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ORIGINAL ARTICLE

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An application of mixed-effects model to evaluate the effects of initial spacing on radial variation in wood density in Japanese larch (*Larix kaempferi*)

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Abstract The effects of initial tree spacing on wood density at breast height were examined for 22-year-old Japanese larch (*Larix kaempferi*). The experiment involved the use of three plots with different initial tree spacing densities (300, 500, and 1000 trees/ha). For five trees selected from each plot, the total tree height, diameter at breast height, height to the base of the live crown, and crown diameter were measured. Ring width and wood density for individual growth rings were determined by X-ray densitometry. A mixed-effects model was applied for fitting the radial variation in wood density in relation to initial spacing. Models having various mean and covariance structures were tested in devising an appropriate wood density model. The model, consisting of the mean structure with quadratic age effects and heterogeneous first-order autoregressive covariance, was able to describe the radial variation in wood density. Closer spacing of trees (1000 trees/ha) resulted in a faster increase in wood density from the pith outward than for more widely spaced trees, indicating that initial tree spacing may influence the age of transition from juvenile to mature wood.

Key words Japanese larch · Silvicultural treatment · Initial spacing · Linear mixed model · Wood density

Introduction

Japanese larch (*Larix kaempferi*) shows rapid growth and good adaptability to cold climates, and has been planted in subalpine regions and the northern area of Japan for several decades.[1] The area afforested with *L. kaempferi* accounts for about 30% of all plantation forest areas in Hokkaido, northern Japan.[2] Wood products from the immature stands were low in quality owing to the large volume of juvenile wood, and their primary use was limited to piles, civil engineering lumber, pallets, and packing materials. However, as the stands matured, the timber has been recommended for use as construction material, including structural glued laminated timber. Consequently, Japanese larch has good potential as an important wood product for sustainable harvest from intensively managed plantations.[3,4]

Numerous studies have examined the effects of silviculture practices on wood properties.[5] Of these, tree spacing (encompassing initial planting density and thinning treatment) is one of the most common silviculture practices for controlling the growth and form of individual trees, and has been studied intensively. Wood density was found to decrease following thinning treatment of *Pseudotsuga menziesii*,[6] *Pinus banksiana*,[7] *Pinus radiata*,[8] and *Picea abies*,[9] but in other studies, thinning had minor or no effects on the wood density of *Pinus taeda*,[10–12] *Pinus ponderosa*,[13] and *Picea rubens*.[14] It has also been reported that thinning increased wood density in *Pinus resinosa*,[15] *Larix occidentalis*,[16] and *Pseudotsuga menziesii*.[17] In Japanese larch, Koga et al.[18] found that heavy thinning significantly affected the growth rate and tracheid length at breast height, but had little effect on wood density. There are some reports concerning the effects of the initial spacing on wood properties in *Pinus taeda* and *Pinus ellioti*,[19] *Picea abies*,[20] *Pinus resinosa*,[21] and *Pinus banksiana*;[22] however, results are not consistent. These inconsistencies could be due to species variation, genetic variation, climatic factors, precision of measurement, and sampling techniques.[5,23,24]

Wide initial spacing of trees and thinning treatments decrease competition among trees, improving light availability and access to water and nutrients in the soil, thus increasing plant growth.[5,25] Relationships between growth rate and wood properties have also been investigated in many studies, but the results have been controversial. Growth rates affect wood properties at different plant ages,

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and ignoring this effect could result in growth rates being incorrectly identified as the cause of differing wood properties.[26,27] In black spruce (*Picea mariana*), Zhang[28] found that the negative correlation between ring density and ring width tended to be weaker with increasing age, and suggested that fast growth has a less negative effect on wood density with increasing tree age. Similar trends have been reported in *Abies balsamea*[29] and *Larix* species.[30,31] Thus, it is essential to consider initial tree spacing, and the optimum tree age and time for thinning treatments in the management of tree plantations during a rotation age.[5,23]

Sequences of yearly measurements of wood characteristics are considered as longitudinal (time series) data,[32] and the analysis of longitudinal data is able to evaluate the age effect on variation of these characteristics. In this case, these data are repeated measures made of the same characteristic on the same observational unit (tree, disk, and ring), and such data generally present temporal autocorrelation, heteroscedasticity, and nonstationarity of the mean.[24,32,33] Objections are frequently raised to statistical analyses that ignore correlation among observations due to bias in the variance of estimated coefficients and hypothesis tests.[34] Gregoire et al.[35] introduced the mixed-effects analysis technique as a means of accounting for correlation among observations. Correlations among observations made on the same subject or experimental unit can be modeled using random effects, random regression coefficients, and through the specification of a covariance structure.[36] Recent studies have developed models predicting variation in wood properties within a stem or cross section using the mixed-effects analysis for many species.[37–43] In this article, we develop a model describing the radial variation in wood density in relation to initial spacing and discuss the effect of spacing on wood density based on the model predicted value.

