# Bivariate Modelling of the Long-Short Axis System for the Study of Eccentric Growth and Its Effect on Wood Specific Gravity Variation

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#### Abstract

The specific gravity of wood (WSG), a variable property, has a strong influence on the quality of the wood. Eccentric growth contributes to the variation of WSG within a tree but is poorly understood. To clarify the effects of eccentric growth on WSG variation, two opposite sides of the same tree, representing a differential growth rate, were used for the bivariate modelling of the long-short-axis system. The WSG values on the long and short axes were considered two distinct traits, and their common biological architecture was examined. By jointly modelling the long-short axis, correlations between aspect (spatial correlation) and contemporaneous correlation (within aspect) were examined. The variances of WSG in the long-short axis were different and non-zero. The spatial correlation was -0.03 in the outer wood modules and 0.52 in the core wood modules, averaging 0.25 for the entire WSG profile between the long-short axis. The contemporaneous correlation ranged from 0.79 to 0.86. The results suggest a spatial correlation between the long-short axis and this spatial correlation change with the developmental stage of the tree. The bivariate mixed model method provides the underlying physiological, genetic, and environmental mechanisms related to the long-short axis to explain, clarify, and predict the behaviour of complex wood formation associated with eccentric growth. When young, wood formed on opposite sides may be controlled by the same gene set, but in the outer wood shell, the cambium can be controlled by different and unrelated gene sets that drive WSG variation between aspects. It may be that cambium evolves to meet the needs of a changing crown architecture or local environment over time.

#### Introduction

Wood formation in a tree occurs in a spacetime pattern (Fayle 1973; Manceur et al. 2012). Formed wood occupies a relative position and direction, and time is a continuum in which wood sheaths follow one another from the past, through the present, into the future with the environment as the regulatory web. Wood sheaths increase in quantity and quality around and along the trunk, changing variability and dependency in both space and time. The changes in variances and covariances describe the changing morphogenetic properties during ontogeny (Zobel et al. 1989). The two elements (space and time) integrate to form the shape by sharing some common features, e.g., physiology and or genetics. The physical environment also induces a shared response for a tree or a group of trees (van der Maaten et al. 2013). The spatiotemporal correlations are of interest for two reasons: they contain physiological information (Fritts 1976; Larson 1969) and they can be used to represent genetic correlations (Savidge 2003) because the correlation between the two sides of the same tree can give the degree a given trait shares the same genetic basis (Via 1984, 1991). The interaction between spatial and temporal elements determines the spatiotemporal structure of tree growth and development. Correlations measure the relationship between two variables, but how wood modules are correlated both in space and in time are not well understood.

The environment is a major cause of fluctuations in wood quantity and quality, as the environmental conditions are not constant over space or time (Larson 1964; Burdon 1977; Bell and Lechowicz 1994). To adapt to their environment, trees constantly change their morphology as part of their growth and development process, resulting in more complex and heterogeneous wood (Niklas, 1992). The value and performance of the usable timber are determined by the level of heterogeneity. Heterogeneity results in property variation of the wood between trees of the same species and within the stem of the same tree. Within the tree (both vertical and horizontal space) represents a major source of variation in wood properties (Larson, 1967). In the horizontal space (i.e., diameter growth), a cause of variation within the tree is eccentric growth, which creates asymmetry between two sides of a tree trunk (Clair and Thibaut 2014; Ruelle 2014). In trees, the pith can be found eccentrically in the trunk because of the trunk deviation from its vertical position, unbalanced crown, and the environment (Akachuku 1991; Leavitt 1993; Hellgren et al. 2004; Telewski 2006).

Eccentric radial growth induces pronounced growth on one side compared to the opposite side of the same tree, resulting in heterogeneity at both the microscopic and macroscopic level. It is formed mostly in stems and branches. Eccentricity can be viewed as an inherent evolutionary mechanism of trees' response to environmental heterogeneity (Bell and Lechowicz 1994; Pruyn et al. 2000). Chave et al. (2009) added that eccentric growth strongly affects the function of the tree ecologically. These properties can vary due to growth eccentricity (differential cambial activity). Previous studies have reported that the anatomical, physical, chemical, and mechanical properties of the overgrown side can be very different from the opposite side (referred to as normal wood) (Stokes and Berthier 2000; Rodriguez et al. 2001; Andersson-Gunneras et al. 2006; Heinrich and Gartner 2008; Sultana et al. 2010). However, the role of eccentric growth in WSG variation remains unclear. From a user viewpoint, it brings difficulties and problems, especially when sawing and drying, which can lead to differential stresses and shrinkage that affect the use of lumber from these trees for structural applications. Therefore, understanding the property variation within the tree, particularly in eccentric stems, is critical to making optimal use of wood and enhancing properties.

