# APPLICATION OF MIXED MODELS TO STUDY WOOD PROPERTIES OF TEAK PLANTED IN GHANA

アジチュム ジェリー オポン

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# APPLICATION OF MIXED MODELS TO STUDY WOOD PROPERTIES OF TEAK PLANTED IN GHANA

JERRY OPPONG ADUTWUM

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# ABSTRACT

Trees develop in space and time. Wood occupies space (both area and height), and wood is formed sequentially in time from the start (planted), annual growth, and end of wood formation (cut). During tree growth and development, the primary meristem (responsible for height growth) and secondary meristem (responsible for diameter growth) are unified by a signaling system controlled by endogenous and exogenous factors. As a result, wood exhibits complex heterogeneity in their properties, especially wood specific gravity and heartwood color. Wood quality data typically include both spatial and temporal interdependencies that can reveal key dynamical and statistical information of the tree growth process. This dissertation investigates the spatiotemporal process of wood formation and its development in Teak (*Tectona grandis* L.f).

The variation in wood properties is an observable phenomenon (of interest to wood scientists) and is influenced by underlying and unobserved factors. We cannot possibly measure these factors accurately and account for all factors that affect the tree growth process. All that can be seen explicitly are the effects of these processes, which appear in the wood data as intricate patterns of correlations and independence. Models should accommodate the principal sources of variability in the data, including random fluctuations that cannot be ascribed to measured parameters. The correlation structure models the complex evolutionary nature that the meristems have traversed in space and time to form the tree and wood. The physics of the first formed wood is encoded in the correlations between both spatial and temporal structures at late times. Traditionally, these aspects of information have been largely ignored in the wood science literature, which may have led to confusing conclusions as they are a source of variability that must be accounted for.

Mixed-effect models are developed and applied to address both spatial and temporal correlations embedded in wood data to gain insight into the processes underlying the observed

patterns in wood properties variations. Mixed models contain both fixed and random effects. The fixed effect models the signal while random effect models the noise in the data and captures the covariance structure of the noise. Data from six height levels, two aspects (opposite sides of the same tree), and ten relative radial positions (time factor) were used to illustrate the implementation of the repeated measures analysis method. Spatial correlation can be seen in the among height levels and between aspect whereas temporal correlation is embedded in the within aspect. The spatial correlation models the development of the apical meristems while the temporal correlation models the development of the lateral meristems.

The spatial and temporal correlations were mostly significant, implying that models chosen to clarify the variation in wood properties should account for the correlations inherent in the wood data. This research further shows that the spatial correlation among height levels increased from bottom to top, a phenomenon attributed to the maturation mechanism of the apical meristems. The decreasing temporal correlation from the center (pith) to the cambium (bark) is attributed to the decreasing influence of the crown of the cambium meristems. The correlation between opposite sides of the same tree was relatively low, likely indicating a strong environmental influence on the cambial genotype and wood formation. In many cases, the radial growth rate had little influence and statistically insignificant effect on wood specific gravity and heartwood color. Age and height were found to be decisive factors that control the wood specific gravity in teak. The implications are further discussed.

The results of this research provided remarkable correlations (physiological correlations) responsible for the variation in wood properties within trees. The spatial correlations, which measure the evolutionary relationship between the cambium separated by aspect, were generally low i.e., r smaller than 0.30. This indicates that wood traits in each aspect are influenced either by some different genes or differently by the same sets of genes and thus wood traits formed by the same cambium separated by aspect can have some degree of independent development. Also, the low spatial correlations can be a signal that external conditions under which trees developed are not constant in space. Similarly, spatial correlations among height levels were low a phenomenon attributable to the relative distance among height levels which was measured in meters. Furthermore, these correlations could be used to predict spatial distributions of biomass and yield by exploiting the correlation at lower height levels. The models explained the growth and physiology of the study trees much better. When seen in this light, spatial and temporal correlations should not only be accounted for by our models but also be considered as a significant piece of background information of the wood formation process that may be used by wood researchers to create a more precise distribution of wood properties throughout the tree.

This research contributes to the advancement of the statistical science of analyzing multivariate wood data (repeated measurements) for wood scientists, providing a new window into the fundamental physics of wood formation and wood property variation. There are correlations in the wood data we gather, so the main task facing modern wood scientists is to create a coherent tree history that explains these relationships.

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# CHAPTER 1

# INTRODUCTION

This thesis deals with the selected wood properties of planted teak in Ghana.

Ghana used to be mostly covered with natural forest but is shrinking by 135,000 hectares annually over the 20 years from 1990 to 2010 (FAO 2010a, FAO 2010b). However, according to Hansen et al. 2009, is so fast that estimating the forest area in Ghana has become a challenge. The Ghanaian forest products industry may face trouble and difficulty in acquiring the resources they need in the future if the deforestation rate is maintained. Changes in land use, compounded by shortages of large, naturally grown hardwoods, may result in lower inventories as timber demand keep rising. Promotion of fast-growing tree plantations is seen as a crucial strategy to overturn the decline and boost the availability of timber resources in Ghana (FC 2010). However, planted trees are grown in short rotations and can produce poor quality wood with a high proportion of core wood, a natural consequence of rapid growth (Clark 1997). The value (intrinsic quality) of these resources is generally considered to be low and cannot be used for structural purposes. The forest products industry may become increasingly dependent on fast-growing plantations of trees. Therefore, it is crucial to determine the distribution of wood properties in this new wood supply correctly (Zhang 1997).

Teak (*Tectona grandis* Linn. F., Lamiaceae) is an exotic tree species that was first introduced to Ghana between 1900 and 1910 (FAO 1981) and its large-scale plantations commenced in the late 1960s (Prah 1994). Today, teak is well planted by public and private companies with more than 150,000 hectares since 2002 (FSD-FC, Ghana 2017) and is one of the most economically important exotic tree species in Ghana. This species is highly sought after and is grown in several tropical regions, including Asia, Africa, and Latin America. It occurs naturally in Myanmar, Laos, Thailand, and India, but it is estimated that there are between 4.35 and 6.89 million hectares planted worldwide (Sasidharan and Ramasamy 2021), making it the most widely grown tropical hardwood in the world. Due to its excellent visual properties and biological and mechanical integrity, there is an increasing demand for teak wood products that is accompanied by decreasing stock of natural stands. Consequently, planting teak trees is considered a profitable investment opportunity (Ball et al. 2000). Teak is accepted worldwide for a variety of purposes, from general hardware and fittings to furniture and furniture making, from veneers to building applications, including railways and shipbuilding (Bhat 1998; Bailleres and Durand 2000). Teak is mostly processed in Ghana for the export market (TIDD-FC, Ghana 2021), processed locally for furniture and was previously used as the main source of electric transmission poles for the rural electrification project. Teak has not only economic value, but it is also fascinating for its ability to store atmospheric carbon. This highlights the importance of teak in reducing the release of carbon into the atmosphere. In 20-year-old teak plantations in Panama and a 14-year-old stand in Ghana, studies found an atmospheric carbon storage capacity of 120 $tC.ha^{-1}$ and 72 $tC.ha^{-1}$, respectively (Kraenzel et al. 2003; Watanabe et al. 2009). Ghanaian teak is currently harvested at varying ages from 15 to 20 years (Adu-Bredu et al. 2018) and this practice has contributed to the low quality of teak wood in Ghana coupled with poor forest management practices (Djagbeletey and Adu-Bredu 2007). The magnitude of the change in the distribution of wood properties within the logs is not known, although it is recognized that shortening the rotation will affect basic wood properties (e.g., Bhat et al. 2001; Bhat and Florence 2003). Despite the lack of information on the biological maturation of Ghanaian teak, teak tree harvesting occurs only based on economic needs and incentives. Consequently, sustainable use of this plantation resource is necessary to improve teak wood quality. One way to get the most out of wood resources is to effectively study the distribution pattern of wood properties within the tree. Knowledge of the qualities and characteristics of teak wood is crucial in deciding if additional research on teak grown in Ghana is necessary.

Trees are sessile biological systems that are unable to escape environmental stresses. The tree’s morphology changes over time and space as it grows into space and evolves in response to its ever-changing environment in response to a multitude of factors as like, light, temperature, wind, or nutrients, resulting in a more complex and heterogeneous wood (Larson 1964; Niklas 1992). Variation in quantitative traits (e.g., tree height and diameter) and wood properties is accepted as the tree's adaptive mechanism to its environment due to its sessile nature (Larson 1964; Bell and Lechowicz 1994; Friml 2003). Advances in molecular genetics have observed that certain genes and proteins are expressed differently in ways that contribute to wood plasticity (Dejardin et al. 2010). Wood is known to be very heterogeneous (Zobel and van Buijtenen 1989). This lack of uniformity is one of the main problems for manufacturers, reducing the efficiency of wood as a raw material compared to alternative materials such as steel. Within a given species, variation within a tree represents a major source of variation (Larson 1967). Variation within the tree is further classified into horizontal variation, i.e., radially from pith to bark, and vertical variation, that is, axially from the tree stump to apex. These changes are analogous to the progression of the physiological age of the cambium at the tree base and at the tree apex (Lachenbruch et al. 2011). Predicting wood performance and end use is very difficult due to its variability. However, due to their variability, trees offer great potential for genetic improvement and diverse end uses (Zobel and van Buijtenen, 1989; Koga and Zhang, 2004). Therefore, a better understanding of the variability within a tree is central to optimizing the wood value chain and improving the properties of the wood.

For teak planted in the tropics, particularly Costa Rica and Togo, there are several studies on the effects of growth on wood quality, but they are somewhat scattered and inconclusive. There is also no comprehensive information on the properties of the teak wood grown in Ghana. This means that the wood industry in Ghana does not have basic information on the efficient, sustainable, and potential use of the age of the species, and the influence of rotation (15 – 20 years) on the extent of change in the basic properties of wood is not known. Trees grown in intensively managed forests over a short period have a higher proportion of core wood compared to trees from old growth.