Materials and methods

Experimental site and sampling

The trees used in this study were obtained from an experimental site (43°14′ N, 143°33′ E; approximately 220 m elevation) in the Ashoro Research Forest of Kyushu University (Hokkaido, northern Japan). The annual average precipitation and temperature in the research forest are 782 mm and 5.9°C, respectively. Japanese larch seedlings were planted in 1984 at an initial plant density of 2000 trees/ha. When the stand was 9 years old (1992; stand density 1000 trees/ha), three plots (each 625 m^2; 25×25 m) were established in the stand. Two treatment plots were thinned (plot A: 300 trees/ha; plot B: 500 trees/ha), and the third plot (plot C) was retained as a nonthinned control. At the time of treatment, crown closure had not occurred in the stand, and consequently the effects of the thinning treatment were similar to the effects of initial spacing. The stand density at 9 years old was relatively low, but the reason for this was unknown (perhaps vole browsing).

In June 2005, when the stand was 22 years old, five trees were randomly selected from each of the three plots. The diameter at breast height (DBH) of each selected tree was measured, and the tree was harvested. Total height (TH), height to the base of the live crown (HB), and crown diameter (CD) were measured (Table 1). A 5-cm-thick, knot-free sample disk was excised at breast height (1.3 m) from each harvested tree, and the disks were transported to the Hokkaido Forest Products Research Institute for processing.

Wood density measurements

A 2-mm-thick (longitudinal direction) strip that included the pith was cut from each sample disk along the arbitrary radial direction. Resin was extracted from the strips for 1 week in a solution of benzene–ethanol (2:1), and the strips were then dried to an equilibrium moisture content of about 12%.

Wood density and ring width measurements were obtained using X-ray densitometry.[44,45] Although this technique can provide various wood density and width characteristics for individual growth rings (e.g., earlywood density, latewood density, and latewood proportion), the mean wood density within ring and annual ring width data were used in this study. Each strip was scanned from the pith toward the bark in two radial directions, and the wood density and width for individual rings were expressed as the

Table 1. Characteristics of the sample trees at harvest

Plot	NTA (trees/ha)		TH (m)	HB (m)	DBH (cm)	H/D ratio	CD (m)
A	300	Mean	18.75	6.41	27.55	68.23	3.46
		Min	17.24	4.80	25.47	65.38	2.73
		Max	20.27	8.30	30.78	74.22	4.25
		SD	0.98	1.18	2.07	3.16	0.49
B	500	Mean	18.60	8.06	25.66	73.42	3.05
		Min	18.05	6.12	22.92	57.86	2.65
		Max	19.19	9.42	31.20	83.34	3.61
		SD	0.49	1.08	2.87	8.54	0.33
C	1000	Mean	18.90	11.06	20.33	95.01	1.96
		Min	16.50	10.30	15.60	76.88	1.63
		Max	20.30	11.90	25.89	107.54	2.48
		SD	1.49	0.57	3.79	11.13	0.31

NTA, Number of trees per unit area after treatment; TH, total tree height; HB, height to base of live crown; DBH, diameter at breast height; H/D ratio, tree height divided by diameter at breast height; CD, crown diameter; SD, standard deviation mean of both values. In order to determine whether the wood density pattern varied with ring position in terms of cambial age, wood density of individual rings were averaged into 5-year groups. The number of annual rings included in the sample disks was 19 or 20, and thus the total number of observations was 60 (15 trees × 4 groups).

Statistical analysis

Observations from the same unit (tree, disk, and growth ring) tend to be correlated. As the wood density measurements were made ring by ring at breast height, it is reasonable to assume that they would be temporally correlated.[24,33] The mixed-effects analysis technique is frequently used to account for correlations among observations.[35,46,47] In the mixed model, the correlation structure of the dependent variable can be taken into account by allowing the parameters to vary randomly from one individual to another around the fixed population mean.[48] A linear mixed model for expressing the wood density of a specific tree is:

$$\begin{cases} \boldsymbol{Y}_i = \boldsymbol{X}_i\boldsymbol{\beta} + \boldsymbol{Z}_i\boldsymbol{b}_i + \boldsymbol{\varepsilon}_i \\ \boldsymbol{b}_i \sim N(\boldsymbol{0}, \boldsymbol{D}) \\ \boldsymbol{\varepsilon}_i \sim N(\boldsymbol{0}, \boldsymbol{\Sigma}_i) \end{cases} \tag{1}$$

where $\boldsymbol{Y}_i$ is the n_i dimensional vector of density observations for tree i, $1 \le i \le N$, N is the number of trees, $\boldsymbol{X}_i$ and $\boldsymbol{Z}_i$ are $(n_i \times p)$ and $(n_i \times q)$ dimensional matrices known covariates, $\boldsymbol{\beta}$ is the p dimensional vector containing the fixed effects, $\boldsymbol{b}_i$ is the q dimensional vector containing the random effects, and $\boldsymbol{\varepsilon}_i$ is a n_i dimensional vector of residual components. $\boldsymbol{D}$ is a general $(q \times q)$ covariance matrix with (i, j) element $d_{ij} = d_{ji}$ and $\boldsymbol{\Sigma}_i$ is a $(n_i \times n_i)$ covariance matrix that depends on i only through its dimension n_i, which means the set of unknown parameters in $\boldsymbol{\Sigma}_i$ will not depend upon i.