The assessment of wood properties at the macrolevel offers an interesting opportunity to elucidate the spatial and temporal scales of cambial cells within the stem and their interaction with their microenvironment. Wood specific gravity (WSG) is considered dependent on wood anatomy (Wang and Aitken 2011; Wimmer and Grabner 2000; Elliott 1970) and provides biomass estimation, tree function history, genetic expression, and ecological character (Morel et al. 2018). WSG reflects three key roles: the safe and effective transport of water from roots to leaves, mechanical support for the plant body, and as a reservoir for biological chemicals. It is generally used to estimate wood yield, quality, and potential end uses. WSG, a first-order factor that correlates with several other properties, is a useful trait to compare among trees. However, its association becomes fundamentally indeterminate when properties are compared as WSG in a single tree, and particularly in eccentric trees, where the underlying heterogeneity becomes of greater importance for wood behaviour (Clair and Thibaut 2014).

Interestingly, the radii of different lengths within individual disks from same sampling height of a tree are thought to be constant in genetic makeup, age, and microenvironment (Taylor 1968; Williamson and Weimann 2011; Savidge 2003). Thus, they provide an opportunity to disentangle the genetic regulation of wood formation (Groover 2016). Traits in eccentric disks would tend to correlate because of shared genetic material, physiological and microenvironmental factors (Larson 1969; Fritts 1976). The correlation function can track the changes the vascular cambium has undergone in the course of time giving us a cue to the relation between traits in a spatially heterogeneous environment. To gain insight into the tree growth process, it is imperative to model changes in variances and covariance in time and in space. Therefore, it is crucial to consider the correlations between radii (spatial autocorrelation) and within radii (temporal autocorrelation) and to model them jointly. Joint analysis can reveal unknown associations between aspect-separated traits and potentially improve our understanding of the biology of eccentric wood formation by clarifying the patterns and processes associated with environmental heterogeneity in tree growth. This information is also necessary for future timber management.

Previous studies (Nylinder 1953; Olesen 1973; Williamson and Wiemann 2011; Zeidler and Sedivka 2015; Eberhadt et al. 2018) on azimuthal variations within stems are based on a univariate analysis that ignores the correlations between and within the aspects. Recently, Adutwum and Matsumura (2022) have established a spatial correlation between two opposite sides of the same tree for heartwood colour. Here, we propose the joint modelling of WSG repeatedly measured over time and in eccentric disks (space) from planted teak

trees in Ghana. A bivariate mixed model for WSG variation is developed, representing two opposite sides of the same tree. The approach allows assessing the evolution of the association between the two sides for a trait that can provide better insight into wood biology. Specific questions asked were: (1) Does spatial autocorrelation exist in eccentric growth data? (2) How strong is the spatial autocorrelation? (3) Does the spatial autocorrelation of eccentric growth vary with time (changes with development)? The authors firmly believe that this approach is the key to understanding WSG variation within the trunk and would provide estimates of correlations among WSG evolutionary changes occurring in the two aspects and further understand the coordinated evolutionary relationship between cambium only separated by aspect. This is to improve our understanding of wood uniformity, which is a fundamental requirement for wood quality, particularly of planted trees. Our research focuses on the correlation analysis between the two opposite sides of the same tree and its evolution over time. The biological and statistical importance of application of bivariate mixed modelling approach for wood data analysis are discussed.

#### Materials and methods

# Wood Samples

Three trees were randomly selected from an even-aged plantation in Ghana. The plantation was 18 years old; at this age, Ghanaian teak is believed suitable for harvesting (Adu-Bredu et al. 2018). In each tree discs 5 cm thick were taken at every metre from 0.3 m ground level using a chainsaw. Two opposing radial strips were taken in random cardinal directions from each disc. The two orthogonal radii represent the longest and shortest axes of the tree at a particular height level. Radial (pith to cambium) sample blocks were taken from each disk. From the radius, a thin section (5 mm in size on the tangential direction and 30 mm thick on the longitudinal direction) was cut and then seasoned at 20°C and 65% relative humidity for more than two weeks. Pith eccentricity averaged a factor of 1.3 as computed by the ratio of two radii (long/short).

#### Gravimetric procedure

The gravimetric density was measured using an electronic densimeter MD-300S (ALFA MIRAGE, Osaka, Japan) with a density resolution of 0.01gcm<sup>-3</sup>. The device was calibrated to compensate for the water temperature (since the water is 1 gcm<sup>-3</sup> at 4°C). This device measures the air-dry density. It measures the density according to the Archimedean principle. The densimeter can measure the specific gravity of samples such as wood floating in water instantly (it takes about 10 seconds to measure). Each disc was analyzed as two separate halves, separated by the pith. Each disc was then divided into 10 consistent parts across the radius and the mean value for each fraction was calculated using the relative distance approach (RRD) following (Hans et al. 1972; Chowdhury et al. 2009; Makino et al. 2012; Hidayati et al. 2014). Two orthogonal (long- and short-axes) radial density profiles were obtained. The data were then divided into core wood and outer wood to reflect the growth stages of the trees. The total number of samples used in this study was 360 (3 trees x 2 aspects x 6 height levels x 10 RRD).

# Statistical analysis

#### The Linear Mixed-Effects Model

Repeated measurements for the same tree are correlated in time and space. Wood traits in related trees and aspects are always subject to correlations due to shared genetic, physiological, and environmental effects. Additionally, the wood properties of related trees at different points in time also correlate due to the above factors. The long-short-axis data consist of two components: spatial and temporal dependencies. By jointly modelling the long-short-axis data, the dependency between the two aspects is accounted for in two ways: one for that between the aspects (i.e., *purely spatial dependence*) and the other for correlation within the long-short axis (i.e., *purely temporal dependence*). This modelling approach reveals the underlying pattern of wood formation and thus the WSG for the two aspects.