The present study focuses on the influence of different sources (i.e., tree age, growth rate, stem heights, tree effects) on the change in wood properties. The general aim of this study was to use mixed effects models to describe how properties change within individual trees, from stump to merchantable top and from pith to bark. It also aimed to clarify the factors that control the change in wood properties. This study is designed to complement growth and yield studies. They are essential for optimizing forest management and maximizing yields from teak plantations. The models adopted in this study provide an underlying mechanism for tree growth and observed variations, physiological patterns for the evolution of wood properties in both axially and radially, and prediction of the changes that will occur in wood properties, allowing biologists and wood users to quantify the properties of the spatial location of a tree. With a better understanding of how wood properties are regulated, it is possible to manipulate growth rates which can improve utilization by increasing its uniformity. This study focuses on two properties of wood, namely specific gravity, and heartwood colour, because these properties are complex and depend on basic chemical, physical and cell organization at the anatomical level. Specific gravity is closely related to the physiology of tree growth. Specifically, the objective of the study was as follows:

1. To clarify patterns of variation over time in tree height and across stem diameter.
2. Quantify the variation in wood property between individual trees.
3. Clarify the factors that control the evolution of wood properties and the mechanism of maturation of xylem, in particular wood specific gravity.
4. Clarify the effect of eccentric growth on the variation of the wood property.
5. Using statistical analysis tools that consider the expected correlation (physiological correlation) in the wood specific gravity data by modelling the covariance structure and presenting the broad physiological organization of the wood formation process.

**Thesis Outline**

This thesis is written in "Integrated Article Format". Brief descriptions of each are presented below.

Chapter 1: Presents the research background, identifies the research gaps, and presents the research goals.

Chapter 2: Provides a literature review focusing on wood specific gravity, space-time analysis of wood data, and physiological aspects of wood formation.

Chapter 3: Presents information, research methods, and data analysis used to assess the temporal variation and covariation of specific gravity of wood and identify the physiological basis while establishing the temporal control of xylem maturation of wood specific gravity of teak. The chapter dealt with modelling of the temporal variance-covariance matrix, and criteria for choosing among several correlation structures were discussed.

Chapter 4: A novel approach to clarifying the longitudinal variation of wood specific gravity is presented. The approach used a space-time technique to clarify the variation and covariation in the distribution of wood specific gravity at each presumed time-point along the tree height. The approach provides detailed information about evolution of both apical and lateral meristems.

Chapter 5: Joint modelling of heartwood color on the long-short axis of the same tree was examined. We incorporated the correlation between the two axes (so-called spatial correlation), and contemporaneous correlation was also modelled. The joint modelling of multivariate data enabled the decomposition of the sources of shared spatial structures.

Finally, Chapter 6 summarizes the work contained in this thesis and discusses the implications for future research.

# CHAPTER 2

# LITERATURE REVIEW

The literature review focuses primarily on the wood properties (specifically wood specific gravity) examined in this study. These are widely recognized as useful indicators of wood quality, especially for structural purposes.

## 2.1 Relevance of Wood

Trees are complex biological organisms that have existed for millions of years, with the evolution of wood formation occurring around 380 million years ago (Willis and McElwain 2002). Wood is a valuable natural resource that is used for a variety of purposes such as construction, transportation, art, and sports. Trees also play a crucial role in the carbon cycle, which is the foundation of life on earth. Carbon is a common chemical element (Ren et al. 2013) and is used in food, civilization, economy, and transportation systems. Trees store carbon in their above and below-ground structures through photosynthesis, which converts carbon dioxide in the form of cellulose, hemicellulose, and lignin (Unwin and Kriedemann 2000). Carbohydrates are the basic molecular building blocks used to build the bulk of the tree. Climate change has highlighted the importance of trees in the carbon cycle and their conservation is becoming increasingly important. To efficiently use and conserve wood resources, plantation is one solution, and it is necessary to understand the mechanism of wood formation (xylogenesis) and find the optimal environmental conditions for their growth in order to maximize the economic value of trees.

## 2.2 Wood and its Function

The importance of wood products for the global bioeconomy cannot be overstated. Wood is a product of the metabolic activity of the cambial meristem, which originates from a highly structured developmental process in living trees (Panshin and de Zeeuw 1980). Wood is produced under the bark in the trunks and branches of trees and shrubs (Webster and McKechnie 1980). Trees deal with the problem of gravitational force by strengthening their trunk axis through wood formation. The development of wood is a result of a series of phases, including cell division, differentiation, expansion, secondary thickening, and maturation, all coming together to create wood (Larson 1969). Wood cells are made of cellulose and lignin, two structural materials that give the tree its strength, and are made in the leaves through photosynthesis. Cellulose is the most abundant biological compound on earth. The vascular cambium, a thin layer of meristematic cells located between the secondary phloem (i.e., living bark) and secondary xylem (i.e., wood), is responsible for forming a continuous sheath around the trunk, branches, and roots of trees and producing xylem inward and phloem outward (Wilson 1984). These cells vary in size and shape, depending on their physiological role in the tree. Wood cells perform four main functions inside the tree: mechanical support, transport of water, carbon, and nutrients, support and allocation of photosynthesis and storage and distribution of defense chemicals to protect the tree from pathogens. These functions have opposing structural requirements that impact the cells produced and thus wood properties. In hardwoods, different cell types perform these three functions. Specialized parts in the wood called vessels and fibers play specific roles in the tree. Vessels are involved in moving water vertically and fibers provide mechanical support. Meanwhile, cells called parenchyma cells, which are only living cells are arranged horizontally in rays, help with the transfer of nutrients and energy between the phloem and xylem, as well as store food in the form of starch and lipids for future growth. The variation and pattern of different cell types and their anatomy directly influence wood traits such as density, strength, or stiffness. A detailed description of the wood formation in hardwoods is given in Dejardin et al 2010.

## 2.3 The Concept of Wood Quality

The characteristics of wood can have a significant impact on its suitability for different uses and its ability to withstand transformation. However, the concept of wood quality does not have a clear, objective definition, as the relative importance of different characteristics depends on the intended end use (Larson 1969; Larson et al. 2001; Bowyer et al. 2007). Wood quality is a composite expression of several properties, such as its anatomical, physical, chemical, and mechanical properties of a piece of wood for a specific product (Punches 2004). Therefore, the concept of wood quality is dependent on its intended use (Cown 1997). For example, in structural applications, the main criteria are stiffness, strength, and dimensional stability on drying (Porteous and Kermani, 2007), which in turn are strongly dependent on intrinsic wood properties such as wood specific gravity (the mass of wood cell wall material per unit volume), microfibril angle, and others. In summary, the quality of wood can be defined as a spectrum of properties that are considered to varying degrees based on the intended use of the wood.

## 2.4 Wood Specific Gravity

In the field of wood science, the measure of wood specific gravity, has been the focus of much attention and is commonly used to assess the quality of wood. Wood specific gravity is the construction cost of tissue per unit volume and is often found to be a good first order approximation in predicting variations in mechanical properties of trees. In simple terms, it is a measure of the solid wood substance (fiber wall) in wood. It is associated with its suitability for use in making paper, its ability to be treated chemically, its dimensional stability, its ability to insulate against sound, electricity, and heat (Wiemann and Williamson 1988). The specific gravity of wood is the ratio of two densities: the density of wood to the density of pure water at 4° C (Koch 1972; Williamson and Wiemann 2010). Wood specific gravity is the wood mass per unit volume. The density of the water is assumed to be 1 g/cm$^3$. Therefore, the specific gravity of a wood substance becomes numerically equal to its density. It is dimensionless. Information about wood specific gravity of trees is valuable for both arborists and wood users. The wood specific gravity of trees, together with estimates of the volume of wood, allows us to predict the dry weight productivity of a unit area of land or the productivity potential of tree stands. As a heritable trait, wood specific gravity can be influenced by environmental factors, silvicultural treatments, and varies as tree age (Zobel and Rhodes 1955; Paul 1963; Briggs and Smith 1986). The link between stem biomass and stem volume is reflected in the fundamental form of wood specific gravity. Large cell lumens are produced more quickly by species that emphasize stem volume expansion, which lowers the specific gravity below the theoretical maximum density of 1530 kg/m$^3$ (Bamber and Burley 1983). The specific gravity of wood is increased in species that emphasize biomass accumulation by producing smaller lumen or thicker cell walls. An increase in wood specific gravity by 0.02 units leads to an increase in dry pulp of 22.7 kg per ton of round wood (Mitchell 1964) and an increase in the modulus of rupture or modulus of elasticity by 31.15 kg/cm$^2$ and 3516 kg/cm$^2$ (Wahlgreen and Schuman 1975). Therefore, achieving high wood specific gravity should be the goal of management practices when growing high quality wood for industrial purposes. Recently, ecologists have become interested in the intricacy of specific gravity as they explore functional traits and determine their significance in terms of ecology and evolution. They pay attention to specific gravity to better understand how trees adapt to their environment (Falster and Westoy 2005; Jacobsen et al. 2007; Chave et al. 2009; Poorter et al. 2010). Regardless of timber use, specific gravity is now recognized as an important ecological trait of tree function, as it encompasses the expression of the genome, ecological character, the tree function history (e.g., Morel et al. 2018), the physiological functioning and the economic value of tree boles (e.g., Thomas et al. 2005).

The wood specific gravity is a highly variable property, showing considerable variation within a single tree and between trees within a species, which has been the subject of extensive research. According to Panshin and de Zeeuw (1980) three trends of vertical variation in wood specific gravity have been reported. They are:

1. As the height increases, the density decreases evenly.
2. Decreasing in the lower trunk and then increasing in the upper trunk.
3. Increasing in the trunk from the base to top in a nonuniform pattern.

