial age of juvenile-mature wood transition in Scots pine sample trees from slow-grown stands. Mean ring density, carlywood, and latewood density profiles from 99 trees were determined by X-ray densitometric analysis of disks taken at 4-m stem height. The cambial age of transition from juvenile to mature wood is described according to segmented regression models based on latewood density profiles. The time series nature of the density data was considered by using generalized nonlinear regression and restricted maximum likelihood regression procedures. The quadratic-linear fit shows the transition at cambial age of about 22 with a standard deviation of 5 to 7 yr. Segmented regression models are an effective tool to get objective estimates of the juvenile-mature wood transition from density profiles.

Keywords: Segmented regression, wood density, juvenile wood, mature wood, juvenile-mature wood transition, Scots pine.

INTRODUCTION

Juvenile wood is an important source of between-tree and intra-tree wood variation, especially in conifers (Krahmer 1986). Independently of whether the effects of juvenile wood characteristics on end-uses are positive or negative, it is necessary to have an accurate estimation of the proportion and size of the juvenile wood core in a tree or sawlog. This

Wood and Fiber Science, 31(4), 1999, pp. 416–425 © 1999 by the Society of Wood Science and Technology permits the separation of juvenile from mature material, thus minimizing the negative influences on end products (Sauter 1992).

The concept of juvenile wood and its formation is documented in numerous publications. Definitions and descriptions of juvenile wood can be found in Rendle (1959, 1960). Zobel and van Buijtenen (1989) give a comprehensive overview of the state of knowledge about juvenile wood. Zobel and Talbert (1984) describe juvenile wood as forming a central core around the pith from the base up to the top of the tree. This central core includes growth rings up to a certain cambial age. Further, the basic information for the juvenile wood formation is located in the genetic code of each species. Most authors attribute control of the growth process to the growth hormone auxin produced in the live crown of the tree (Larson 1969). In summary, the proportion of juvenile wood in a tree is influenced by tree species, size of growth rings up to a distinct cambial age, and relationship between the changes of the live crown and the radial growth along the stem (Paul 1960; Bendtsen 1978). For second-growth Douglas-fir, Di Lucca (1989) concludes, "... the size and length of the active live crown seemed to regulate the quantity and quality of juvenile and mature wood in the stem." Kučera (1994) found in Norway spruce a close relationship between the formation of juvenile wood and annual height increments of the tree, which also suggests that the control mechanism of juvenile wood is related to crown activity.

The point at which the transition from juvenile to mature wood occurs is a basic issue affecting wood quality and product value. However, it is often difficult to estimate with sufficient scientific reliability. Di Lucca (1989) pointed out that species of the genera spruce (*Picea* spp.), fir (*Abies* spp.), and cypress (*Cupressus* spp.) show an "indistinct juvenile-mature transition zone," whereas "Douglas-fir and most hard pines" show a more distinct transition from juvenile to mature wood.

The issue is further complicated by the fact that the transition point varies with the wood characteristic under investigation (Bendtsen and Senft 1986). Variables that have been considered are fiber length, fibril angle, longitudinal shrinkage, lignin/cellulose ratio, and wood density. These characteristics are closely related to the tracheid differentiation, which changes with cambial age. While the transition point or zone for each of these characteristics is of scientific interest, for practical purposes, we are more concerned with those properties that are closely related to end-product quality and that can be repeatably and economically measured. X-ray densitometry, developed by Polge (1966), provides a very efficient method for measuring pith-to-bark density profiles, and because product quality is closely related to wood density, most research into the juvenile-to-mature transition has been based upon density criteria.

A simple way to identify the transition between juvenile and mature wood on the basis of density profiles from pith-to-bark is to visually locate a point (cambial age) on the plotted curve where the increase in density becomes noticeably smaller. However, this method cannot provide reliable scientific results. A statistical approach to the problem is the application of segmented regression models, used by Di Lucca (1989), Cook and Barbour (1989), Abdel-Gadir and Krahmer (1993) on second-growth Douglas-fir and Danborg (1994) on Norway spruce. A principal statistical problem arises when segmented regression models are used without consideration of the time series nature of growth ring data from a pith-to-bark profile. Possible interdependencies in data from adjacent rings could lead to poor estimates of the cambial age of the juvenile-mature wood transition. Statistical methods considering this fact can lead to transition point estimates that have smaller bias and variability.