A general linear mixed model has the form (Laird and Ware 1982; Henderson 1984; Searle et al. 1992) as shown in Eq. 1:

 $\psi = \Xi \beta + Z \beta + \epsilon, (1)$  b ~ N(0, G) $\epsilon ~ N(0, P)$ 

where y is the vector of observations,  $\beta$  is a px1 vector of fixed effects with incidence matrix X, b is aqx1 dimensional vector of random effects with corresponding design matrix Z, R is the variance-covariance matrix of errors and the random effects covariance matrix G. The expected value and variances are  $E[y] = \Xi\beta$ ,  $var[b] = G = \sigma_b^2 A$  and  $var[\epsilon] = R = \sigma_{\varepsilon}^2 I$  for A the numerator relationship matrix and I an identity matrix.

# Bivariate analysis

In the bivariate case, Eq. 1 was expanded to accommodate WSG values in the two aspects (stacking up the vectors), in such a way that  $\beta$ , b and  $\epsilon$  now contain the values for both radii (aspects). The bivariate linear mixed model can be expressed as the following:

 $\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & amp; 0 \\ 0 & amp; X_2 \end{bmatrix}$   $] \ddagger \begin{bmatrix} Z_1 & amp; 0 \\ 0 & amp; Z_2 \end{bmatrix}$   $\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} (2) \end{bmatrix}$ 

 $G = A \otimes G_0$ ;  $R = I \otimes R_0$ ; (The symbol  $\otimes$  is the Kronecker product). The distribution of the random effects and error terms is assumed to be normal with mean zero and variance-covariance matrix:

 $G_0 =$ 

];  $[R_0 =$ 

],[(3)

where;  $G_0$  and  $R_0$  are the between-aspect and within-aspect variance-covariance matrices, respectively.

 $\sigma_{b_1}^2$  and  $\sigma_{b_2}^2$ : variances of the aspects 1 and 2, respectively.

 $\sigma_{b_{12}}:$  random treatment effects of covariance between a spects 1 and 2.

 $\sigma_{\varepsilon_1}^2$  and  $\sigma_{\varepsilon_2}^2 \colon$  residual variance of the aspects 1 and 2, respectively.

 $\sigma_{\varepsilon_{12}}$ : residual covariance between aspects 1 and 2. The nonzero covariances of random effects and error terms induce an association between the responses. These represent the association of cambium development between the aspects or the development of cambium association over time.

Note that the two aspects are independent under joint normality if  $G_0 =$ 

 $\begin{bmatrix} 0 & amp; \sigma_{b_2}^2 \end{bmatrix} \quad (4).$ 

This implies that there is no correlation at all between the means of the trait in the two aspects.

The zero-order Pearson correlation  $(r_{12})$  between the two aspects was estimated using the standard formula from the long-short-axis variances and covariance components as the following:

$$r_{12} = \frac{Cov(b_1, b_2)}{\sqrt{var(b_1) \ x \ var(b_2)}} = \frac{\sigma_{b12}}{\sqrt{\sigma_{b_1}^2 x \ \sigma_{b_2}^2}}, (5)$$

where  $\sigma_{b12}$  is the covariance between the aspects,  $\sigma_{b1}^2$  is the variation for trait in aspect 1 and  $\sigma_{b2}^2$  is the variation for trait in aspect 2. These correlations are referred to hereafter as spatial correlations. This measures the degree to which WSG change in one aspect is associated with WSG change in the opposite aspect.

We compute var(z), which serves as a measure of the stability of the WSG in the two aspects, where 'var' means variance. Low variability means that the ratio  $\frac{\sigma_{b_1}^2}{\sigma_{b_2}^2}$  is nearly constant, i.e., for all observations the two aspects show about the same ratio. The var(z) can be used as an estimate of similarity (fixed) or difference (plastic). The coefficient of variation is given  $CV = \frac{\sqrt{\sigma^2}}{\mu} \ge 100$  (6)

Where  $\sigma^2$  and  $\mu$  are the variance and mean of an aspect's property.

The model (UN@AR (1)) adopted in this study assumes that the covariance matrix within a subject has the following structure:

]⊗[

 $\begin{bmatrix} 1 & amp; \rho & amp; \rho^2 \\ \rho & amp; 1 & amp; \rho \\ \rho^2 & amp; \rho & amp; 1 \end{bmatrix} = \\ \begin{bmatrix} 1 & amp; \rho & amp; \rho^2 \\ \rho & amp; 1 & amp; \rho \\ \rho^2 & amp; \rho & amp; 1 \end{bmatrix}$ amp; $\sigma_{b_{12}} *$  $\begin{bmatrix} 1 & amp; \rho & amp; \rho^2 \\ \rho & amp; 1 & amp; \rho \\ \rho^2 & amp; \rho & amp; 1 \end{bmatrix}$ Iamp; $\rhoamp; \rho^2$  $\rhoamp; 1amp; \rho$  $\rho^2amp; \rhoamp; 1$ close@rowamp;  $\sigma_{b_2}^2 *$  $\begin{bmatrix} 1 & amp; \rho & amp; \rho^2 \\ \rho & amp; 1 & amp; \rho \\ \rho^2 & amp; \rho & amp; 1 \end{bmatrix}$ 

The UN (unstructured) takes care of the spatial correlation (dependency between aspects) and AR(1) (firstorder autoregressive) represents the correlation over time, which is assumed to be same for evolution of wood in the two aspects.