When we consider how trees grow, we can understand radial variation. The wood corresponding to earlier ontogenetic stages remains closer to the pith as cambial activity adds new sheaths to the wood towards the outer edge. Radial variation may reflect changing environmental conditions as well as biomechanical needs placed on wood as tree age and/or increase in size. In the horizontal spatial dimension, a general classification of the pattern of wood-specific gravity pattern of variation from pith outward has been described in the literature and is as follows:

1. Specific gravity increases from the pith outwards.
2. Specific gravity decreases from the pith for the first few years and then increases with increasing age from the pith.
3. Specific gravity increases near the pith and then remains more or less constant or sometimes decreases again near the bark.
4. Specific gravity generally decreases from the pith outwards.

Biological logic suggests that wood properties should be classified in two dimensions: stump-to-tip and pith-to-bark and their interactions (Olesen 1978, 1982; Burdon et al. 2004): up the stem and radially from pith to bark. This argument is based on the theory of age changes in both the apical and lateral meristems (Olesen 1972, 1982). Although not as obvious as the pith outwards variation, the differences in wood quality along the stem can have significant consequences, particularly for the bottom logs of rapidly grown trees and in estimating the overall distribution of wood properties in the entire stem. The way that wood properties are distributed vertically and radially is complicated and has intricate details. Understanding the arrangement and distribution of wood properties in trees requires advanced mathematical techniques like tensor and vector calculus.

## 2.5 Wood Variation and Its Causes

The complete life history, as well as its environmental series of changes, is preserved in wood. Wood anatomy, chemistry, and consequently its physical qualities are affected by environmental variations. These changes can occur not only between tree sections (such as stems, branches, and roots), but also inside individual tree parts. Variation in wood occurs at several scales and spatial locations in the stem and crown. First, the progressive change from the pith (middle of the tree) to the bark, referred to as “the core / outer wood or juvenile/mature wood pattern” or, as Lachenbruch et al. 2011 phrased it, “typical radial pattern” is the most well-known and studied within-tree variability in wood. Second, the vertical variation considered on a cross-sectional disk as a function of tree height from stump to apex, which has not received much attention, especially in African tropical species. Third, between normal and tension wood (that is, clear wood versus wood formed in response to gravity). The influence of environmental variation on the radial pattern of wood production is significant. Because wood property evolves radially and are depending on the specific tree and geographic region (Cown et al. 1991; Fabris 2000; Kojima et al. 2009), there is no common spot within a stem to designate the transition from core to outer wood. Because all tree populations can be classed according to age and growth rate, regardless of environmental or geographic location, it is important to look at variation in wood specific gravity within a given species in relation to these two parameters: age and size.

## 2.6 Tree Age versus Tree Size

The formation of tree wood evolves in reaction to the external forces it faces at each stage of its development. The age of the cambium or elements that alter as the tree grows in diameter or height can impact how the properties of the wood change radially and vertically. The age vs. size effect is commonly discussed in wood biology when discussing fixed and plastic mechanisms. We can better understand the components that influence wood structure and function by determining whether tree age or tree size controls wood property along the radial or vertical change. A size effect could be explained by the changing demand for the mechanic function of wood; in contrast an age effect could point to an intrinsic control of wood development such as the number of dormancy periods experienced (Lachenbruch et al. 2011). To separate the impact of age and size on wood properties, either trees of varying ages but similar sizes or trees of different sizes but the same age can be compared. The former is more difficult to encounter and has never been used; hence, the latter has been used in most studies. Williamson and Wiemann (2011) proposed a new method for evaluating the age versus size dichotomy for wood property variation in wood specific gravity, namely, different sides of the same tree exhibiting different sizes. The goal of this strategy is to minimize the unknown reasons for differences in growth in a forest made up of trees of the same age, which could be due to the genetics of each tree and the specific environmental conditions they grew in. In tropical species, some studies indicated that wood specific gravity was more closely related to age than to size (Rueda and Williamson 1992; Castro et al. 1993; Williamson and Wiemann 2010, 2011). In the case of age-dependence, a time-related metric, such as the number of dormancy periods experienced, causes the cambium to produce wood with mature cambium thus higher specific gravity; on the other hand, a size-related metric, such as the number of periclinal divisions experienced, determines wood structure and functions (e.g., Kojima et al. 2009).

Fast growth does not always mean a tree is mature. The tree might grow quickly, but he cells it produces may be less dense, resulting in lower specific gravity. Harvesting faster grown trees at an earlier age because they have reached a certain average diameter sooner may hinder wood utilization as they would contain a larger proportion of lower specific gravity. Young trees will have fewer growth rings closer to the center of the tree compared to older trees of the same size. The knowledge of tree age or tree size of tropical trees and its relation to wood structure is poorly studied. It is important to understand how age and size impact variations in wood properties in order to improve plantation growth. The maturity of the tree plays a role in determining the quality of the wood it produces. Maturity may be influenced by the rate of production (which is spatially controlled) or the physiological intensity (age or temporally controlled). Gaining knowledge of how age and size influence the properties of wood can give us the tools necessary to manage tree growth and development, particularly with regards to the core wood which is not suitable for structural purposes (Lachenbruch et al. 2011).

## 2.7 Mixed Effects Model

### *2.7.1 Tree as Space-time Domain*

The tree is a biological system that operates in both space and time (Fayle 1972; Manceur et al. 2012). The concept of space-time is fundamental to understanding the complex formation of wood. Space is multi-dimensional in which wood formed occupies a relative position and direction. Time is a continuum in which layers of wood follow one another from the past, through the present to the future. The trunk as a geometric figure represents space (position in the tree), while the beginning, evolution, and end of the wood production process are represented by time. Time is integrated within the tree. The tree trunk has both a vertical and a horizontal spatial dimension, created by the primary growth from the apical meristem and the secondary growth from the vascular cambium, respectively. Modeling appears to be a key tool for gaining insight into the primary mechanisms controlling wood formation and variations in wood properties, which a complex process that is tightly regulated over both space and time. The growth pattern of the tree involves organizing the shape-forming events in a specific order over space and time, forming a hierarchical system of processes that take place at all levels of the tree's structure.

### *2.7.2. Wood Formation Mechanism*

The physiology of wood production is separated into two distinct aspects. The primary stage of the process of producing wood involves the growth of the overall structure and height growth. The main stem lengthens because of active cell division in distant apical meristems. During the secondary stage, meristematic activity of the vascular cambium causes the stem to increase in diameter. The renewal of tissues is necessary for their survival and is achieved by the addition of modules of primary and secondary growth to the crown, trunk, and roots annually (Lanner 2017). Cambial activity in a stem often increases in a tapered fashion as it descends from the apex where hormones are produced. Much of the variability in growth hormone, such as auxin availability and photosynthate, is explained by physiological gradients (which decrease with distance from the apical meristem, this is known as basipetal polar flow of hormones) within a stem (Aloni 2001; Aloni and Zimmerman 1986). A change in the hormonal balance influences the gene activity and gene pattern (Olesen 1978). This changes the expression of specific genes/proteins during wood formation contributing to the plasticity of wood property both in space and time (Mizrachi and Myburg 2016; Dejardin et al. 2010; Savidge 2003). Savidge (2003) adds that the genetic makeup of the cambium may remain the constant through a tree, the way genes are expressed, and the resulting output cam vary based on the physical and chemical conditions that cambium cells are subjected to in different spatial locations within the tree. Any differentiated tissue structure that is the result of a well-defined series of actions are intricately linked both temporally and spatially within the growing tissue mass (Goodwin and Cohen 1969). There is a strong connection between the concentration of hormones present and the way genes are expressed, and how these factors affect the properties of wood produced (Lachaud 1989). These processes create some dependencies and patterns in wood formation and can affect both radial and vertical variation in wood formation and hence specific gravity. The basic mechanism that coordinates tree growth and wood formation both spatially and temporally is still poorly understood.

Our understanding of the factors affecting wood properties variation is limited due to the lack of precise and high-resolution measurements of the underlying process (Grigera 2021). However, according to Thorson and Minto (2015), statistical techniques can be utilized to make inferences about the "hidden" unseen biological processes of the cambium from wood quality data (that is, "*statistical models are often used to count invisible moving trees").* The physiological component, critical to understanding the temporal and spatial pattern of wood formation is largely overlooked in traditional wood specific gravity analyses. The distribution of specific gravity of the wood is determined by stem analysis (Duff and Nolan 1953; Forward and Nolan 1964; Fritts 1977). Wood cores are taken at different heights or aspects within a tree for measurement of one property. Stem analysis enables the understanding of changes in wood structure within the tree over time. Disks are taken up the stem of the sampled trees at specified intervals. The data obtained from stem analysis is both complex and involves multiple variables and aspects of time and space (that is, multivariate and spatio-temporal). We can view the specific gravity observations as repeated measurements to expect that there is a correlation between the multiple measurements made on the same tree (e.g., Manceur et al. 2012). The initial step in analyzing autocorrelation is to examine the variation and correlation of the data (Manceur et al. 2012). Autocorrelation is the property of correlating a variable with itself at different time intervals in different spatial intervals. Autocorrelation of variables and crosscorrelation between variables are well known in tree ring analysis (Wimmer 2002), and the dendrochronological literature underscores the need to correctly evaluate error values: "Proper statistical treatment of data, for example accounting for non-independence of variables (often a major problem in structural research), will allow more correct interpretation of actual patterns" (Gartner et al. 2002). There may be three sources of autocorrelation. Multiple measurements on the same disk can be correlated since the cambial initials are always formed in the previous season (Fritts 1976). This implies that the specific gravity of the wood formed in one year is influenced by the wood specific gravity of the wood formed in the previous year. The second autocorrelation is longitudinal correlation, in which specific gravity measurements from two adjacent disks are more similar than those from two more distant disks. According to Duff and Nolan (1953), vertical growth is affected by the climatic conditions of the previous season since the food supply is then being stored and made available for new tissue growth in the current year. Furthermore, this longitudinal correlation may possibly be explained by the longitudinal gradient in growth hormones and photosynthate in the top-down approach and the movement of nutrients from the bottom-up. The third source of correlation is temporal dependency. Due to climatic effects on specific gravity, specific gravity of wood grown in the same year but at different position in a tree will be correlated in both the longitudinal and radial direction. Also, individuals that are genetically similar may also have unmodelled correlations in wood specific gravity and shared environmental changes may cause synchronous changes in individual wood specific gravity variation. In general, there is relativity in the variation of wood properties; for example, the variance can change more in one dimension or the position in the dimension. These can be taken care of by modeling the variation between and within trees. In statistical modeling, these are causes of errors that must be addressed by identifying the corresponding variance-covariance matrix (which embodies both the variability and the interdependencies) in order to perform valid tests of significance for mean value in a spacetime example of a tree stem. These sources of variation can be modelled using mixed modeling by considering them as random effects as they are influenced by a common physiological process. Linear regression models often presume statistical independence (absence of correlation) between residuals for distinct data points, however, unmodeled correlations undermine this assumption (Manceur et al. 2012; Aitken et al. 2009). Mixed effects models come in handy in this situation. Any model with a combination of fixed and random effects is referred to as a mixed-effects model. The mixed modeling approach combines the estimation of both fixed and random parameters in one analysis, leading to accurate and effective results for the fixed parameters (Pinheiro and Bates 2000). These selected references provide a full treatment of spatiotemporal process modeling with mixed effects: Stroup et al. (2018); Dutilleul (2011); Verbeke and Molenberghs (2012). Models help us explain the variation in properties within a tree by revealing the underlying physics behind wood formation and are important for making better management decisions. They also help the forester make the best use of available resources and plan for efficient product sorting and use (Lindstrom 2002). In summary, modeling the physiological growth correlations allow for a more detailed approach to study the effects of environment, growth conditions and temporal effects on wood formation and thus wood specific gravity (Larson 1969). It is crucial to understand that all evaluation of wood quality is based on statistics and can be misleading unless the biological sources of variation are taken into consideration and made clear. By understanding the growth needs of teak and how it interacts with the environment and utilizing information about the connections between growth in different parts of the tree and their physiology during the growing season, geneticists can identify the most favorable traits for improvement.