The model has two types of error terms: the $\boldsymbol{b}_i$ are the random subject effects and the $\boldsymbol{\varepsilon}_i$ are observation level error terms. In the linear mixed model we assume only that the $\boldsymbol{b}_i$ and $\boldsymbol{\varepsilon}_i$ are independently distributed with zero mean and variances $\boldsymbol{D}$ and $\boldsymbol{\Sigma}_i$, respectively. On the basis of this model, the observations vector $\boldsymbol{Y}_i$ has a multivariate normal distribution with an expected value of

$$\mathrm{E}(\boldsymbol{Y}_i) = \boldsymbol{X}_i\boldsymbol{\beta} \tag{2}$$

and variance

$$\mathrm{var}(\boldsymbol{Y}_i) = \boldsymbol{V}_i = \boldsymbol{Z}_i\boldsymbol{D}\boldsymbol{Z}_i^{\mathrm{t}} + \boldsymbol{\Sigma}_i \tag{3}$$

where superscript notation t indicates the transposed matrix.

The classical approach to inference is based on estimators obtained from maximizing the marginal likelihood function (Eq. 4) with respect to $\boldsymbol{\theta}$, which is the vector of all parameters in the marginal model for $\boldsymbol{Y}_i$.[36]

$$L_{\mathrm{ML}}(\boldsymbol{\theta}) = \prod_{i=1}^{N}\left\{(2\pi)^{-n_i/2}|\mathbf{V}_i(\boldsymbol{\alpha})|^{-1/2} \times \exp\left(-\frac{1}{2}(\boldsymbol{Y}_i - \boldsymbol{X}_i\boldsymbol{\beta})^{\mathrm{t}}\boldsymbol{V}_i^{-1}(\boldsymbol{\alpha})(\boldsymbol{Y}_i - \boldsymbol{X}_i\boldsymbol{\beta})\right)\right\} \tag{4}$$

In Eq. 4, $\boldsymbol{\alpha}$ is the vector of all variance and covariance parameters found in $\boldsymbol{V}_i$, which means that $\boldsymbol{\alpha}$ consists of the $q(q + 1)/2$ different elements in $\boldsymbol{D}$ and of all parameters in $\boldsymbol{\Sigma}_i$. If $\boldsymbol{\alpha}$ was known, the maximum likelihood (ML) estimator $\boldsymbol{\beta}$, obtained from maximizing Eq. 4, conditional on $\boldsymbol{\alpha}$, is then given by:[47]

$$\hat{\boldsymbol{\beta}} = \left(\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{W}_i\boldsymbol{X}_i\right)^{-1}\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{W}_i\boldsymbol{Y}_i \tag{5}$$

and its variance–covariance matrix then equals:

$$\mathrm{var}\left(\hat{\boldsymbol{\beta}}\right) = \left(\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{W}_i\boldsymbol{X}_i\right)^{-1}\left(\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{W}_i\,\mathrm{var}(\boldsymbol{Y}_i)\boldsymbol{W}_i\boldsymbol{X}_i\right)\left(\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{W}_i\boldsymbol{X}_i\right)^{-1} \tag{6}$$

$$= \left(\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{W}_i\boldsymbol{X}_i\right)^{-1} \tag{7}$$

where $\boldsymbol{W}_i$ equals $\boldsymbol{V}_i^{-1}(\boldsymbol{\alpha})$. If $\boldsymbol{\alpha}$ is not known but an estimate $\hat{\boldsymbol{\alpha}}$ is available, it is possible to set $\hat{\boldsymbol{V}}_i = \boldsymbol{V}_i(\hat{\boldsymbol{\alpha}}) = \hat{\boldsymbol{W}}_i^{-1}$, and to estimate $\boldsymbol{\beta}$ by using the Eq. 5, in which $\boldsymbol{W}_i$ is replaced by $\hat{\boldsymbol{W}}_i$.

A common method for estimating $\boldsymbol{\alpha}$ is the restricted maximum likelihood estimation (REML). This method enables estimation of the variance components, explicitly taking into account the loss of the degrees of freedom involved in estimating the fixed effects. The REML estimator for the variance component $\boldsymbol{\alpha}$ is obtained from maximizing the likelihood function of a set of error contrasts $\boldsymbol{U}$:

$$\boldsymbol{U} = \boldsymbol{K}^{\mathrm{t}}\boldsymbol{Y} = \begin{pmatrix} Y_1 - \bar{Y} \\ Y_2 - \bar{Y} \\ \vdots \\ Y_{N-2} - \bar{Y} \\ Y_{N-1} - \bar{Y} \end{pmatrix} \tag{8}$$

where $\boldsymbol{K}$ is an $[n_i \times (n_i - p)]$ full-rank matrix with columns orthogonal to the columns of the $\boldsymbol{X}$ matrix. The vector $\boldsymbol{U}$ then follows $N(0,\boldsymbol{K}^{\mathrm{t}}\boldsymbol{V}(\boldsymbol{\alpha})\boldsymbol{K})$. The likelihood function of the error contrasts can be written as follows:[49]