The objectives of this study were to find the growth-related density variable that best identified the juvenile-mature wood transition, and to fit an appropriate segmented regression model to pith-to-bark density profiles typical of slow grown Scots pine, considering the time series nature of the data.

MATERIAL AND METHODS

A total of 100 trees were sampled from five different Scots pine stands in southwest Germany. The stands are typical of the existing resource of this species in the state Rhineland-Palatinate. Four of the stands are from the

'Pfaelzer Wald' and grow on very poor sites in terms of tree-available nutrients and water supply. The fifth stand represents slightly better growth conditions in the Rhine Valley. In both areas the soils are predominantly sandy. Tree age ranged from 70 to 129 yr. All trees were dominant or codominant individuals in the stands, and the tree diameter at breast height including the bark, ranged from 32 to 35 cm. A rough overview of the average growth rates in 4-m stem height of the 100 sample trees is given by the following data: growth period of cambial age 1-20 yr: 2.68 mm (range 0.51-8.14 mm); cambial age 21-50 yr: 1.15 mm (range 0.24-3.47 mm); cambial age 51-100 yr: 0.86 mm (range 0.11-3.08 mm). After the first 80-100 yr, most sample trees produced very small growth rings in the range of 0.1 to 0.25 mm. This effect can be interpreted as a lack of vigor of the crown caused by changes in water supply and intertree competition. This kind of wood, known as 'starved wood,' is characterized by very narrow growth rings and small latewood percentages.

From each tree a 4-cm-thick disk was taken at 4-m stem height for analysis of the density variation from pith-to-bark. A stem height of 4 m was chosen instead of breast height, because other project objectives required the butt log to be used for lumber tests. The radial pith-to-bark strips for the X-ray densitometry were taken from disk areas free of compression wood, mostly perpendicular to the slope direction of the terrain or to the largest radius of the tree crown.

Density profiles were obtained from each disk using the X-ray densitometer at the 'Station de Recherches sur la Qualité des Bois,' I.N.R.A. in Champenoux, France. Polge (1978) described the measurement method in detail. Density measurements were calibrated to 12% moisture content (weight at 12% MC/ volume at 12% MC). Each ring was divided into 20 equal length intervals, each representing 5% of the ring width, and average density values were computed for each interval. These averages were used in all further analyses as they are more stable than the raw measurements (Danborg 1994). Because Scots pine has a clearly defined growth ring boundary, specially adapted software could be used to eliminate false growth rings almost entirely (Leban and Dedeckel 1995). A comprehensive discussion of possible shortcomings of X-ray densitometry can be found in Schweingruber (1983).

In order to do a detailed assessment of both pith-to-bark and intra-ring density profiles, it was necessary to distinguish earlywood from latewood. In addition to the standard definition by Mork (1928), which is based on the ratio of cell-wall thickness to lumen diameter, there are two techniques for automatically identifying the earlywood-latewood boundary during the X-ray scanning process. The simplest is to use a predefined density threshold; the advantages of this method are outlined in Jozsa et al. (1987). A ring-specific threshold was used in this study, computed as the average of the minimum and maximum density values within each ring.

WOOD DENSITY TRENDS

The sampling method produced usable density profiles for 99 sample trees, which included the whole range of growth rings from pith-to-bark. The data obtained and processed consisted of average values for ring width, mean ring density, earlywood width, earlywood density, latewood width, and latewood density for each growth ring. The density variables reflect the textural changes of the tracheids caused by age-dependent development of the cambium cells and are thus suitable for further consideration (Danborg 1994). The first step of the analysis was to select the appropriate density variables in order to determine the transition between juvenile and mature wood for the Scots pine material. For each sample tree, all density variables were plotted as pith-to-bark profiles and visually assessed.