# CHAPTER 3

# AN APPLICATION OF MIXED-EFFECTS MODELS TO EVALUATE THE ROLE OF AGE AND SIZE ON RADIAL VARIATION IN WOOD SPECIFIC GRAVITY IN TEAK (*Tectona grandis*)

### 3.1 Abstract

To test whether radial WSG is controlled by tree age or tree size in teak (*Tectona grandis* L.f) plantation trees, opposing different-length pith-to-bark strips which represents the differential lateral growth rate was compared using mixed-effects model which considers the heterogeneity of variances and dependency in the data to gain insight into the stochastic processes that govern the wood formation process. Various models were tested in devising an appropriate radial WSG model. Models that accounted for serial correlation in WSG data performed better than the simple structure that assumes zero correlation between measurements. The autoregressive plus random tree effect structure performed better in describing the radial variation pattern. The variability of the data related to random fluctuations during tree development and wood formation process is modelled by the autoregressive parameter revealing the intrinsic complexity of wood formation. Since they cannot be attributed to observed factors, models should consider temporal or serial correlations when assessing wood quality. The results revealed that tree age is a decisive factor in controlling the WSG of wood, while tree size is statistically less important. Furthermore, the core wood production period varies with the growth rate. It is shown that the core wood area decreased with slow growth. Findings presented here appear to provide the first demonstration of radial variation in WSG with respect to growth rate and age for planted teak growing in Ghana.

**Keywords**: *Tectona grandis*, Tree age, Tree size, Growth rate, Radial variation, Xylem maturation, Wood specific gravity, Linear mixed model, Temporal autocorrelation.

## 3.2 Introduction

Teak (*Tectona grandis* L.f) is a tropical pioneer species growing on more than 260000 hectares (FAO 2010) in Ghana and accounts for approximately 70% of the exotic species in the plantation base (Apertorgbor and Roux 2015). Teak in Ghana has been reported to be genetically associated with those in central Laos (Verhaegen et al. 2010). Teak is the most commercially important plantation tree species in Ghana, grown in even shorter rotations to keep up with timber demand and reduce restoration costs. However, there is a concern that this practice will produce trees with a large volume of core wood, which will affect usable timber. Lachenbruch et al. (2011) defined core wood as wood close to the pith with relatively large radial wood property gradients, and outer wood as wood lying outside the core wood with more uniform wood properties. Core wood is characterized by a low wood specific gravity (WSG), a high microfibril angle, and short fibers, which causes problems in processing and utilization (Zobel and Sprague 1998). The need for sustainable plantation resources is amplified by increasing their economic value by providing them as suitable for building, construction, and high-value-added products such as furniture. Therefore, it is important to clarify when and where wood maturation occurs and what is the controlling factor is for xylem maturation. Knowing what, when and where xylem maturation occurs can be critical to the successful development of plantations (Kojima et al. 2009).

Tree growth is a classic spatiotemporal process. The vertical dimension exists due to the primary growth from the apical meristem and the horizontal dimension exists due to secondary growth from the cambium. However, how these processes are spatially and temporally remains unclear. Tree development involves two types of processes at the cellular level: an increase in cell number through division and a change in size through growth, resulting in an increase in height and diameter over time. As part of the tree growth process, there is some interdependence between the cambium sheaths within the trunk (Manceur et al. 2012) since cambium initials are always formed in the preceding growing season (Fritts 1976). These correlations should be viewed as physiological growth correlations rather than mathematical correlations (Larson 1969). This provides the physiological basis for autocorrelation in the tree growth process. Analysis of the variation (variance) over time in the wood properties assessed must allow modeling of the changes in variances and correlation (covariance) with tree age. This modeling process provides a key understanding of the physiological control of wood formation (Manceur et al. 2012). After a period of tree growth, the young cambium, which forms the core wood, gradually ceases, and the mature cambium which produces the outer wood, is formed thereafter. This has been termed radial shift (Wiemann and Williamson 1989a,b; Williamson and Wiemann 2010, 2011). Trees undergo physiological and morphological changes through ontogeny. However, the physiological relationships between the life stages of teak trees are poorly understood although this species is of great ecological and economic interest (Bouriaud et al. 2004). The factors known to cause cambium maturity are spatial, temporal, and/or the interaction of both (spatial temporal).

WSG has been described as a function of cell size, shape, proportion, and thickness of cell walls at the anatomical level (Wang and Aitken 2001; Elliott 1970). A direct relationship between WSG and tree growth or productivity is expected (Williamson and Wiemann 2011; Bouriaud et al 2004). Thus, the radial pattern of the WSG of a tree offers a record of changes in the biomass allocation during growth and development. This record can tell us whether the WSG is controlled spatially or temporally. Clarifying the spatial and temporal factors in WSG variation can give us the requisite knowledge needed to manipulate the pattern of wood development, particularly in the case of core wood which affects the value and utilization (Lachenbruch et al. 2011).

Longitudinal analysis of data using ordinary least squares assumes that the error term is independent (Hermann et al. 1998). This leads to biased estimates of the model parameters and reduces the efficiency of the estimated parameters, leading to invalid statistical conclusions (Johnston 1984; Judge et al. 1988; LeMay 1990). This challenge has increased the popularity of mixed-effects models for analyzing longitudinal data due to their flexible variance-covariance structures that allow for heterogeneity of variance and dependence within observations (Pinheiro and Bates 2000; He 2004). The estimated variance-covariance matrix allows valid tests for the significance of mean values (Gregoire 1987; Manceur et al. 2012). The covariance model is the level of association between consecutive wood increments within a core (Meng et al. 2012; Verbeke et al. 2014). However, few studies have evaluated the autocorrelation between errors between successive wood increments for temperate species (Sauter et al. 1999; Mutz et al. 2004; Jordan et al. 2005; Koubaa et al 2005; Antony et al. 2010), but none for tropical hardwoods. Therefore, since the radial variation of WSG is based on repeated wood increments at different time, it becomes imperative to model the temporal autocorrelation in the data. With the mixed modeling approach, unbiased insights can be gained. Therefore, the objectives of this study were to determine: (1) to develop a model describing the radial variation in teak WSG by determining an appropriate variance-covariance structure; (2) to clarify the effects of age and size on radial variation in teak WSG; and (3) to clarify the mechanism of xylem maturation and to discuss the broad physiological control in the process in teak WSG using a mixed modeling approach. Effective utilization of woody material requires reliable information on the quality distribution (proportion and size of the core wood and outer wood) in a harvested stem. In addition, we subjected our data to Bayesian analysis, which assumes that model parameters come from a broader distribution and do not rely on large sample theory (Muthén and Asparouhov 2012). This was done to solve the small sample problem in this study (He et al. 2021). As a guide this work and based on the literature (de Castro et al. 1993; Kojima et al. 2009; Nock et al. 2009; Williamson and Wiemann 2010, 2011), our working hypothesis is that age-dependent radial increases should lead to slopes that are steeper in the short radius than in the long radius.