$$L(\boldsymbol{\alpha}) = (2\pi)^{-(n-p)/2}\left|\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{X}_i\right|^{1/2} \times \left|\sum_{i=1}^{N}\boldsymbol{X}_i^{\mathrm{t}}\boldsymbol{V}_i^{-1}\boldsymbol{X}_i\right|^{-1/2}\prod_{i=1}^{N}|\boldsymbol{V}_i|^{-1/2} \times \exp\left\{-\frac{1}{2}\sum_{i=1}^{N}\left(\boldsymbol{Y}_i - \boldsymbol{X}_i\hat{\boldsymbol{\beta}}\right)^{\mathrm{t}}\boldsymbol{V}_i^{-1}\left(\boldsymbol{Y}_i - \boldsymbol{X}_i\hat{\boldsymbol{\beta}}\right)\right\} \tag{9}$$

where

$$\hat{\boldsymbol{\alpha}} = \frac{1}{n_i - p}\sum_{i=1}^{N}(\boldsymbol{Y}_i - \boldsymbol{X}_i\boldsymbol{\beta})^{\mathrm{t}}\boldsymbol{V}_i^{-1}(\boldsymbol{\alpha})(\boldsymbol{Y}_i - \boldsymbol{X}_i\boldsymbol{\beta}) \tag{10}$$

It should be noted that closed-form solutions for the REML estimators of variance components can be obtained only in particular cases.[36] In most cases the restricted log-likelihood must be maximized in an iterative way such as the Newton–Raphson algorithm.[50]

The statistical analyses and model parameter estimations were performed using the MIXED procedure of the SAS V8 software (SAS Institute Inc.).[51] Under the linear mixed model (Eq. 1), the data vector $\boldsymbol{Y}_i$ for the ith tree is assumed to be normally distributed with mean vector $\boldsymbol{X}_i\boldsymbol{\beta}$ and covariance matrix $\boldsymbol{V}_i = \boldsymbol{Z}_i\boldsymbol{D}\boldsymbol{Z}_i^{t} + \boldsymbol{\Sigma}_i$. Therefore, fitting of linear mixed models implies that an appropriate mean structure and a covariance structure need to be specified. Selection of the appropriate mean and covariance structures were based on maximum-likelihood criteria, Akaike's information criterion (AIC),[52] Bayesian information criterion (BIC),[53] and the Likelihood Ratio Test. The AIC and BIC were calculated as:

$$\mathrm{AIC} = -2\ln(L) + 2q \tag{11}$$

$$\mathrm{BIC} = -2\ln(L) + q\ln(N^*) \tag{12}$$

where L equals the maximized ML or REML likelihood function, q is the number of variance components in the model (i.e., the number of parameters in $\boldsymbol{\alpha}$), and N^* is N (total number of observations) in case of ML estimation and $N - p$ in case of REML estimation (p is the number of fixed parameters). The AIC and BIC were used to discriminate among models having the same fixed effects (variables), but different covariance structures.

The likelihood ratio statistic ($-2\ln\lambda_N$) was defined as:[36]

$$-2\ln\lambda_N = -2\ln\left[\frac{L_{\mathrm{ML}}\left(\hat{\boldsymbol{\theta}}_{\mathrm{ML},0}\right)}{L_{\mathrm{ML}}\left(\hat{\boldsymbol{\theta}}_{\mathrm{ML},1}\right)}\right] \tag{13}$$

where L_{ML} equals the likelihood function (Eq. 4), and $\hat{\boldsymbol{\theta}}_{\mathrm{ML},0}$ and $\hat{\boldsymbol{\theta}}_{\mathrm{ML},1}$ are the maximum likelihood estimates under the null hypothesis and the alternative hypothesis, respectively.

Results and discussion

Radial trends in growth and wood density

The radial (cambial age) trends from pith to bark for ring width and wood density measurements at breast height in the trees from each spacing group are shown in Fig. 1. The