The plots show more or less uniform curve patterns for the density variables mentioned above. Mean ring wood density increases from

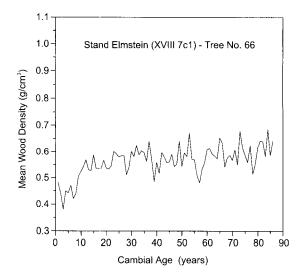


FIG. 1. Development of mean wood density from pithto-bark for test tree No. 66 at 4-m stem height.

pith-to-bark with a slightly steeper slope in the first 20 yr from the pith (e.g., tree No. 66, Fig. 1). Such a trend was expected, although differences between growth zones near the pith and towards the bark in Scots pine are not as strong as usually found in most conifers, e.g., Douglas-fir. This type of curve is not suitable for a clear differentiation between juvenile and mature wood. Once the segmented regression models, described later, were applied, it was deduced that the use of mean density was not appropriate, because of low coefficients of determination and a large range of ages for transition from juvenile to mature wood.

In a second approach, earlywood density was considered. The earlywood density profiles taken from the Scots pine disks showed very low variation and curves without increasing or decreasing trends (e.g., tree No. 66, Fig. 2). This type of curve characterized all the sample trees, with very few exceptions. These findings are similar to those for western hemlock (Jozsa et al. 1997); however, we observed a slight decrease of earlywood density for the first few growth rings. Abdel-Gadir and Krahmer (1993) reported for second-growth Douglas-fir, a decreasing earlywood density for the first rings near the pith, followed by an in-

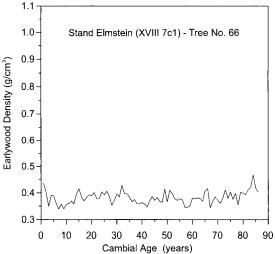


FIG. 2. Development of earlywood density from pithto-bark for test tree No. 66 at 4-m stem height.

crease until stable mature wood conditions were reached.

Latewood density curves of the analyzed Scots pine trees first increased rapidly for about twenty years and thereafter either remained at a relatively high density level (Fig. 3), increased slightly, or decreased. The radial development of latewood density can be divided into two different zones interpreted as

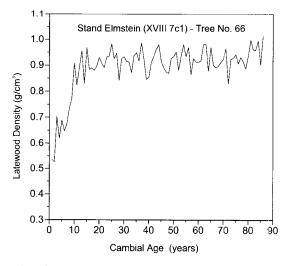


Fig. 3. Development of latewood density from pithto-bark for test tree No. 66 at 4-m stem height.

juvenile and mature growth. This indicates the need for two separate regressions to obtain reasonable fits for the whole profile from pithto-bark. The juvenile section is best described by a quadratic curve. Regardless of the trend direction, the mature part of the curve can be described best with a linear expression, although large yearly density variations are observed. For the purpose of determining the juvenile-mature wood transition, only the latewood density data gave reasonable results, and produced visibly identifiable breakpoints in the segmented regression models applied to the pith-to-bark density profiles.

STATISTICAL PROCEDURES

The first step was to analyze the time series nature of the data using the ARIMA (Autoregressive Integrated Moving Average) concept, developed by Box and Jenkins (1970), which determines the most suitable model for the data set of individual sample trees. The objective of this step was to find a general time series process that generates most of the individual tree time series. The second step of the statistical analyses was a simulation. Data sets were generated corresponding to the time series derived in step one, and segmented nonlinear regressions were then performed and used to estimate the parameter x_0 , the juvenileto-mature transition point. The following statistical procedures were compared; the first two considered the time series nature of the data and the third did not:

- a) nonlinear segmented regression after data transformation corresponding to the time series model found (GNLIN)
- b) restricted maximum likelihood segmented regression considering the time series nature of the data (REML)
- c) nonlinear segmented regression (NLIN)

To determine the most suitable statistical approach, the three procedures were applied to data sets with known x_0 and time series structure, and the bias and variability of the resulting parameter estimate x_0 were compared. In a third step, the estimated transitions at cam-

TABLE 1. Frequencies of ARIMA (p,O,q)-models after selection according to SBC-criterion for n = 99 trees.