## 3.3 Materials and methods

### *3.3.1 Sampling, wood specimen preparation and wood specific determination*

Three straight-bole 18-year-old *T. grandis* trees were randomly selected from a private plantation with a spacing of 3 m by 3 m in Dormaa Ahenkro, Bono Region, Ghana. 10-cm thick discs were sampled from each tree every meter starting at 0.3 m from the ground level. From these discs, two radii being the opposite sides of the tree were selected randomly (see Fig.1). The discs were eccentric by at least 1.3. Subsequently, a strip approximately 1-2 cm wide was cut from the disc. The strips were conditioned for several months at 20 $^{o}$C, 65% relative humidity until achieving 12% dry-base moisture content (MC). Then, the strips were cut into two 1-cm segments (from the pith to the bark) collected from the opposite sides. The air-dried specific gravity (weight at 12% MC / volume at 12% MC), here referred to as wood specific gravity (WSG), was measured with an electronic densimeter (Alfa-Mirage MD-300S) calibrated to compensate for the water temperature (as water is 1 g/cm$^3$ at 4 $^{o}$C). Each disc was analysed as two separate halves, referenced as disc long and disc short, separated by the pith. Each disc was then divided into 10 consistent parts over the radius and the mean value for each fraction was calculated using the relative distance approach (Hans et al. 1972; Chowdhury et al. 2009; Makino et al. 2012; Hidayati et al. 2014). The relative radial distance (RRD) approach has been used to clarify xylem maturation. This was done as it was very difficult to distinguish the annual rings. Using this method, wood strips of different lengths were standardized. The ages at given RRD along a radius were unknown, so we assumed that RRDS along the radius were the same age, for example, at 10% RRD from the pith on both short and long radii the wood should be the same age. To clarify whether the radial WSG pattern is controlled spatially or temporally, the two sides at a height level of the same tree were evaluated using linear mixed models (Williamson and Wiemann 2011). The different length radii at the same sampling height of a tree represent growth rate differences in tissues that are uniform in genetic makeup, cambial age, height in the tree, and microenvironment, although aspect and illumination can differ (Taylor 1968). These differences reflect how trees respond to local environmental conditions and the orientation of the stems for better access to light may lead to eccentric growth (Pruyn et al. 2000). The total number of observations was 360 (3 trees × 2 radii × 6 replicates × 10 RRD levels).

### *3.3.2 Statistical analysis*

The resulting data constitute spatiotemporal repeated measures on the tree, with RRD as a time factor and aspect as a space factor. Observations from the same unit (tree, disc, and age) tend to be spatially and/or temporally correlated (Hermann et al. 1998; Tasissa and Burkhart 1998). In the mixed model, the correlation structure of the dependent variable is considered by allowing the parameters to vary randomly from one individual to another around the fixed population mean (Searle et al. 1992). The analysis of experimental data with mixed-effects models requires decisions about the specification of the random-effects structure (Bates et al. 2015). This implies that in a repeated measures modelling, the best covariance structure describing the correlation among the repeated measures should first be identified. A mixed linear model for expressing the wood specific gravity of wood for a specific aspect/radius following (Laird and Ware 1982) is as follows:

$$\boldsymbol{Y_i = X_i\beta + Z_iU_i + \varepsilon_i} \qquad (1)$$

$$\boldsymbol{U_i} \sim N\,(\mathbf{0}, \boldsymbol{G})$$

$$\boldsymbol{\varepsilon_i} \sim N\,(\mathbf{0}, \boldsymbol{R})$$

where:

$\boldsymbol{Y_i}$ = vector of observations,

$\boldsymbol{\beta}$ = p × 1 vector of fixed effects with incidence matrix X; p = number of levels for fixed effects

$\boldsymbol{Z_i}$ = q × 1 dimensional vector of random effects with corresponding design matrix Z; q = number of levels for random effects

$\boldsymbol{U_i}$ = n × 1 vector of residual effects

**R** = variance-covariance matrix of errors

**G** = random effects covariance matrix

The expected value and variances are $E[\boldsymbol{Y_i}] = X\beta$, var $[\boldsymbol{U_i}] = G = \sigma_b^2 A$ and $var[e] = R = \sigma_e^2 I$ for $A$ the numerator relationship matrix and $I$ an identity matrix.

### 3.3.4 Model development

The longitudinal data (time series) of WSG were analyzed using linear models to determine the effects of the differential growth rate on radial trends. In model development, it is imperative to find a parsimonious model that specifies the covariance structure of the data and to obtain unbiased statistical tests of fixed effects. Hence, our major focus is on modelling the covariance structure following Littell et al. 2000.

Conceptually, the design is a split plot in which trees and aspects are the main plot treatments and radial positions (cambial age) the minor plot treatments. The effect of RRD and the differential growth rate on the WSG was examined using a mixed-model approach with repeated measures (Littell et al. 2006; Littell et al. 1996) as follows:

$Y_{ijk} = \mu + \alpha_i + d_{ij} + \tau_k + (\alpha\tau)_{ik} + e_{ijk}$ (2)

Where $Y_{ijk}$ is the SG measured in RRD $k$ on the $j$th tree assigned to the $i$th radius (growth category); $\mu$ is the overall mean effect; $\alpha_i$, $\tau_k$, $(\alpha\tau)_{ik}$ are parameters corresponding to the radii $i$, RRD $k$ and the interaction of $i$ radii and RRD $k$, respectively; $d_{ij}$ is the random effect of the $j$th tree within $i$th radii; $d_{ij}$ is normally distributed random variable with mean zero and $\sigma^2_d$ corresponding to tree $j$ in radii $i$, and $e_{ijk}$ is a normally distributed random variable with mean zero and variance $\sigma^2_e$, independent of $d_{ij}$, corresponding to tree $j$ in radii $i$ at RRD $k$. We used the MIXED procedure of the SAS software (SAS Institute, Cary NC) to fit the model with a restricted maximum likelihood (REML) method. Degrees of freedom were determined using the between-within method. The homogeneity and normality of the residuals were checked to ensure that assumptions were met. We determined the statistical significance ($\alpha = 0.05$) of fixed effects with the *F*-test. The variables components of random effects and their standard errors were expressed as a percentage of the total variation of all random effects. As a result of small tree replication, the results of the *Z*-test must be considered indicative only (Littell et al. 2006). Moreover, a quadratic evolution of WSG for each radius, with tree-specific intercepts and with correlated errors within radii was modeled as follows:

$$Y_{ij} = (\beta_{A0} + b_i) + \beta_{A1}t + \beta_{A2}t^2 + \varepsilon_{ij}(t) \text{ in radius 1} \quad \text{or} \qquad (3)$$

$$(\beta_{B0} + b_i) + \beta_{B1}t + \beta_{B2}t^2 + \varepsilon_{ij}(t) \text{ in radius 2}$$

Where $t$ is the RRD = 0.1, 0.2, … , 1; $\varepsilon_{ij}$ is the random error term associated with *the j*-th rrd of the *i*-th radii, and it is assumed that $\boldsymbol{\varepsilon}_i \sim N(0, \Sigma)$, where the bold character of $\boldsymbol{\varepsilon}_i$ denotes the vector of $\{\varepsilon_{ij}\}$ specific to *the i*-th radii, and $\Sigma$ is a symmetric positive definite variance-covariance matrix. Graphical techniques were used to check for normality and homoscedasticity of the residuals. We used PROC BGLIMM of the SAS software (SAS Institute, Cary NC) to generate the model parameter estimates with their associated errors and the random effects variance based on Hamiltonian Monte Carlo algorithm. The model ran for 500 burn-in iterations and $50^5$ sampling iterations, saving every 100th iterations for a total of 5000 generated posterior distributions of the model parameters. Along with the WSG estimates computed from the fitted model and applied to new data, a prediction uncertainty interval was also constructed, represented here by the range between 2.5 and 97.5% of the estimated distribution density.

## 3.4 Results and discussion

### *3.4.1 WSG Mean and Variability*

Table 1 gives the descriptive statistics of the WSG values for each radius. Figure 2 shows the WSG distribution across the radial direction for each growth category. The pooled mean WSG value was 0.666, ranging from 0.610 to 0.715 between trees with a coefficient of variation (CV) of 11.23%. WSG increased with height from 0.673 at 0.3 m to 0.704 at 5.3 m. This translates to an increase in WSG of about 11.6% from bottom to top. However, at 2.3 m height level, WSG was strikingly low (0.625). With radial variation, WSG increased from pith to bark across all height levels, averaging 0.603 to 0.687 from pith to cambium representing about 14% increase in WSG with time. Spatially, the radial dimension showed higher variation than the axial dimension in WSG. The results presented here are similar to those described in the literature (Bailleres and Durand 2000). Our mean WSG value was higher than those reported by (Sanwo 1987; Bhat 2000; Miranda et al. 2011) but similar to those reported by (Kokutse et al. 2004; Wanneng et al. 2014).