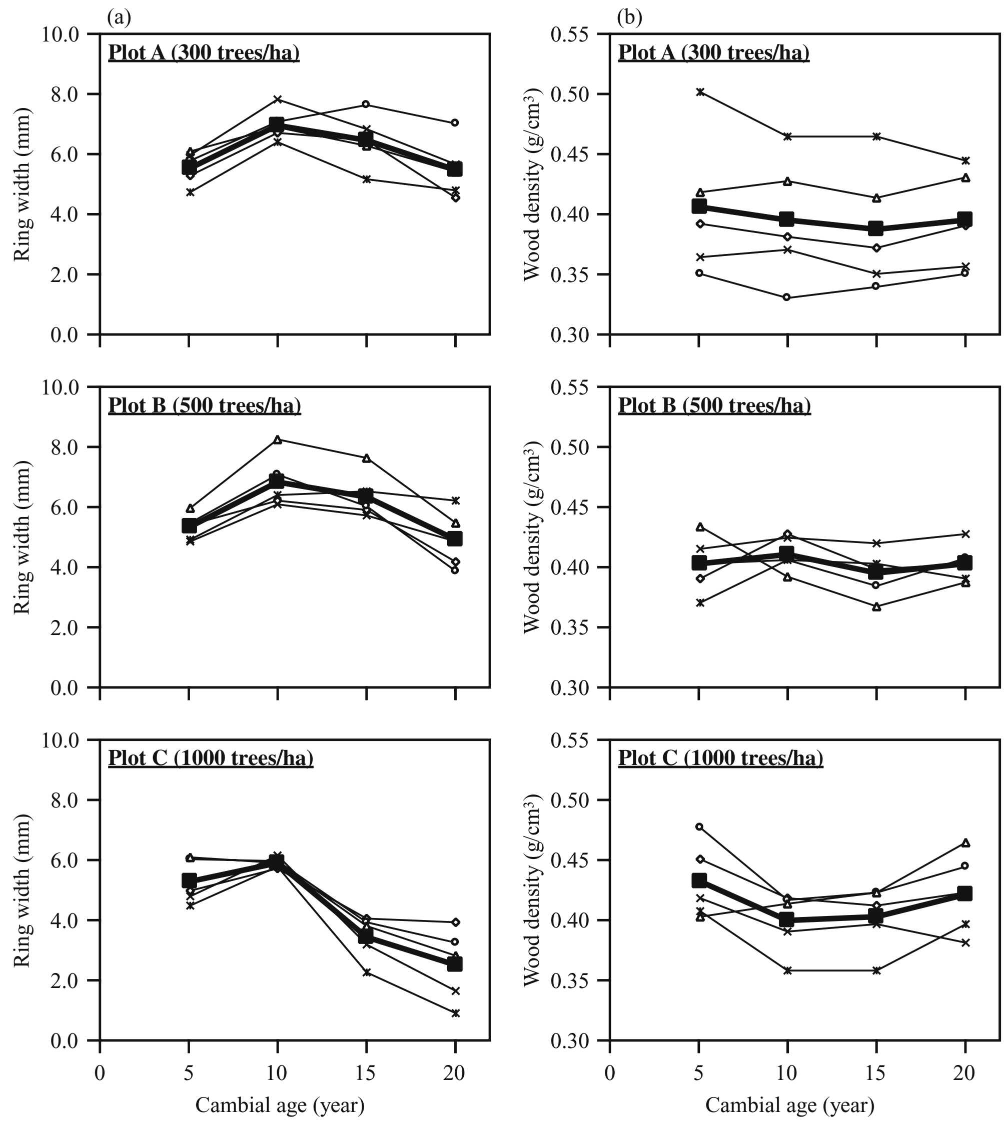

Fig. 1a, b. Radial trends in **a** ring width and **b** wood density at breast height for each spacing plot. *Thick solid lines*, mean value of each plot. *Symbols* represent each five individuals within the plot trends in ring width for plot A (300 trees/ha) and plot B (500 trees/ha) were quite similar (Fig. 1a); the values increased with cambial age up to about 10 years of age and then declined gradually. The ring width in the control trees (plot C; 1000 trees/ha) showed the same trend as those for the other two plots up to about 10 years of age, but then decreased markedly with further age.

Although the effects of initial tree spacing on the radial growth rate were quite evident, the effects on the wood density were unclear. Wood density for the control trees (plot C) decreased to 10 years of age and then steadily increased with further age (Fig. 1b). In contrast, wood density for trees in plots A and B were almost stable with age and showed no clear increase in radial variation.

Model development

The longitudinal (time series) data on wood density were analyzed using linear mixed models (Eq. 1) to determine the effects of initial spacing on the radial trends. In model development, an appropriate mean structure was first selected from the next three models. The first preliminary model (model 1) is the saturated mean structure, incorporating a separate parameter for the mean response at each 5-year group within each spacing group:

$$\begin{aligned} Y_{ij} = \beta_0 &+ (\beta_1 \mathrm{SA}_i + \beta_2 \mathrm{SB}_i + \beta_3 \mathrm{SC}_i) \\ &+ (\beta_4 \mathrm{SA}_i + \beta_5 \mathrm{SB}_i + \beta_6 \mathrm{SC}_i) \times \mathrm{AGE}_{ij(=5)} \\ &+ (\beta_7 \mathrm{SA}_i + \beta_8 \mathrm{SB}_i + \beta_9 \mathrm{SC}_i) \times \mathrm{AGE}_{ij(=10)} \\ &+ (\beta_{10} \mathrm{SA}_i + \beta_{11} \mathrm{SB}_i + \beta_{12} \mathrm{SC}_i) \times \mathrm{AGE}_{ij(=15)} \\ &+ (\beta_{13} \mathrm{SA}_i + \beta_{14} \mathrm{SB}_i + \beta_{15} \mathrm{SC}_i) \times \mathrm{AGE}_{ij(=20)} \end{aligned} \tag{14}$$

where Y_{ij} is the density observation of the ith tree, measured at jth age (AGE_{ij}). SA_i, SB_i, and SC_i are indicator variables defined as 1 if the ith tree was obtained from Plot A, Plot B, and Plot C, respectively, and 0 otherwise. β are the parameters for each fixed effect.