The models in this paper were implemented in PROC MIXED of SAS 9.04 (SAS Institute, Cary NC) and solved using Restricted Maximum Likelihood (REML), assuming a normal distribution of the random effects. The Kenward-Roger method (Kenward and Roger 1997) for determining the degrees of freedom was used in the modelling. The REML variance components were estimated. From the modelling output, the best linear unbiased predictions (BLUPs) of the random effects were used further in the simulation. The homogeneity and normality of the residuals were checked to ensure that the assumptions were met through visual inspection, as per Schabenberger (2004). F-test was used to determine the statistical significance of the fixed effects (a = 0.05).

Analysis of variance in which three types of heterogeneity (i.e., mean, variance, autocorrelation) are considered as follows:

 $\Psi_{\imath\vartheta\kappa} = \mu + T_{\kappa} + a_{\imath} + \rho_{\vartheta} + (a \ \xi \ \rho)_{\imath\vartheta} + \epsilon_{\imath\vartheta\kappa} \ (8)$ 

where  $Y_{ijk}$  denotes the WSG for tree k = 1, ..., 3 in relative radial position  $r_j = 0.1, ..., 1$  along aspect  $a_i = 1, 2$  at a given height level, m is the overall mean and  $(a \ x \ r)_{ij}$  is the interaction of aspect and relative radial position. The experimental error is denoted by  $\epsilon_{i\partial\kappa}$ . The spatial and temporal variation in WSG, within and between trees was statistically assessed using an ANOVA approach. Large-scale and small-scale heterogeneities were considered by the tree and radii (aspect) factors, respectively, while the relative radial position factor accounted for temporal heterogeneity.

After fitting the bivariate model, the data from Aspect 1 and 2 BLUPs were simulated and used to construct graphs with the aim of examining the relationship between the two aspects (same genotype; different environments). The simulation was implemented using PROC IML (SAS Institute Inc., Cary NC). Aspect 2 (short axis) WSG values were plotted against Aspect 1 (long axis). A regression line of aspect 2 against aspect 1, which is implicit in the bivariate variance structure for the evolution effects, was drawn. The slope is given by

$$\beta = \rho_{12} \ge \sqrt{\frac{\sigma_2^2}{\sigma_1^2}}(9)$$

The slope is useful if we want to predict the magnitude and direction of changes the WSG values in aspect 2 given the aspect 1 WSG values.

### Results

Table 1 shows the performance of the model as given by the AIC and BIC.

Table 2 lists the variance-covariance and correlation estimates. The variances describe the variation of WSG in the two aspects while the covariance between the two aspects measures the extent to which they share similar physiology, genetic, morphological, and environmental basis (Falconer 1981). The bivariate model included a correlation structure for both spatial effects (between-aspect) and the temporal effects (within-aspect). The estimated spatial correlations were less than 0.7, implying a weak linear association between the aspects. Temporal correlations were greater than 0.7. These high temporal correlations reflect the impact of the repeated measures nature of the data and the sequential nature of wood formation. The variance-covariance estimates were simulated to ascertain the 95% credible intervals (see Table 3).

Table 4 assesses the degree of uncertainty of the spatial correlation estimate. The lower and upper limits do not contain 0.

The residuals appeared normal and well behaved (Fig 1a,b,c).

# Full variability of the WSG profile

WSG averages were 0.6673 and 0.6649 for aspects 1 and 2, respectively. WSG was up only 0.36% on the fast-growing side. The CV were 9.75% and 8.62% for aspects 1 and 2, respectively. The WSG variation can change more in one aspect/direction even on the same spatial dimension (horizontal dimension). The ratio of variance was 1.29. WSG can be seen as plastic. The covariance, which is the measure of how WSG varies in the two aspects together, was weak, although positive. From Table 4, RRD (temporal within-subject effects), the main effects are highly significant (P < 0.0001), the difference between yearly mean values is significant. The temporal heterogeneity of the mean WSG appears similar for both aspects (representing growth categories), since the interaction of Aspect \* RRD with the F-test has not been shown to be significant. The main effects are not statistically significant for WSG, the mean differences between the long and short axes retain the same sign and are almost constant in size over time (temporally).