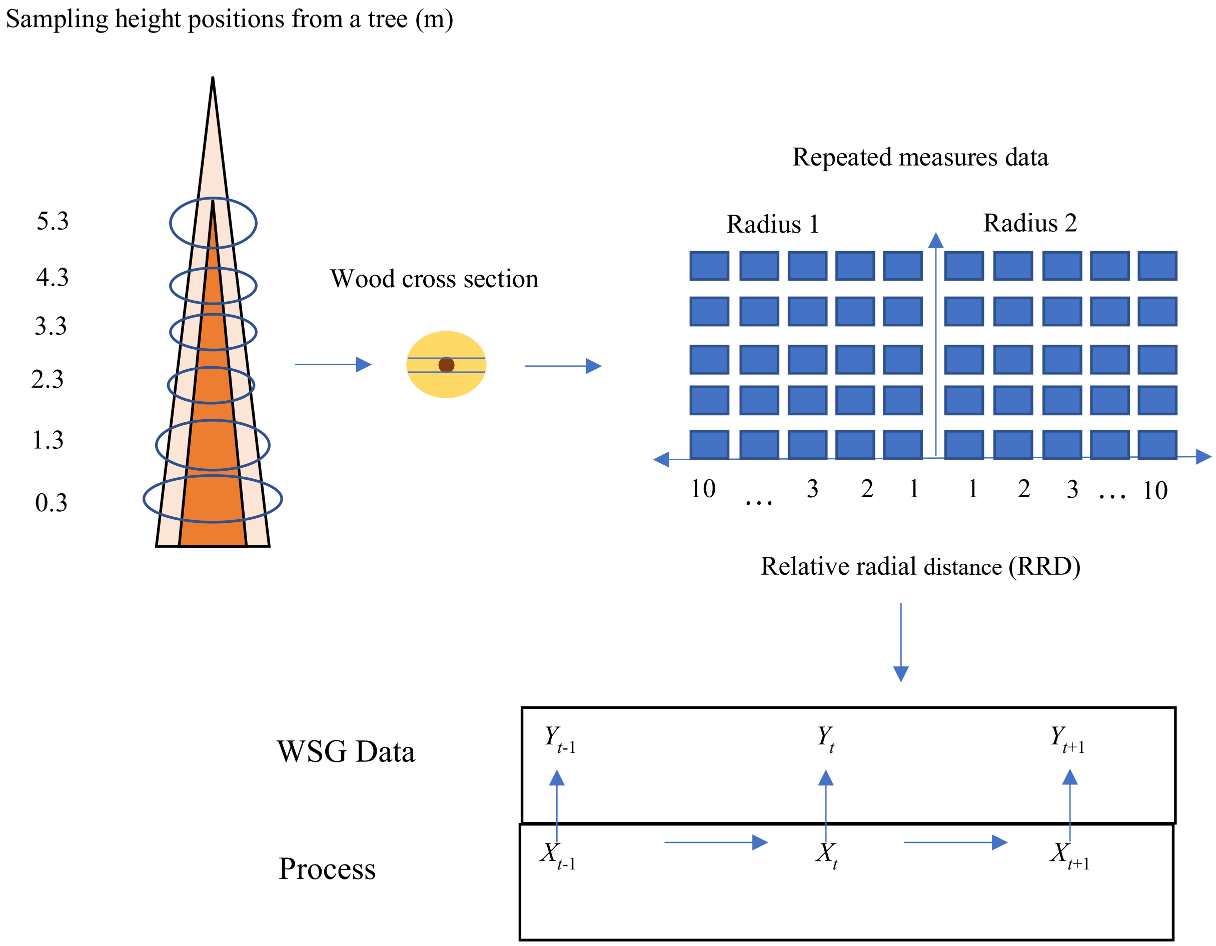


Figure 1: Schematic diagram of sample preparation and repeated measures data illustration

*RRD 1: represents wood close to the pith; RRD 10: close to the bark. The repeated measures data represent the time series character of the data and wood formation (multiple observations accumulate for each radius over time). The process represents the latent or unmeasured factors that explain the variation in WSG measurements over time and are not included in the model. The process is a hidden layer that captures the randomness introduced by wood formation dynamics. The process is captured by the temporal correlation structure.*

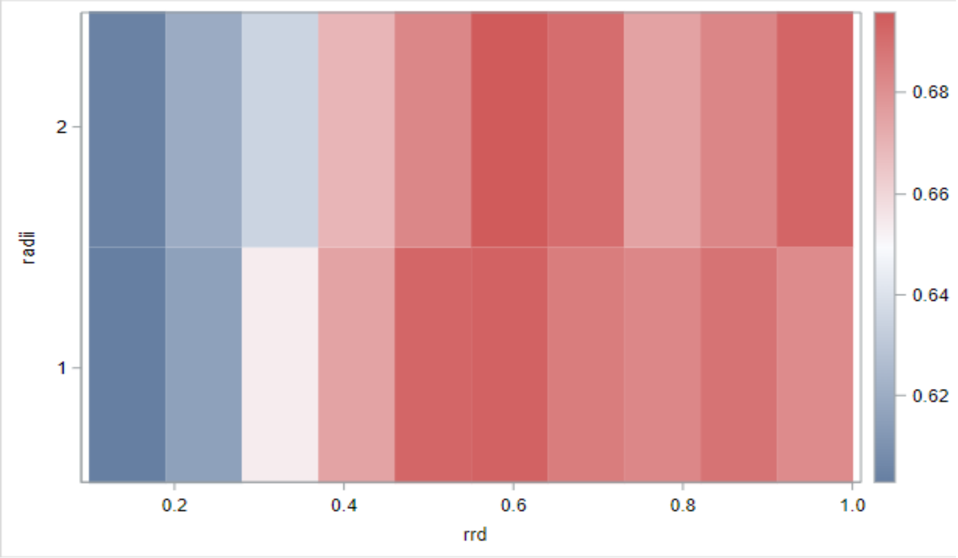


**Figure 2**: Contour plot visualizing the WSG variation with relative radial distance per radius ((rrd) × $100, \%$).

### *3.4.2 Observed correlation (Pearson) and REML covariance and correlation estimates*

Table 2 gives the Pearson correlation between WSG measured at different radial positions. REML covariance and correlation are printed above and below the diagonal, respectively, of the matrix in Table 3. The correlations between WSG at RRD 1 and later times are in the first column of the matrix. Correlation generally decreased over time. Covariance and correlations between adjacent WSG measurements on the same strip are more correlated at later time periods than at earlier times, for example, the covariance and correlation between adjacent WSGs of RRD 9 and 10 are 0.0049 and 0.8609, respectively, which are much larger than their corresponding covariance and correlation between adjacent WSG measurements of 0.0021 and 0.6932 at RRD 1 and 2. The correlations of the WSG formed in the early ages of the tree (RRDs 1 and 2) decreased rapidly with the WSG formed later. This indicates the phase where the trees are growing faster (high annual increment). The low correlation of RRD 1 with later ages suggests that early growth is probably not a good predictor of later WSG. Additionally, the low correlations of RRD 1 with later ages suggest that whatever causes these early differences, they do not persist and are not scaled up as the trees grow. The temporal positive-to-negative and negative-to-positive shifts in the correlations may indicate intrinsic differences in the underlying wood formation processes during the young and adult growth stages. The correlations increased substantially after RRD 4. The strength of correlation increases from RRD 5, implying that the WSG changes only slightly after RRD 5. From RRD 5, the tree can be said to have entered the mature phase. The stability of the correlation implies that no meaningful change in genotypic ranking is expected to occur after RRD 5. The results indicated that the most rapid change within the trajectories occurred before RRD 5. This is approximately the termination point of the juvenile core wood as the tree starts to produce high WSG. The correlation matrix can be seen as the pattern of cambial activity during tree growth. The diagonals are the estimated variances of the errors associated with each RRD measurements.

Note that they increase marginally from 0.0026 at RRD 2 to 0.0062 at RRD 6. After RRD 6, the variances stabilized (Fig. 3). This trend is consistent with most growth data, and so the covariance structure models that we consider for these data should accommodate heterogeneous variance with time, however, it is reasonable to assume homogenous variances across time. The phenomenon may be due to the initial fast growth of the tree at a younger age resulting in wider volume increments (growth rings), low correlations, and high variation. At later stages in the tree’s life, high WSG is produced, slowing down growth resulting in smaller wood increments and hence high correlation and low variation. Adult slow growth produces relatively uniform wood in its wood anatomy while young fast growth produces more complex wood because of the changing anatomical patterns from year to year. Cambial aging can be seen as a positive process because it brings order out of chaos.

| Radii | Mean | Variance | Std Dev | Std Error |
|---|---|---|---|---|
| 1 | 0.67 | 0.01 | 0.08 | 0.01 |
| 2 | 0.66 | 0.01 | 0.07 | 0.01 |

Std Dev: Standard deviation; Std Error: Standard error

*Radii 1 and 2 stand for the fast growth category and slow growth category, respectively.*

**Table 1:** Descriptive statistics of the WSG between the two radii

|  | RRD1 | RRD2 | RRD3 | RRD4 | RRD5 | RRD6 | RRD7 | RRD8 | RRD9 | RRD10 |
|---|---|---|---|---|---|---|---|---|---|---|
| RRD1 | 1 | <0.0001 | 0.2176 | 0.4085 | 0.9970 | 0.7674 | 0.4434 | 0.4738 | 0.3628 | 0.6625 |
| RRD2 | 0.6930 | 1 | <0.0001 | 0.0005 | 0.0936 | 0.3478 | 0.8260 | 0.9592 | 0.8947 | 0.8354 |
| RRD3 | 0.2106 | 0.6976 | 1 | <0.0001 | <0.0001 | 0.0042 | 0.0440 | 0.0565 | 0.0876 | 0.1819 |
| RRD4 | 0.1420 | 0.5476 | 0.8777 | 1 | <0.0001 | <0.0001 | <0.0001 | 0.0002 | 0.0004 | 0.0046 |
| RRD5 | -0.0006 | 0.2836 | 0.6927 | 0.9241 | 1 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| RRD6 | -0.0511 | 0.1611 | 0.4658 | 0.7392 | 0.8831 | 1 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| RRD7 | -0.1318 | 0.0379 | 0.3377 | 0.6199 | 0.7833 | 0.9272 | 1 | <0.0001 | <0.0001 | <0.0001 |
| RRD8 | -0.1233 | -0.0088 | 0.3207 | 0.5826 | 0.7575 | 0.8376 | 0.9218 | 1 | <0.0001 | <0.0001 |
| RRD9 | -0.1562 | -0.0229 | 0.2888 | 0.5621 | 0.7465 | 0.8138 | 0.8471 | 0.9435 | 1 | <0.0001 |
| RRD10 | -0.0753 | -0.0359 | 0.2276 | 0.4611 | 0.6416 | 0.7514 | 0.8539 | 0.8580 | 0.8551 | 1 |

RRD, relative radial distance (%), *P*-value in the upper triangular part of the matrix

**Table 2**: Observed WSG correlation between relative radial distance groups (Pearson correlation)

| RRD1 | RRD2 | RRD3 | RRD4 | RRD5 | RRD6 | RRD 7 | RRD8 | RRD9 | RRD10 |
|---|---|---|---|---|---|---|---|---|---|
| 0.0035 | 0.0021 | 0.0007 | 0.0006 | 0.0000 | -0.0002 | -0.0006 | -0.0006 | -0.0007 | -0.0004 |
| 0.6932 | 0.0026 | 0.0021 | 0.0019 | 0.0011 | 0.0006 | 0.0001 | 0.0000 | -0.0001 | -0.0002 |
| 0.2154 | 0.7151 | 0.0034 | 0.0036 | 0.0030 | 0.0022 | 0.0016 | 0.0014 | 0.0012 | 0.0011 |
| 0.1426 | 0.5500 | 0.8843 | 0.0049 | 0.0048 | 0.0041 | 0.0034 | 0.0031 | 0.0029 | 0.0025 |
| 0.0000 | 0.2871 | 0.6931 | 0.9243 | 0.0054 | 0.0051 | 0.0045 | 0.0042 | 0.0040 | 0.0037 |
| -0.0512 | 0.1607 | 0.4749 | 0.7403 | 0.8860 | 0.0062 | 0.0057 | 0.0050 | 0.0047 | 0.0046 |
| -0.1322 | 0.0368 | 0.3477 | 0.6218 | 0.7872 | 0.9273 | 0.0061 | 0.0055 | 0.0048 | 0.0052 |
| -0.1229 | -0.0067 | 0.3169 | 0.5818 | 0.7568 | 0.8396 | 0.9250 | 0.0058 | 0.0053 | 0.0051 |
| -0.1560 | -0.0213 | 0.2865 | 0.5615 | 0.7462 | 0.8151 | 0.8493 | 0.9435 | 0.0053 | 0.0049 |
| -0.0763 | -0.0390 | 0.2439 | 0.4655 | 0.6494 | 0.7524 | 0.8544 | 0.8653 | 0.8609 | 0.0060 |

Variances on the diagonal, covariances above diagonal, correlation below diagonal.