Second, the model was simplified by assuming a linear trend between the observation and age (model 2):

$$\begin{aligned} Y_{ij} = \beta_0 &+ (\beta_1 \mathrm{SA}_i + \beta_2 \mathrm{SB}_i + \beta_3 \mathrm{SC}_i) \\ &+ (\beta_4 \mathrm{SA}_i + \beta_5 \mathrm{SB}_i + \beta_6 \mathrm{SC}_i) \times \mathrm{AGE}_{ij} \end{aligned} \tag{15}$$

From the radial trends shown in Fig. 1b, third model is assumed to have a linear as well as a quadratic age effect within each spacing treatment (model 3):

$$\begin{aligned} Y_{ij} = \beta_0 &+ (\beta_1 \mathrm{SA}_i + \beta_2 \mathrm{SB}_i + \beta_3 \mathrm{SC}_i) \\ &+ (\beta_4 \mathrm{SA}_i + \beta_5 \mathrm{SB}_i + \beta_6 \mathrm{SC}_i) \times \mathrm{AGE}_{ij} \\ &+ (\beta_7 \mathrm{SA}_i + \beta_8 \mathrm{SB}_i + \beta_9 \mathrm{SC}_i) \times \mathrm{AGE}_{ij}^2 \end{aligned} \tag{16}$$

AGE was expressed in decades rather than years as in the original dataset (i.e. 0.5, 1.0, 1.5, and 2.0 years). This was done to avoid the possibility that the random slopes for the linear and quadratic time effects show too little variability, which might lead to divergence of the numerical maximization routine.[36]

The results of fitting three different mean structures to the wood density data are shown in Table 2. It was assumed that these three models have an unstructured covariance structure. The likelihood ratio statistic ($-2\ln\lambda_N$) is the difference between $-2L_{\mathrm{ML}}$ of the current and reference model. The ML likelihood ratio test comparing model 2 with model 1 rejected the null hypothesis of linearity ($P = 0.017$), and thus the saturated mean structure should not be simplified. In contrast, the quadratic model (model 3) was well fitted and was acceptable compared with model 1 ($P = 0.197$). Furthermore, the fixed effect of spacing was not significant, based on the type III tests[51] (null hypothesis H_0: $\beta_1 = \beta_2 = \beta_3 = 0$; $P = 0.569$; data not shown). The quadratic model without spacing effect (model 3–2) was also acceptable compared with model 1 ($P = 0.384$) and model 3 ($P = 0.801$, data not shown). Hence, the mean structure of model 3–2 (Eq. 17) was used for further inference and simplifying of the covariance structure.

Table 2. Summary results for fitting three different mean structures to wood density data for models with an unstructured covariance structure

	Par	$-2L_{\mathrm{ML}}$	$-2\ln\lambda_N$	df	P
Model 1	16	–315.0			
Model 2	7	–294.9	20.1	9	0.017
Model 3	10	–306.4	8.6	6	0.197
Model 3-2	7	–305.4	9.6	9	0.384

Par, Number of parameters; $-2L_{\mathrm{ML}}$, minus twice the maximized ML log-likelihood value; $-2\ln\lambda_N$, likelihood ratio statistic testing vs model 1; df, degree of freedom; P, P-value corresponding to the likelihood ratio test statistic

$$\begin{aligned} Y_{ij} = \beta_0 &+ (\beta_4 \mathrm{SA}_i + \beta_5 \mathrm{SB}_i + \beta_6 \mathrm{SC}_i) \times \mathrm{AGE}_{ij} \\ &+ (\beta_7 \mathrm{SA}_i + \beta_8 \mathrm{SB}_i + \beta_9 \mathrm{SC}_i) \times \mathrm{AGE}_{ij}^2 \end{aligned} \tag{17}$$

The profile of the ordinary least squares (OLS) residuals ($\boldsymbol{r}_i = \boldsymbol{y}_i - \boldsymbol{X}_i\hat{\boldsymbol{\beta}}_{\mathrm{OLS}}$) and the variance function of these residuals are shown in Fig. 2. This OLS estimator $\hat{\boldsymbol{\beta}}_{\mathrm{OLS}}$ is consistent for $\boldsymbol{\beta}$ from the theory of generalized estimating equations (GEE).[54] The OLS residuals varied greatly for each tree, and the variance was not stable over time (heterogeneous). The estimated covariance matrix obtained from fitting of model 3–2 is:

$$\begin{pmatrix} 0.0018 & 0.0010 & 0.0010 & 0.0007 \\ 0.0010 & 0.0010 & 0.0010 & 0.0008 \\ 0.0010 & 0.0010 & 0.0011 & 0.0008 \\ 0.0007 & 0.0008 & 0.0008 & 0.0009 \end{pmatrix} \tag{18}$$

and the corresponding correlation matrix is:

$$\begin{pmatrix} 1.000 & 0.733 & 0.742 & 0.593 \\ 0.733 & 1.000 & 0.953 & 0.853 \\ 0.742 & 0.953 & 1.000 & 0.845 \\ 0.593 & 0.853 & 0.845 & 1.000 \end{pmatrix} \tag{19}$$