Core WSG Variability

WSG mean values were 0.648 and 0.6423 for aspects 1 and 2, respectively. WSG increased only slightly by 0.89% on the fast-growing side. The CV of WSG were 9.05% and 9.12% for aspects 1 and 2, respectively. The variance of WSG produced at the tree's juvenile stage remained relatively stable for the two aspects. The variance ratio was 1.00. This indicates that the SG of the core wood may be ontogenetically fixed implying there may be no changes in the degree of genetic variation. The WSG correlates strongly and positively between the two aspects. The WSGs formed in the juvenile modules are strongly connected between the two aspects. Table 5 contains the hypothesis tests for the significance of each fixed effects. This is shown by the test for a significant regression relationship between WSG and RRD, and insignificant WSG and Aspect\*RRD. An insignificant Aspect\*RRD, which is a space-time interaction, indicates that the temporal constructions of WSG is not different from aspect to aspect, or that the spatial formations of WSG do not differ from time to time. Between the two aspects, there was no statistically significant difference with WSG. This could be interpreted as the effect brought by differential cambial production is not significant to the WSG variation.

#### Outer WSG Variability

The mean values of the WSG were 0.687 and 0.688 for aspects 1 and 2, respectively. WSG increased only 0.13% on the slow growth side. The CVs of WSG were 9.73% and 7.11% in aspects 1 and 2, respectively. The variance ratio was 1.87, indicating that the outer WSG is very plastic. This plasticity may be explained by the differences in wood structure and chemical composition (Clair and Thibaut 2014). Furthermore, there may also be changes in the degree of genetic variation between the aspects. The covariance was negative but very weak, suggesting that WSG may not be associated in the two aspects. WSGs of the outer modules of the long-short axis are independent of each other. Table 6 shows the tests for a nonsignificant regression relationship between the WSG formed at later stages and the predictor variables. This may reveal that there may be some other factors that control the WSG in the outer wood modules.

#### WSG associations between radii

This measures the direction and strength of associations between the WSG values. We can understand how the rapid production of cambium in aspect 1 is related to the development of WSG in aspect 2 (the slowgrowing side). This relationship is important in understanding how cambium physiology and development would produce predictable changes in one aspect, as expressed in the opposite aspect. The BLUP data were simulated 5000 times using the eigen-decomposition technique to measure the association between the radii. The bivariate approach has shown the existence of variation among aspects for WSG, which can be seen in the scatter plots of predicted WSG mean values (Figs. 2a,b,c). This information is lost in the traditional approach i.e., univariate analysis. A regression line of the full WSG on aspect 2 (short axis) versus aspect 1 (long axis) was plotted (Fig. 2a), had a slope value of 0.22 and a simulated correlation of 0.23. The two opposing sides share about a quarter of the similarity in WSG. The positive slope indicates that the factors that increase WSG on the long axis also increase those on the short axis. The coefficient of determination was 0.064, which means that about 6.4% of the short-axis variation is explained by the long-axis WSG. The WSG tend to move in the same direction, but with relatively large fluctuations around the line of association. A regression line of WSG was plotted in aspect 2 versus aspect 1 in the core wood section (Fig. 2b), had a slope value of 0.52 and a simulated correlation of 0.49. The two axes share about 50%-degree similarity. The positive steep slope indicates increases in WSG in the two aspects that go together. The coefficient of determination was 0.267, indicating that about 27% of the WSG variation on the short axis is explained by the long axis. There appears to be relatively less variation around the of association. A regression line of WSG was recorded in aspect 2 versus aspect 1 in the outer wood modules (Fig. 2c), had a slope value of -0.02 and a simulated correlation of -0.03. The slope was almost zero, indicating that the change in WSG on the long axis is not or only weakly associated with the changes in WSG on the short axis. The coefficient of determination was 0.001, indicating that only 0.1% of the variation in WSG variation in the short axis is explained by the long axis. A low correlation between the aspects means more variation in the outer wood WSG data.

Spatial and temporal correlations

The association of the wood trait on two opposite sides is determined by correlations at two different levels: between and within radii. The main drivers of these correlations are physiological, genetic, and environmental mechanisms. Correlations between aspects (i.e., purely spatial) were 0.253, 0.52, and -0.03 for full WSG, core WSG, and outer WSG, respectively (Table 2). This characterizes the association between the aspect means. The spatial correlations were significant for the complete WSG and core WSG but insignificant in the outer WSG (see Table 3). The between aspect correlations of +0.25, +0.52 and -0.02 indicate that a tree which is 1 standard deviation (s.d) above the average WSG in one aspect is expected to be 0.25, 0.52s.d. above the average and -0.02 s.d. below the average WSG in the opposite aspect, respectively. The spatial correlations between aspects were generally weak (r < 0.7). This indicates that even though wood at the ends of the two radii are formed by same cambium, they are still poorly correlated. But at the young stage, we can say that there exists a strong local spatial trend in WSG variation with autocorrelation values greater than 0.3. The evolution of WSG in the outer wood modules between the opposing aspects is independent. Contemporaneous correlations (i.e., *purely temporal*) indicate the strength of the association between the change in one aspect between time t and time t+1 with its change in the opposite aspect over the same time. The intra-radius correlations (i.e., purely temporal) were 0.837, 0.7898, and 0.8566 for the full WSG, core WSG, and outer WSG, respectively. These correlations were highly significant. These correlations underscore the physiological basis of the tree growth process (Fritts 1976; Larson 1969). The inter-aspect correlation and the intra-aspect correlation reveal the underlying physiological associations in eccentric wood formation. The correlations within each aspect were significantly higher than the correlations between the aspects. For example, wood of the same presumed age on opposite sides has a similar WSG (r=0.84), in contrast, the WSG correlate poorly with distance or size (r=0.25). This finding contributes to our understanding that the xylem production on opposite sides of a tree may not necessarily be of equal quality in terms of physiology, genetic, and morphology as the tree may not grow and develop evenly around the trunk. In fact, we expect the greater the differential xylem production (eccentricity), the less association between opposite radii, but wood produced simultaneously on opposite sides of the tree would show greater similarity. Both sides of the tree may have had the same number of years to reach the current structural integrity, and both may have similar morphology and perhaps physiology (Lachenbruch et al. 2011). The greater similarity between contemporaneous woods on opposite sides shows that the cambium meristems may exhibit age-dependent behaviour. This reinforces the results of Williamson and Wiemann (2011). Estimates of the inter-aspect correlations were effectively low. This implies that when estimating the specific gravity for a tree, sampling could not be undertaken using only one direction.