**Table 3**: REML covariance and correlation estimates for unstructured covariance structure for WSG repeated measures data**.** This can be seen as the evolutionary variance-covariance of the lateral meristem.

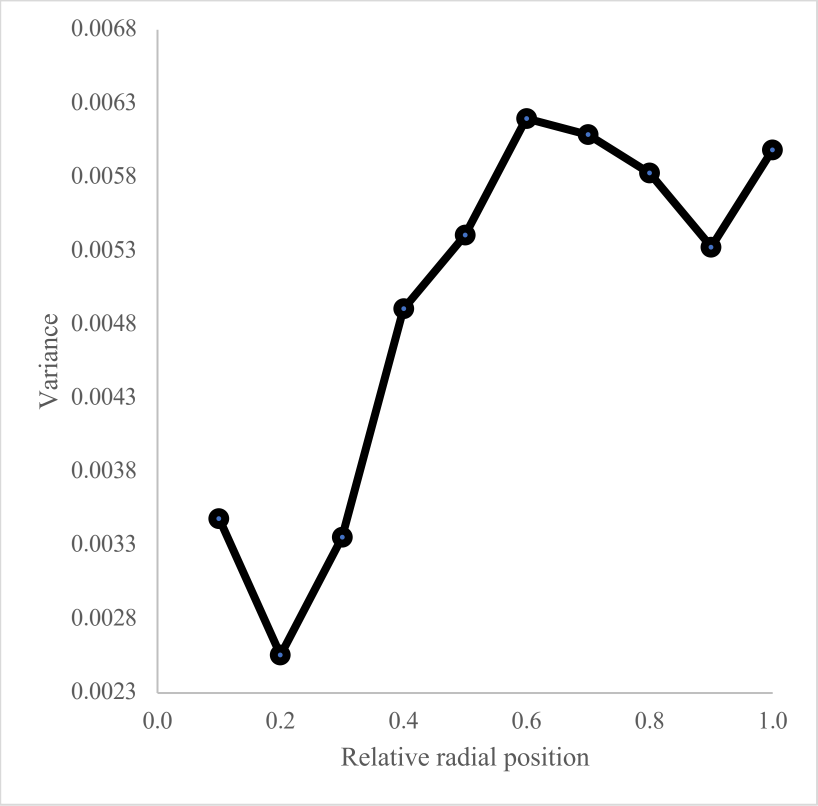


**Figure 3**: Variance function in the WSG data

Relative radial position (× 100, %).

### *3.4.3 Estimated concentration matrix for the unstructured covariance model*

As shown in Table 4, the inverse of the covariance matrix for the unstructured model yielded larger (absolute) values along the first off-diagonal band. This gives us an indication of a first-order structure, justifying the use of the first-order autoregressive correlation structure. First-order structures model conditional independence, since any pair of measurements made on the same strip that are more than a time interval apart are conditionally independent (Machiavelli and Moser 1997). The covariance and correlation matrices displayed as a function of lag for simple, compound symmetric, autoregressive (1), autoregressive (1) plus random tree effect, Toeplitz and antedependence structures are summarized in Table 5. Figure 4 shows the correlation function of lag for unstructured, autoregressive (1), compound symmetric and autoregressive (1) plus random effect correlation structures. We expect that traits separated by developmental changes will be uncorrelated; however, for dissociation to occur, the correlations need not be zero (Aguirre et al. 2014), justifying the importance of the first-order autoregressive structure. The correlation structure can be viewed as the physiological correlations in wood formation.

| RRD1 | RRD 2 | RRD 3 | RRD 4 | RRD5 | RRD 6 | RRD 7 | RRD 8 | RRD 9 | RRD10 |
|---|---|---|---|---|---|---|---|---|---|
| 1239.96 | -1750.4 | 1257.01 | -123.17 | -402.91 | -403.93 | 1196.32 | -1067 | 1055.17 | -568.91 |
| -1750.4 | 3741.13 | -2076.7 | -1376 | 2189.15 | -72.878 | -1218.5 | 1381.62 | -1388.8 | 655.62 |
| 1257.01 | -2076.7 | 4412.7 | -3961.6 | 1247.63 | -848.41 | 2213.52 | -1769.9 | 1812.71 | -1104.6 |
| -123.17 | -1376 | -3961.6 | 9706.47 | -7202.3 | 2075.34 | -2347.8 | 1279.59 | -973.09 | 1166.77 |
| -402.91 | 2189.15 | 1247.63 | -7202.3 | 7522.56 | -2713.2 | 1731.67 | -770.09 | 34.3874 | -587.48 |
| -403.93 | -72.878 | -848.41 | 2075.34 | -2713.2 | 3479.4 | -3545 | 2063.37 | -1591.3 | 850.39 |
| 1196.32 | -1218.5 | 2213.52 | -2347.8 | 1731.67 | -3545 | 5951.02 | -4255.9 | 3088.98 | -1733.1 |
| -1067 | 1381.62 | -1769.9 | 1279.59 | -770.09 | 2063.37 | -4255.9 | 5073.19 | -3644.1 | 947.22 |
| 1055.17 | -1388.8 | 1812.71 | -973.09 | 34.3874 | -1591.3 | 3088.98 | -3644.1 | 3781.56 | -1318.9 |
| -568.91 | 655.62 | -1104.6 | 1166.77 | -587.48 | 850.39 | -1733.1 | 947.22 | -1318.9 | 1327.85 |

**Table 4:** Estimated concentration matrix or inverse of the covariance matrix for the unstructured covariance model. It tends to larger (absolute) values along the first off-diagonal band.

| RRD 1 | RRD 2 | RRD 3 | RRD 4 | RRD 5 | RRD 6 | RRD 7 | RRD 8 | RRD 9 | RRD 10 |
|---|---|---|---|---|---|---|---|---|---|
| *1. Simple (Variance components)* | | | | | | | | | |
| 5.913 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *2. Compound Symmetric* | | | | | | | | | |
| 4.913 | 2.526 | 2.526 | 2.526 | 2.526 | 2.526 | 2.526 | 2.526 | 2.526 | 2.526 |
| 1.000 | 0.514 | 0.514 | 0.514 | 0.514 | 0.514 | 0.514 | 0.514 | 0.514 | 0.514 |
| *3. Autoregressive (1)* | | | | | | | | | |
| 4.843 | 4.239 | 3.711 | 3.249 | 2.844 | 2.49 | 2.18 | 1.909 | 1.671 | 1.463 |
| 1.000 | 0.876 | 0.766 | 0.671 | 0.580 | 0.510 | 0.450 | 0.394 | 0.345 | 0.302 |
| *4. Autoregressive (1) with random tree effect* | | | | | | | | | |
| 4.124 | 3.520 | 3.004 | 2.564 | 2.188 | 1.867 | 1.594 | 1.360 | 1.116 | 0.099 |
| 1.000 | 0.853 | 0.728 | 0.622 | 0.530 | 0.453 | 0.386 | 0.330 | 0.281 | 0.240 |
| *5.Toeplitz (banded)* | | | | | | | | | |
| 4.965 | 4.357 | 3.476 | 2.737 | 2.078 | 1.392 | 0.647 | 0.078 | -0.420 | -0.610 |
| 1.000 | 0.878 | 0.699 | 0.551 | 0.419 | 0.280 | 0.130 | 0.016 | -0.085 | -0.012 |
| *6. Antedependence (1)* | | | | | | | | | |
| 3.485 | 2.557 | 3.356 | 4.907 | 5.405 | 6.198 | 6.088 | 5.828 | 5.325 | 5.985 |
| 1.000 | 0.693 | 0.715 | 0.884 | 0.924 | 0.886 | 0.927 | 0.925 | 0.944 | 0.861 |

Variances ( $\times 10^{-3}$) and covariance in the top line; correlations in bottom line.