There was no clear evidence for a particular trend in the matrices, although the covariance between two measurements showed a slight decrease as a function of the time lag between them. Hence, the following six models were fitted to explore the covariance structure; (1) unstructured, (2) random intercepts, AGE and AGE^2, (3) random intercepts and AGE, (4) random intercepts, (5) heterogeneous Toeplitz, denoted by TOEPH, and (6) heterogeneous first-

Table 3. Summary of results for fitting of various covariance models to wood density data for models with a quadratic mean structure without spacing effects (model 3–2)

Model	$-2L_{REML}$	AIC	BIC	df	P
Unstructured covariance	−249.7	−229.7	−224.5	10	
Random intercepts, AGE and AGE^2	−241.0	−227.0	−224.5	7	0.034
Random intercepts and AGE	−235.3	−227.3	−226.5	4	0.025
Random intercepts	−230.3	−226.3	−226.0	2	0.013
TOEPH	−240.8	−226.8	−224.3	7	0.031
ARH (1)	−240.5	−230.5	−229.2	5	0.101

$-2L_{REML}$, Minus twice the maximized REML log-likelihood value; AIC, Akaike's information criterion; BIC, Bayesian information criterion; df, number of parameters (degrees of freedom) in the corresponding covariance model; P, P-value corresponding to the likelihood ratio test statistic compared with the unstructured covariance structure; AGE, tree age; TOEPH, heterogeneous Toeplitz; ARH (1), heterogeneous first-order autoregressive

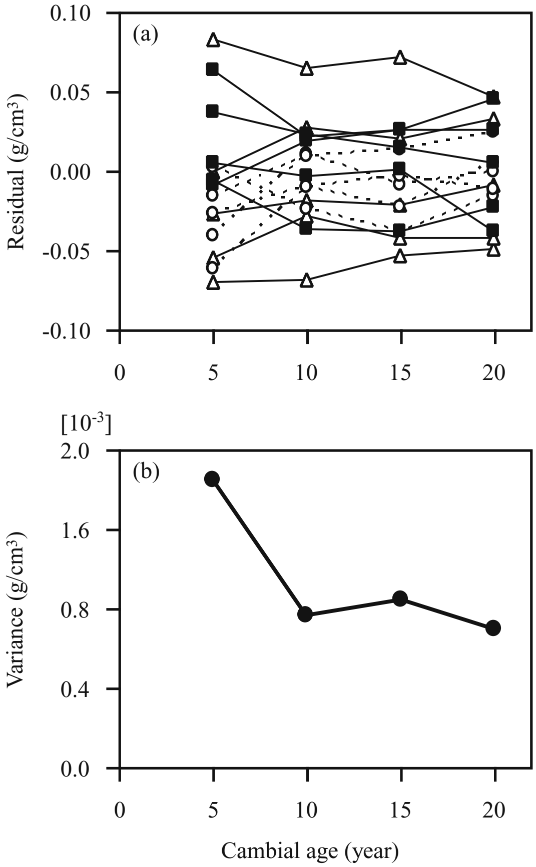

Fig. 2a, b. Profiles of the ordinary least squares (OLS) residuals (**a**) and the variance in OLS residuals (**b**) for wood density at breast height. *Open triangles*, plot A (300 trees/ha); *open circles*, plot B (500 trees/ha); *filled squares*, plot C (1000 trees/ha)

order autoregressive, denoted by ARH (1). The last two covariance structures assume the correlations to be a function only of the time lag between the measurements.[36] In addition, the Toeplitz structure assumes no relation among all correlations in different bands. The ARH (1) structure assumes all correlations to be of the form ρ^u, where ρ is the correlation coefficient between two measurements and u is the time lag between the measurements. Table 3 shows the results of fitting of these covariance models to wood density data for models with the quadratic mean structure (model 3–2). Except for the ARH (1) model ($P = 0.101$), no model was acceptable at the 5% level of significance compared with the unstructured covariance structure (P = 0.013–0.034). The AIC and BIC criterions also supported the ARH (1) covariance structure. Consequently, it was concluded that the model consisting of the quadratic mean structure and ARH (1) covariance structure best described the radial variation in wood density at breast height. Table 4 shows the restricted maximum likelihood estimates and standard errors for all parameters in model 3–2 with ARH (1), denoted by model 4. Figure 3 shows the fitted average profiles of wood density for each spacing group.

Table 4. Restricted maximum likelihood estimates and standard errors (SE) for all fixed effects and covariance components in model 4

Effect	Parameter	Estimate	SE
Intercept	β_0	0.4437	0.0185
AGE × spacing effect			
SA	β_4	−0.0671	0.0270
SB	β_5	−0.0327	0.0270
SC	β_6	−0.0968	0.0270
AGE^2 × spacing effect			
SA	β_7	0.0221	0.0104
SB	β_8	0.0090	0.0104
SC	β_9	0.0402	0.0104
Covariance			
Var (AGE = 5)	σ_1^2	0.0023	0.0009
Var (AGE = 10)	σ_2^2	0.0012	0.0005
Var (AGE = 15)	σ_3^2	0.0012	0.0005
Var (AGE = 20)	σ_4^2	0.0010	0.0004
Correlation	ρ	0.8664	0.0573