# Discussion

The answers to all three questions in this study are (1) spatial correlation exists in wood density data from trees exhibiting eccentric growth; (2) the spatial correlation between opposite sides is stronger during the early stage of tree growth and weaker in the adult stage; and (3) the spatial correlation evolves with time (i.e., with developmental stage). In the juvenile phase, the variability in WSG between the two opposing aspects was low or almost fixed, with the spatial correlation being the greatest. In the adult stage, the outer wood is more variable and spatial correlation occurs at its weakest. The spatial correlation between the two opposite sides for the full WSG data was positive but weak, and the variability was high.

# **Overall Findings**

Bivariate analysis allows us to assess the variations in each aspect (spatial dimensions). In our analysis, the variance components for both aspects (long and short axis) were non-zero for all properties considered (see Table 2). The variation of WSG along the long axis was greater than that for the short axis for all traits except wood formed at the young stage, where the variances were almost comparable. WSG variation can change more in one aspect than another, even in the same spatial dimension (horizontal dimension). Slow growth can improve the uniformity of desired plantation resources. A small variability within the core WSG was found by Lamy et al. (2012) for pine species. The greatest WSG variation occurred in the outer wood, where the increase in long axis variation was approximately 87% on the short axis. Since WSG is largely determined by the microstructure of the wood, the greater variation in WSG along the long axis would

reveal greater anatomical variability and consequently strength and possibly chemical properties (Wimmer and Johansson 2014). The WSG variance between the aspects increases with increasing age. This occurrence was previously identified in *Pinus radiata* by Apiolaza (2011) and Zamudio et al. (2002).

The large variation in WSG observed in the long axis can be largely attributed to competition for food between cells (Larson 1973) and rapid cambium activity, in which cambium cells have less time to expand and do not accumulate enough photosynthetic material to thicken cell walls (Lachenbruch et al. 2011), consistent with Cote and Day (1965) that lignification of longer axes occurs least in hardwoods. Fully developed crown at maturity may create small canopy gaps introducing heterogeneous light environment. We could try to say that the negative covariance produced by the WSG of the outer wood modules is caused by differential lignin allocation partly in response to imbalanced stress distribution due to crown formation (Archer 2013) and differential auxin concentration (Thimann 1972).

The correlations between the two opposite aspects were moderate but significant (r < 0.7) in the core wood area, insignificant and negligible (-0.03) in the outer wood area, and the correlation for the full WSG profile was of weak order (0.25) but significant. The moderate, positive correlation implies that the WSG found in the core area is relatively homogeneous. From a usage point of view, the core wood (cylindrical layer) of teak can have a certain level of stability due to its high degree of uniformity. Particularly in drying and sawing applications, the core wood must not exhibit differential shrinkage and stress as the two sides of a log can be uniform as variation was almost fixed. Over time, the WSG found in the outer wood becomes dissimilar (heterogeneous) between the two aspects. We are tempted to think that this is a response to high residual stresses generated in the tree at maturity because of the fully developed crown. Although the outer wood has an increased WSG, it shows no signs of uniformity between the two aspects. The cylindrical layer of the outer wood and lumber, which contains both long and short axis lumber, can exhibit varying degrees of stress and shrinkage. Extensive precautions must be taken when used in drving and sawing applications. The full WSG profile showed some degree of similarity. Although this spatial correlation was positive and significant, it was of low order (Sokal and Oden 1978). The difference in the radial gradients in WSG of the two pith-to-bark profiles may contribute to this low-order spatial correlation. There was a steeper slope on the short axis (0.1172) than on the long axis (0.1063).