Model	Without trend elimination	With trend elimination		
p = 1	21	67		
p = 1 p = 2	12	7		
q = 1	1	19		
p = 1 q = 1	63	6		
p = 2 q = 2	2	0		

Note: A polynomial of 3rd order serves as trend function

bial age x_0 from juvenile to mature wood were derived for a quadratic-constant function and a quadratic-linear function on the basis of measured data.

STEP ONE: ARIMA-MODEL-SELECTION

The ARIMA (p,d,q)-model is a statistical approach for analyzing univariate or multivariate time series. It is assumed that an output variable y, here latewood density, is a time invariant linear function of the input variable x, here cambial age. That function can be considered a filter. Three time processes are described: autoregressive process of pth order (AR(p)-process), the data in year t depends on the data in year $t-1, t-2, \ldots, t-p$; moving average process of qth order (MA(q)-process), random component in year t are depending on random component in previous years; and an integrated process or component d, if the time series is not stationary. For the time series of each of the 99 sample trees five simple ARI-MA (p,0,q)-models were calculated (Table 1). For model selection, the Bayes-criterion SBC (Schwarz 1978) was used (Mutz 1998).

Table 1 shows that without trend elimination most of the time series models are mixed ARIMA (1,0,1)-models or AR (1)-models. After recommended trend elimination (polynom 3^{rd} order), more than two thirds of the time series for the sample trees can be expressed by simple AR (1)-models. Since ARIMA (1,0,1) and ARIMA (2,0,0) include also an AR (1)process, for the following analyses the most simple case, an AR (1)-process was assumed.

STEP TWO: SEGMENTED REGRESSION ANALYSIS AND SIMULATION

Nonlinear segmented regression analysis (NLIN)

It is assumed that the radial development of latewood density from pith-to-bark can be described by two functions, one for the steep increase over the first years beginning at the pith (juvenile wood) and a second for the latter part of the curve (mature wood). Segmented regression analysis can be used to fit both curve segments, and the transition x_0 from juvenile to mature wood can be determined in one statistical analysis.

Previous researchers have used nonlinear least squares procedure (NLIN) (Di Lucca 1989), where the regression parameters are iteratively determined by a numerical optimization method, e.g., Newton-Raphson, Gaus-Newton (Judge et al. 1985). The procedure NLIN of the SAS software package was used to perform these statistical analyses. This procedure uses derivatives of nonlinear functions, which can be problematic if the derivatives of the functions are not continuous with respect to all of the parameters. The nonlinear regression in this form does not consider the data as a time series, which can lead to poor estimates of the transition x_0 . For better estimates, two further methods will be introduced. Both of them consider the time series nature of wood density data and the above mentioned AR (1)-process.

Two-stage generalized nonlinear regression (GNLIN)

The generalized nonlinear regression (GNLIN) takes the time series nature into account by transforming the nonlinear function, the vector of the dependent variable y, and the error vector ϵ as a first step (Gallant and Goebel 1976; Gallant 1987). This transformation eliminates the autocorrelation. In a second step, nonlinear regression can be applied to the transformed matrixes. As transformation matrix for the data the P-matrix is used, whereas PP^T is the inverse of the covariance-matrix of the residuals (Judge et al. 1985). For autocor-

relation of 1st order, an n × n covariance-matrix of residuals A = (a_{ij}) has $\rho^{|i-j|}$ in location i,j. According to Judge et al. (1985) *P* is:

$$P = \begin{bmatrix} \sqrt{1 - \rho_2} & 0 & 0 & \cdots & 0 & 0 \\ -\rho & 1 & 0 & \cdots & 0 & 0 \\ 0 & -\rho & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 & 0 \\ 0 & 0 & 0 & \cdots & -\rho & 1 \end{bmatrix}$$

A statistical problem of using GNLIN is that the autocorrelation-coefficient is not known but only estimated. Technically GNLIN is performed in two steps. First, the nonlinear regression (NLIN) is applied to each of the data series of the sample trees to determine the residuals. On the basis of the residuals, the autocorrelation of 1st order can be calculated by SAS procedure AUTOREG (SAS 1989). In a further step, the data are transformed and the transition x_0 is determined using SAS procedure NLIN (Gallant 1987).