Effects of initial spacing on wood density

In order to assess the effects of initial spacing on the radial variation in wood density, F-tests for the significance of sets of linear combinations of fixed effects in model 4 were applied. This could simplify the model by reducing the number of fixed effects. A first test assessed whether there was any quadratic age effect in the control or spacing treatments, and whether the slopes for the quadratic age effects differed between treatments. The null hypotheses tested are given by H_1: $\beta_7 = \beta_8 = \beta_9 = 0$ and H_2: $\beta_7 = \beta_8 = \beta_9$ (see Table 5). Both hypotheses were rejected at the 5% level of signifi-

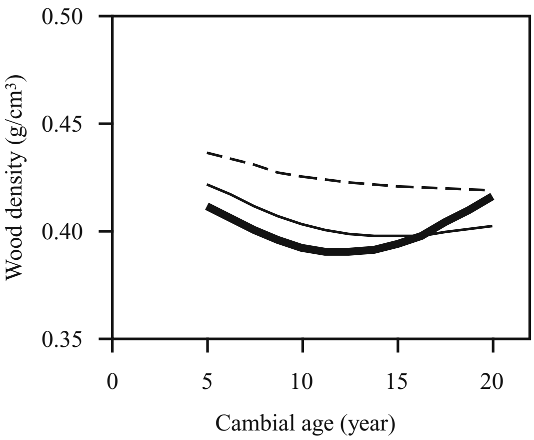

Fig. 3. Fitted average profiles for each spacing plot based on model 4. *Thin solid lines*, plot A (300 trees/ha); *broken lines*, plot B (500 trees/ha); *thick solid lines*, plot C (1000 trees/ha)

Table 5. The null hypothesis and the *P* value resulting from the contrast tests of fixed effects

	Null hypothesis	*p*
H_1	$\beta_7 = \beta_8 = \beta_9 = 0$	0.003
H_2	$\beta_7 = \beta_8 = \beta_9$	0.035
H_3	$\beta_7 = \beta_8$	0.261
	$\beta_7 = \beta_9$	0.128
	$\beta_8 = \beta_9$	0.010
H_4	$\beta_4 = \beta_5 = \beta_6 = 0$	0.006
H_5	$\beta_4 = \beta_5 = \beta_6$	0.050
H_6	$\beta_4 = \beta_5$	0.188
	$\beta_4 = \beta_6$	0.265
	$\beta_5 = \beta_6$	0.018

cance (H_1: $P = 0.003$; H_2: $P = 0.035$). However, all pairwise differences (H_3) were significant only for $\beta_8 = \beta_9$ ($P = 0.010$). This indicates that the variation in wood density did not clearly correspond to the tree spacing intensity. Because the main purpose of this study was to investigate the effects of initial tree spacing, the mean structure with respect to the quadratic effect of age could not be simplified further. The same result was obtained for the tests of linear age effects, which were not zero and had slopes that differed between spacing treatments (H_4: $P = 0.006$; H_5: $P = 0.050$), although all pairwise differences (H_6) were significant only for $\beta_5 = \beta_6$ ($P = 0.018$). These results suggest that wood density at breast height changes quadratically over time for each tree spacing treatment.

The effects of initial tree spacing on wood density have been studied in a number of species. Kang et al.[22] reported in jack pine (*Pinus banksiana*) that wood density decreased with increasing initial spacing, and trees in the medium breast height diameter class were the most significantly affected. Johansson[20] found different results for Norway spruce (*Picea abies*), whereby a decrease in initial spacing from 2.5 × 2.5 m (1600 trees/ha) to 1.5 × 1.5 m (4444 trees/ha) had only a small effect, of little practical importance, on wood density. Larocque and Marshall[21] found similar results in red pine (*Pinus resinosa*) and suggested that closer spacing resulted in a faster increase in wood density from the pith outward. In the present study, wood density in trees in the control plot increased from 10 years of age, and the change was faster than that for trees in the treatment plots (Fig. 3). As Zobel and Sprague[26] defined, the juvenile wood zone is the area of rapid changes in properties near the pith and the mature wood is more uniform toward the bark. It is not possible to interpret the effects of initial spacing on the radial variation of wood density comprehensively through this short-term experiment; however, initial spacing may influence the age of transition from juvenile to mature wood.

The growth and stem-form characteristics (Table 1) were compared among the various tree spacings. For all characteristics except total height (TH), highly significant differences were found between the treatment groups (P = 0.001–0.0014; data not shown). Larocque and Marshall[21] stated that wood density increased more slowly with age, and the crown ratio decreased more slowly as tree spacing increased. A similar trend was found in this study (see Table 1 and Fig. 3). The effects of initial tree spacing on the growth and stem-form characteristics were quite evident, but the effects on the wood density value were unclear despite the radial trends in wood density differing between the treatments.

The model presented in this study is based on measurements at breast height and involved parameters including initial tree spacing and age effects. It is therefore necessary to extend this study to examine variation in wood density within the whole trunk. In addition, if it included parameters related to growth rate, the model will be useful for tree plantation managers in making decisions on when and how much to cut to achieve optimum timber quantity and quality.

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