The spatial correlation in the WSG between aspects may depend strongly on the developmental phase. Reed and Burkhart (1985) first hypothesized that spatial dependence changes with developmental stages. Our data seem to confirm this hypothesis. The high and positive spatial correlation in the young stage can be attributed to the dominance of microsite effects and the lack of competition and relatively unconstrained expression of reaction wood. In other words, if the difference in growth is due to competition from, e.g., light, moisture levels, and nutrient availability, the similarity of the WSG produced on the two opposite axes indicates that the competition which can lead to a differential growth rate (Tilman 1988) may not affect the full WSG and core WSG. Zhang and Zhong (1990) reported similarly on East Liaoning oak. In young teak trees, differences in WSG of different length radii can be attributed to microsite variations, exposing opposite sides of the same tree to similar environmental conditions, thereby creating a positive spatial correlation. The negative spatial correlation found in the outer wood area, a sign of competition (Matern 1960), can be explained by the modular structure of the tree, which represents the physiological unit. Competition is a consequence of limited resources. This competition can be induced by crown closure, which increases competition for space and light (Paul 1957). When the tree grows large, it consists of more modules than when it was younger, which are smaller. The modules of larger trees probably show a stronger competitive effect than smaller ones (Weiner 1990). Over time, the long axis may have more total divisions on the meristem than the short axis (Lachenbruch et al. 2011). When cambium meristem divisions are linked to somatic mutations, the short axis, which exhibits more homogeneity in WSG, may perform poorer at tracking the environment (Lachenbruch et al. 2011). The short axis may have less hydraulic resistance, possibly due to gravity and path length (Lachenbruch et al. 2011). The shorter axis had narrower sapwood width and sapwood width showed negative covariance with the long axis (data not shown).

The shift in spatial dependence from positive to negative can be attributed to the shift from good nutritional

conditions to poor conditions and some age-related decline in forest productivity (Binkley et al. 2002). Fernandez-Moya et al. (2013) found that the concentration of nitrogen, potassium, and magnesium in the trunk of teak trees decreased between 1 and 19 years of age. Our samples have a similar age of 18 years. We found an age-related decrease in the longitudinal rate of change in WSG (data not shown). From 1 to 9 years of age, the longitudinal change rate in the WSG was 0.011 which decreased to 0.005 from 10 to 18 years of age. This age-related decline may be attributed to increasing environmental constraints related to water availability (Dié et al. 2012), nutrition, and respiration (Binkley et al. 2002; Fernandez-Moya et al. 2013) or possibly to the increase in WSG of the outer modules of the tree construct.

Variation and covariation in trait evolution occurs for two reasons: genetic and selective (environmental) covariances. If we follow Falconer (1952), we may be able to view the spatial correlation as genetic correlation. In our case, it can be assumed that the genetic correlations are due to pleiotropy rather than linkage equilibrium. Pleiotropy is simply the property of a gene affecting two or more traits, while linkage equilibrium is more applicable to crosses between different strains (Falconer 1989), which does not apply in this study. The relatively low "genetic" correlation indicates that the cambium and thus WSG values in each aspect are influenced either by some different genes or differently by the same sets of genes and exhibit some degree of independent evolution (Via and Lande 1985).

From the study, we can infer that different genes may be involved at different stages of tree growth. According to Stearns et al. (1991) the shift from positive to negative indicates that one gene is expressed in the young and another in the adult stage. Core wood and outer wood have been shown to be controlled by different genes (Plomion et al. 2001) supporting our findings. In the early growth phase, there is a close correlation between opposite sides of the same tree, and in the later phase there was no or poor correlation between the two aspects, suggesting that the physiological, environmental, and genetic mechanisms in the two aspects are partially different for the stages of growth. In the early stages, the strong correlation between the opposing aspects may indicate that the same genes and physiological factors are driving the increase in WSG typical of light-demanding species. Also, the same environmental conditions may select changes in WSG of the two opposite aspects. In the outer wood modules, different genes may control WSG in both aspects. Wood evolution in one aspect would not affect the ability for adaptive development in the opposite aspect. There may be no or little selective covariances between the two aspects for outer wood modules. The degree to which traits that are separated by axes can evolve independently from one another evidenced by the weak spatial association, may be helpful for evolvability. This supports the theory that wood structure variation may be a result of having genetically different physiology (Gartner 2006). The stem produces specialized reaction wood as a clever response to gravitropism. On the upper side of the stem, tension wood is formed which exerts contractive force and pulls the stem right. Due to its relatively high lignin content, the opposite side is not capable of growth elongation (Groover 2016). The cellulose microfibril angle (MFA) of the cells in tension wood is enriched and close to zero, making the cells and resulting wood resistant to stretching yet permissive to swelling (Clair et al. 2011). The insignificant weak spatial correlation supports the assertion that changes in lignin, MFA and the biochemical makeup of the cell walls may play a significant role in the evolution of tension wood.

Therefore, we can underline the importance of clarifying the interrelationships between wood formation on opposite sides during ontogenesis from young to adult, since the environmental, functional, physiological, or genetic link between the long and short axis expressed at one stage may not be sufficient to validate it throughout the lifespan of the tree. The existence of both spatial and temporal correlations raises an important issue related to the traditional analysis method, regression analysis, which assumes error independence. It is important to recognize that all assessments of wood quality are statistical and can be confusing unless the biological sources of variability are considered and subsequently explained (Larson 1969).