Restricted maximum likelihood regression (REML)

The restricted maximum likelihood regression (REML) can be introduced as an alternative to the nonlinear regression. The advantage is the simultaneous estimation of regression parameters and autocorrelation (Beach and MacKinnon 1978; Jorgensen 1983). To avoid any problems with derivatives as mentioned above, x_0 was set for each data series analysis. From $x_0 = 5$ to x_0 = 70 yr, stepwise 66 segmented maximum likelihood regressions with consideration of an AR (1)-process were calculated for each data series, because in this range the transition from juvenile to mature wood is expected. For each step the concentrated log-likelihood function was determined (Judge et al. 1985). The transition cambial age x_0 for each data series is assumed where the likelihood-value is a maximum. The REML is a restricted log-likelihood regression, because the parameters of the segmented regression are estimated in a way, that x_0 is a maximum of the quadratic function of the segmented regression.

Another advantage of REML is the fact that cambial age is treated as a time-discrete variable, which corresponds to the form of X-ray densitometry data, where there is one density value per growth ring or year.

A data simulation closely related to the real conditions was carried out to find the best fitting method for determining the cambial age of transition from juvenile to mature wood based on latewood density. The following segmented regression model for y_t was assumed: if $x_t < x_0$

$$\mathbf{y}_{\mathrm{t}} = \mathbf{a} + \mathbf{b}\mathbf{x}_{\mathrm{t}} + \mathbf{c}\mathbf{x}_{\mathrm{t}}^{2} + \mathbf{u}_{\mathrm{t}}$$

otherwise

$$y_t = a + bx_0 + cx_0^2 + d(x_t - x_0) + u_t$$

with

$$\mathbf{u}_{t} = \rho \mathbf{u}_{t-1} + \boldsymbol{\epsilon}_{t}$$

The x-values (cambial age) range for t from 1 to T. x_0 is considered the maximum of the quadratic function $x_0 = b/(2*c)$. According to the empirical data series, there are two different T and x_0 assumed, whereas s_{ϵ} is the standard deviation of error component ϵ_{t} .

Simulation I: T = 60 and $x_0 = 20$:

$$a = 0.4$$
, $b = 0.04$, $c = 0.001$,
 $d = 0.002$, and $s_{\epsilon} = 0.1$

Simulation II: T = 110 and $x_0 = 35$:

$$a = 0.4, \quad b = 0.07, \quad c = 0.001,$$

d = 0.002, and $s_{\epsilon} = 0.2$

For the autocorrelation-coefficients $\rho = 0.3$, $\rho = 0.6$, and $\rho = 0.9$, 40 data sets were created for each simulation.

In most simulated cases for the data series T = 60 the calculated bias, which means the deviation from estimated to real transition values, is lowest when the NLIN method is used without considering the time series nature of the data, regardless of the level of autocorrelation (Table 2). In general all three statistical procedures NLIN, GNLIN, and REML underestimate x_0 . However, the procedures GNLIN and REML, which consider the time series na-

TABLE 2. Bias and root mean square error of transition cambial age x_0 for three statistical methods of simulated data sets.