# Conclusion

The bivariate modeling technique used in this study is an attractive way to link information in both space and time, revealing the underlying physics and describing the association and patterns of variation in eccentric wood formation. It is an improvement over the traditional univariate method by decomposing the error variance into within and between components and their covariation. The covariance parameter provides additional information about the relationship between the evolutionary path of traits measured in the longshort axis system. Differences in WSG between the long-short axis are insignificant, meaning that differential growth rate has no statistical effect on WSG. However, the maximum mean WSG occurs on the long axis for the full WSG profile. High mean WSG occurs in the core wood modules on the long axis and on the short axis for the outer wood modules. Estimating within and between correlations provides insight into the shared biology between the two axes. The low WSG of the core wood modules had greater similarity between the two opposite sides, while the outer wood modules, although producing a higher WSG, showed less or no similarity between the long-short axis. The bivariate mixed model approach used in this study would improve our knowledge of why trees evolve into the structures we see by providing a better basis for predicting woody plant behaviour in all aspects. From this study, the long-axis wood genesis is more similar to the short axis in the juvenile stage, but in the outer wood, it is very likely that the long-axis wood genesis differs greatly from the wood formation for the short axis. Statistical tests used to measure the relationship between aspects of a tree must account for these perceived spatial and temporal dependencies. This raises an important problem with respect to the widely used traditional approach, regression analysis, which assumes error independence. These models do not divide the variance component into within-subject and betweensubject variance because they contain no random effects in the regression model. Covariance and correlation may be of great importance to wood technologists seeking to understand the physiological processes that contribute to WSG variability within and between trees. Future research will apply the multivariate mixed model method to WSG data sampled from four axes of the tree trunk.

# **Data Accessibility** :

-Wood specific gravity data: Dryad doi: 10.5061/dryad.x95x69pnk

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#### Abbreviations

WSG: wood specific gravity; AIC: Akaike information criterion; BIC: Bayesian information criterion; CV: Coefficient of variation; RRD: relative radial distance; CI: confidence interval; BLUP: best linear unbiased predictions

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# Author's contributions

JOA and JM conceived and designed the experiment; JOA performed the experiments, analyzed the data, and drafted the paper. JM contributed substantially to the interpretation of the results and to the drafting of the article. The authors have read and approved the final manuscript.

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## Availability of data and materials

Not applicable.

# Declarations

# Ethics approval and consent to participate

The wood samples used in the present study were collected following the laws of Ghana.

#### Consent for publication

Not applicable.

#### **Competing Interests**

The authors declare that they have no competing interests.

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Table 1: Model fit estimates

Trait	Number of Parameters	-2LogLike	AIC	BIC
WSG	5	-1254.9	-1244.9	-1249.4
Core WSG	5	-610.3	-600.3	-604.8
Outer WSG	5	-635.7	-625.7	-630.2

AIC: Akaike information criterion; BIC: Bayesian Information Criterion

Table 2: REML estimates of error variance, autocorrelation parameters (for spatial and temporal factors)

	Error variance	Error variance		Autocorrelation	Autocorrelation
Trait	Aspect 1	Aspect 2	Covariance	Spatial (Between-radii)	Temporal (Within-aspect)
Full WSG	0.004236	0.003286	0.000944	0.253	0.837
Core WSG	0.00344	0.003429	0.001774	0.52	0.789
Outer WSG	0.004462	0.002389	-0.00009	-0.03	0.856

Table 3: Highest Posterior Density (HPD) Interval for the variance-covariance parameters monitored in PROC MCMC for the bivariate data analysis

	Aspect 1	Aspect 1	Aspect 2	Aspect 2	Covariance	Cov
Trait	95% HPD Interval	95%				
Full WSG	0.00438	0.00474	0.00347	0.00376	0.000898	0.0
Core WSG	0.00359	0.00388	0.00363	0.00392	0.00173	0.0
Outer WSG	0.0046	0.00498	0.00257	0.00278	-0.00015	0.0

Table 3: Between-radii correlation (simulated 5000 times)

Trait	Correlation	95% Confidence Interval	95% Confidence Interval	P value
Full SG	0.23	0.21	0.26	<.0001
Core SG	0.49	0.47	0.51	<.0001
Outer SG	-0.02	-0.05	0.004	0.096

Table 4: ANOVA showing the effects of space (aspect), time (rrd), and space-time (aspect\*rrd) interaction factors on the complete WSG

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	$\Pr > F$
Aspect	1	29.7	0.03	0.8604
RRD	9	147	7.19	<.0001
Aspect * RRD	9	165	1.31	0.234

Table 5: ANOVA showing the effects of space, time, and space-time interaction factors on core WSGType 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	$\Pr > F$
Aspect	1	70.2	10.43	0.6215
RRD	4	27.8	0.25	<.0001
Aspect * RRD	4	78.9	2.16	0.0811

Table 6: ANOVA showing the effects of space, time, and space-time interaction factors on outer WSG Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	$\Pr > F$
Aspect	1	23.6	0	0.9614
RRD	4	67.3	1.5	0.2109
Aspect * RRD	4	81.9	0.88	0.4774

# **Figure captions**

Fig. 1 Profiles of the scaled residuals produced from the model (a) Full WSG profile, (b) Core WSG profile and (c) Outer WSG profile

**Fig. 2** Scatter plot illustrating the association of WSG between Aspect 1 and Aspect 2 (a) Full WSG, (b) Core WSG and (c) Outer WSG

Note: Aspect 1 (long axis: fast-growing core) and Aspect 2 (short axis: slow-growing core)















Figure 2