Data set s	imulation	T = 60 :	$x_0 = 20$	T = 110	$x_0 = 35$
	True p	Bias	RMSE	Bias	RMSE
	0.30	-0.22	3.55	-0.20	2.94
NLIN	0.60	-0.22	2.93	-0.22	2.21
	0.90	-0.26	3.37	-0.20	2.36
	0.30	-0.19	3.37	-0.34	2.85
GNLIN	0.60	-0.24	2.65	-0.29	2.00
	0.90	-0.41	2.26	-0.23	1.50
	0.30	-0.30	3.38	-0.25	2.86
REML	0.60	-0.28	2.78	-0.30	2.01
	0.90	-0.35	2.11	-0.28	1.38

 ρ = autocorrelation-coefficient.

ture of the data, show smaller root mean square errors (RMSE). The higher the autocorrelation, the better GNLIN and REML perform against NLIN. There are only slight differences between GNLIN and REML, but with high autocorrelation REML leads to more accurate estimates.

JUVENILE-MATURE WOOD TRANSITION

The three statistical methods were applied to data series from 99 sample trees. The following results are focused on latewood profiles. The set of Figs. 4a to 4f describe, for three arbitrarily chosen sample trees, the latewood density trend curves with condensed data on yearly average values. Further, they contain the fitted regression lines, composed of two regression segments: one for the juvenile growth zone and one for the mature wood zone as well as the iteratively determined cambial age of transition from juvenile to mature wood structures. Although only the transition year is marked, the curves in some cases describe a transition period rather than a distinct point. Each tree is represented by a pair of graphs: one quadratic-constant fit and one quadratic-linear segmented regression.

Descriptive statistics for the estimated cambial ages of transition from juvenile to mature wood for the methods NLIN, GNLIN, and REML are summarized in Table 3 (quadraticconstant fit) and Table 4 (quadratic-linear fit).

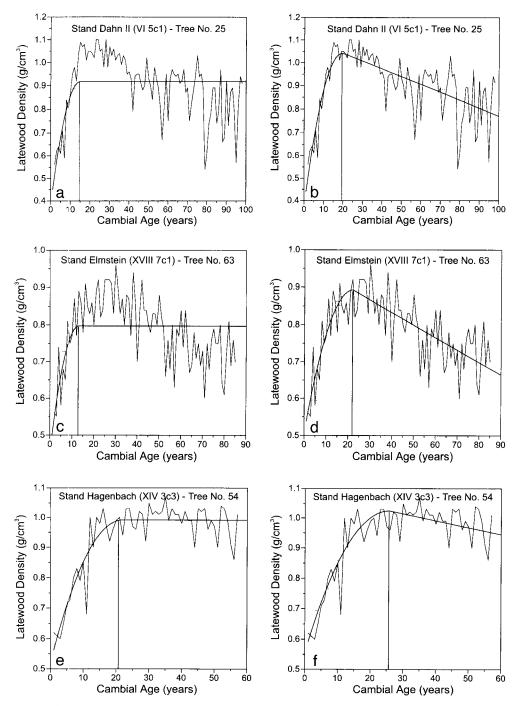


FIG. 4a, b. Quadratic-constant (left) and quadratic-linear (right) fit of the latewood density pith-to-bark profile of test tree 25.

FIG. 4c, d. Quadratic-constant (left) and quadratic-linear (right) fit of the latewood density pith-to-bark profile of test tree 63.

FIG. 4c, f. Quadratic-constant (left) and quadratic-linear (right) fit of the latewood density pith-to-bark profile of test tree 54.

Cambial age of juvenile-mature wood transition x_0 (years)										
Stand	n	NLIN			GNLIN			REML		
		x ₀	SD	R ²	x_0	SD	R ²	x ₀	SD	R ²
Dahn I	19	18.5	5.21	0.53	18.4	5.28	0.56	18.4	5.36	0.57
Dahn II	20	19.1	4.85	0.35	18.9	4.99	0.47	18.0	6.28	0.47
Hagenbach	20	19.2	5.60	0.26	19.1	5.67	0.50	19.3	5.58	0.52
Elmstein-Süd I	20	20.0	4.98	0.55	17.0	4.95	0.63	16.7	5.14	0.63
Elmstein-Süd II	20	14.2	3.73	0.58	14.1	3.29	0.60	14.5	3.64	0.60
All Stands	99	17.5	5.16	0.45	17.4	5.12	0.55	17.4	5.42	0.56

TABLE 3. Descriptive statistics of cambial age of juvenile-mature wood transition for the segmented regression model using quadratic-constant fit.

(number of eliminated outliers: NLIN 3, GNLIN 3, REML 4)

Outliers were eliminated (values exceeding the 95%-confidence interval and values < 0). In summary the three methods converge in the quadratic-constant as well as in the quadratic-linear case. However, the use of GNLIN or REML is recommended because they consider the time series nature of the data and therefore reduce the risk of misleading results.

The quadratic-linear model generally yields higher coefficients of determination than the quadratic-constant model. REML and GNLIN produce in both cases comparable average values for the transition cambial age, whereas GNLIN produces lower standard deviations but also more outliers or data series without convergent estimates. Due to its much better fit, shown in the graphs and by higher coefficients of determination, a quadratic-linear function should be preferred. The juvenile-mature wood transition was determined at cambial age of about 22 with a standard deviation 5 to 7 yr. However, the transition should be assumed as a gradual process that takes place over several years.

CONCLUSIONS

From the three statistical methods described, the generalized nonlinear regression (GNLIN) and the restricted maximum likelihood regression (REML), considering the time series nature of the pith-to-bark latewood density profiles in this study, provided more reliable results than nonlinear regression (NLIN) without consideration of time series nature. Further, segmented regression analysis proved to be a practical and objective method to estimate the cambial age of transition from juvenile to mature wood in a study of Scots pine. This method can likely be used for most conifers, within general statistical restrictions. In addition, these statistical methods may also be used to analyze pith-to-bark trends of other wood properties that are correlated with, and influenced by, annual growth patterns in a tree.

 TABLE 4.
 Descriptive statistics of cambial age of juvenile-mature wood transition for the segmented regression model using quadratic-linear fit.

Cambial age of juvenile-mature wood transition x_0 (yr)										
Stand n		NLIN			GNLIN			REML		
	n	x ₀	SD	R ²	x ₀	SD	R ²	x ₀	SD	R ²
Dahn I	19	21.4	6.72	0.57	20.5	5.93	0.59	21.4	7.08	0.59
Dahn II	20	23.6	5.76	0.47	23.3	5.71	0.51	24.2	6.95	0.52
Hagenbach	20	21.7	8.20	0.49	21.2	5.98	0.56	21.0	7.97	0.56
Elmstein-Süd I	20	20.7	6.52	0.64	20.4	4.68	0.67	20.8	6.48	0.67
Elmstein-Süd II	20	20.9	5.99	0.62	22.4	7.38	0.63	21.8	6.42	0.63
All Stands	99	21.6	6.65	0.56	21.5	5.95	0.59	21.8	6.99	0.60

(number of eliminated outliers: NLIN 3, GNLIN 9, REML 5)

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A more detailed description of the statistical analyses used in this paper will be available from the author, by request.

REFERENCES

- ABDEL-GADIR, A. Y., AND R. L. KRAHMER. 1993. Estimating the age of demarcation of juvenile and mature wood in Douglas-fir. Wood Fiber Sci. 25(3):242–249.
- BEACH, C. M., AND J. G. MACKINNON. 1978. A maximum likelihood procedure for regression with autocorrelated errors. Econometrica 46(1):51–58.
- BENDTSEN, B. A. 1978. Properties of wood from improved and intensively managed trees. Forest Prod. J. 28(10): 61–72.
- , AND J. SENFT. 1986. Mechanical and anatomical properties in individual growth rings of plantationgrown cottonwood and loblolly pine. Wood Fiber Sci. 18(1):23–38.
- BOX, G. E. P., AND G. M. JENKINS. 1970. Time series analysis. San Francisco, CA.
- COOK, J. A., AND R. J. BARBOUR, 1989. The use of segmented regression analysis in the determination of juvenile and mature wood properties. Report CFS No. 31, Forintek Canada Corp., Vancouver, BC. 64 pp.
- DANBORG, F. 1994. Density variations and demarcation of the juvenile wood in Norway spruce. Forskningsserien no. 10-1994. Danish Forest and Landscape Research Institute, Lyngby, Denmark. 78 pp.
- DI LUCCA, C. M. 1989. Juvenile-mature wood transition. Pages 23–38 in R. M. Kellogg, ed. Second-growth Douglas-fir: Its management and conversion for value. Special Publication No. SP-32. Forintek Canada Corp., Vancouver, BC.
- GALLANT, A. R. 1987. Nonlinear statistical models. John Wiley, New York, NY.
- ———, AND J. J. GOEBEL. 1976. Nonlinear regression with autocorrelated errors. J. Am. Stat. Assoc. 71:961–967.
- JORGENSEN, B. 1983. Maximum likelihood estimation and large-sample inference for generalized linear and non-linear regression models. Biometrika 70(1):19–28.
- JOZSA, L. A., J. E. RICHARDS, AND S. G. JOHNSON. 1987. Calibration of Forintek's direct reading X-ray densitometer. Report No. 36a, Forintek Canada Corp., Vancouver, BC. 16 pp.

——, B. D. MUNRO, AND P. SEN. 1997. Basic wood properties of second-growth western hemlock. Report to the British Columbia Ministry of Forests, Forintek Canada Corp., Vancouver, BC. 57 pp.

- JUDGE, G. G., W. E. GRIFFITHS, R. CARTER HILL, H. LÜT-KEPHOL, AND T. C. LEE. 1985. The theory and practice of econometrics. John Wiley, New York, NY.
- KRAHMER, R. L. 1986. Fundamental anatomy of juvenile and mature wood. Pages 12–16 *in* Proc. Technical Workshop: Juvenile wood—What does it mean to forest management and forest products? Forest Products Research Society, Madison, WI.
- KUČERA, B. 1994. A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. Wood Fiber Sci. 26(1):152–167.
- LARSON, P. R. 1969. Wood formation and the concept of wood quality. Bulletin No. 74, Yale Univ. Sch. For. New Haven, CT. 54 pp.
- LEBAN, J.-M., AND A. DEDECKEL. 1995. Intratree modeling of wood density in Douglas-fir. Pages 61–77 *in* EEC Air Project: Forest planning and management tools. Final report.
- MORK, E. 1928. Die Qualität des Fichten-Holzes unter Rücksichtnahme auf Schleif/Papierholz. Der Papier-Fabrikant 26:741–747.
- MUTZ, R. 1998. Inhomogenität des Roh- und Werkstoffs Holz: Konzeptionelle, methodisch-statistische und empirische Implikationen f
 ür holzkundliche Untersuchungen. Kovač, Hamburg, Germany. 336 pp.
- PAUL, B. H. 1960. The juvenile core in conifers. Tappi 43(1):1-2.
- etry. Wood Science and Technology 12:187–196.
- RENDLE, B. J. 1959. Fast-grown coniferous timber—Some anatomical considerations. Quart J. Forestry, April 1959: 1–7.
- SAS Institute Inc. 1989. SAS/STAT User's Guide, Version 6. 4th ed., vol. 2. Cary, NC. 846 pp.
- SAUTER, U. H. 1992. Technologische Holzeigenschaften der Douglasie (Pseudotsuga menziesii (Mirb.) Franco) als Ausprägung unterschiedlicher Wachstumsbedingungen. Diss. Forstwiss. Fakultät Univ. Freiburg, Germany. 221 pp.
- SCHWARZ, G. 1978. Estimating the dimension of a model. Annals Stat. 6:461–464.
- SCHWEINGRUBER, F. 1983. Der Jahrring: Standort, Methodik, Zeit und Klima in der Dendrochronologie. Verlag Paul Haupt, Bern, Switzerland. 234 pp.
- ZOBEL, B. J., AND J. T. TALBERT. 1984. Applied forest tree improvement. John Wiley and Sons, New York, NY.
- ——, AND J. P. VAN BUIJTENEN, 1989. Wood variation. Springer, Berlin, Germany. 363 pp.