**Table 5**: REML covariance and correlation estimates for unstructured covariance structure for WSG repeated measures data

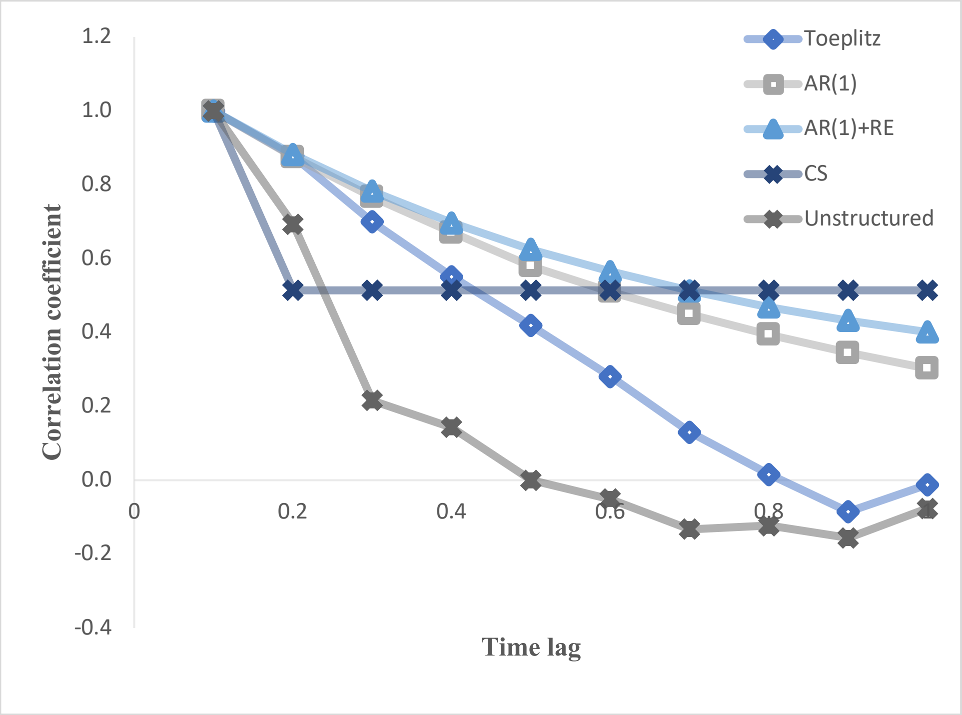


**Figure 4:** Correlograms of the six correlation structures

**Time lag** (× 100, %).

### *3.4.4 Comparison of fits*

To evaluate the impact of accounting for serial correlation (within-tree dependence), models with and without incorporating a function to model the error structure were compared. The results of fitting the seven covariance structures to the data are shown in Table 6. The likelihood ratio statistic ($-2\text{In}\lambda_N$) is the difference between the $-2L_{ML}$ of the current and reference model (simple). The *P* values indicate that there is significant evidence to conclude that the six other covariance structures performed better than the simple ones. Thus, we may conclude that the correlation structure in the data is needed. Heterogeneous models of the compound symmetric and first-order autoregressive models were tested. They did not perform better than the homogenous models (data not shown). The heterogeneous Toeplitz model did not converge in the SAS system.

With the specific goal of a parse modeling of the covariance structure, we use the BIC criterion. AIC and BIC values for the six covariance structures are shown in Table 7. 'Unstructured', it has the largest AIC, but Toeplitz ranks second in both AIC and BIC. AR(1)+RE 'autoregressive with random tree effect' is first in BIC and third in AIC. The discrepancy between AIC and BIC for the UN structure reflects the penalty for the large number of parameters in the UN covariance matrix (55). Overparameterization can lead to uninterpretable and complex models. Based on examining of the correlation estimates in Tables 3 and 7 and the relative values of BIC, we conclude that AR(1)+RE 'autoregressive with random tree effect', is the best choice of covariance structure describing the radial patten of WSG variation. The random tree effect which takes care of spatial variation, significantly improved the model's performance. The scaled residual and the Q-Q plot of the residuals appeared normal and well behaved (Fig. 5). The mixed effects model was able to capture the variation at the different levels considered, that is between-tree variation, within-tree (residual) variation and autocorrelation function, which justified its use as shown in Table 8. The estimated first-order autoregressive process

AR(1) was high with a value of 0.8475. The total variance was 0.005127, which was corrected by autocorrelation of the residuals. Therefore, it is possible to express the variability of each level as a proportion of the total variance: the spatial variation (growth category level variation) was not significant and accounted for about 23% of the total radial variation of the WSG showing that the effects of differential radial growth rate on the WSG were low. This spatial variation is the variation caused by the differential cambium production on the two opposite sides of the same tree. Temporal variation (pith-to-bark) was significant explaining about 77% of the total variation in radial WSG. Overall, there is enough variability at both levels to justify the application of mixed effects models.

The first-order autocorrelation parameter measures the influence of WSG in the previous year on WSG for the current growing season. This parameter was estimated at 0.8475, so observations of WSG from the same strip but one RRD apart are highly correlated by 0.882, observations 2 RRD apart by 0.782 and observations 3 RRD apart by 0.697. The significant first-order autocorrelation parameter implies that the WSG of the wood formed in the previous year (*t*-1) influences the growth in the current year (*t*) and changes over time, which seems to be characteristic of deciduous trees (Kozlowski and Pallardy 1997). This means that if a given year's growing conditions favored thickening and hardening of the cell wall, it is very like that the WSG would be similar in the next growing year, most likely due to stored photosynthates and carbohydrates the cambial meristems use for the next year (Savva et al. 2010). Furthermore, the significant autocorrelation coefficient implies that errors within-tree cannot be assumed to be independent and that precautions must be taken to remove autocorrelations before hypothesis testing to ensure that normality assumptions are met and that statistical tests are unbiased.

|  | Par | $-2L_{ML}$ | $-2\text{In}\lambda_N$ | df | *P* |
|---|---|---|---|---|---|
| Simple | 1 | -912.6 |  |  |  |
| Compound Symmetry | 2 | -1084.3 | 171.66 | 1 | <0.0001 |
| Autoregressive (1) | 2 | -1389 | 476.39 | 1 | <0.0001 |
| Autoregressive (1) with random tree effect | 3 | -1394.3 | 481.70 | 2 | <0.0001 |
| Toeplitz (banded) | 10 | -1428.7 | 516.04 | 9 | <0.0001 |
| Antedependence (1) | 19 | -1424.1 | 511.51 | 18 | <0.0001 |
| Unstructured | 55 | -1538.3 | 625.69 | 54 | <0.0001 |

Par, Number of parameters; $-2L_{ML}$, minus twice the maximum log-likelihood value of ML; $-2\text{In}\lambda_N$, likelihood ratio statistic testing vs model Simple; df, degree of freedom; *P*, *P* value corresponding to the likelihood ratio test

**Table 6**: Summary results for fitting different covariance structures to WSG data

| Structure name | AIC | BIC | Number of Parameters |
|---|---|---|---|
| 1. Simple | -782.7 | -781.7 | 1 |
| 2. Compound symmetric | -942.8 | -939.6 | 2 |
| 3. Autoregressive (1) | -1230.6 | -1227.4 | 2 |
| 4. Autoregressive (1) with random effect for trees | -1235.1 | **-1237.8** | 3 |
| 5.Toeplitz (banded) | -1252.1 | -1236.2 | 10 |
| 6. Antedependence (1) | -1229.8 | -1199.7 | 19 |
| 7. Unstructured | **-1265.6** | -1178.5 | 55 |

**Table 7:** Akaike's information criterion (AIC) and Schwarz's Bayesian information criterion (BIC) for seven covariance structures. The AIC criterion (bold) gives the best fit for the unstructured model, while the BIC criterion (bold) gives the best fit for the autoregressive (1) with random effect for trees.

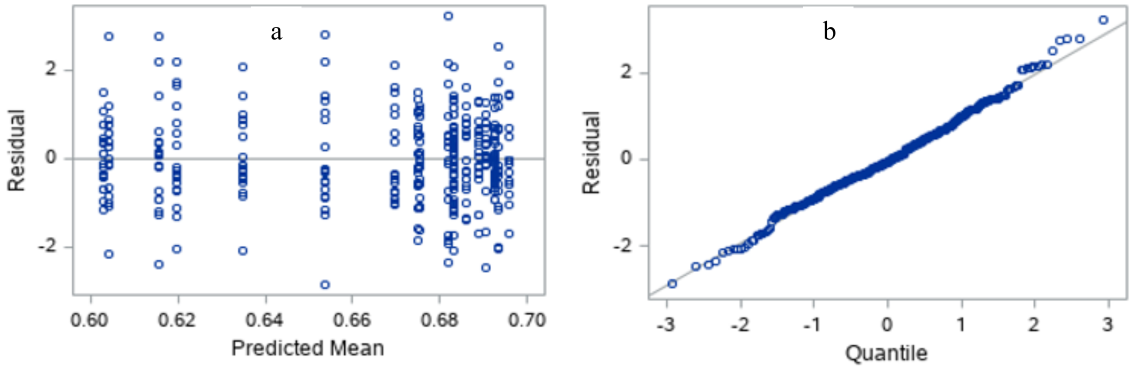


**Figure 4:** Profiles of the scaled residuals (a) and Q-Q plot of the residuals (b) from the AR(1)+RE correlation structure. Residuals examined for adequacy of the normal distribution model.

| Parameter | Subject | Estimate | Std Error | *Z* Value | Pr Z |
|---|---|---|---|---|---|
| Tree | | 0.001160 | 0.001351 | 0.86 | 0.1953 |
| AR(1) | Tree(Radii*Height) | 0.8475 | 0.02570 | 32.98 | <0.0001 |
| Residual | | 0.003967 | 0.000636 | 6.24 | <0.0001 |

**Table 8**: Parameter estimates in the covariance and correlation matrices for the AR(1) + RE structure. Tree gives the between tree variance. Residual gives the within tree variance and AR(1) gives the first-order autocorrelation parameter.

### *3.4.5 Effects of differential growth rate on WSG*

Type 3 fixed effects were used to assess the statistical significance of fixed effects as shown in Table 9. The main effect of growth category (radii), which reflects size effect, was not statistically significant ($p > 0.05$). The lack of statistical significance between the WSG values along the long and short radii indicates that within a tree, factors other than lateral growth rate can drive the shift from low WSG (core wood) to high WSG (outer wood). The radii-by-rrd interaction was not significant ($p > 0.05$). This indicates that there is a similar response in the WSG in both direction and magnitude on opposite sides of the same tree. At an assumed age, the WSG values show no difference from long radius to short radius. The rrd main effect representing presumed age, is highly statistically significant ($p < 0.0001$). This illustrates a high temporal variation of WSG. The shift from low WSG to high WSG, which is analogous to xylem maturity, is likely driven by cambium age rather than distance (size) in the selected teak trees. WSG increases with tree age until it reaches an asymptote. This suggests that the changes follow a fixed trajectory on both the long and short radius. The long-radius WSG mean values were slightly larger than the short-radius mean values, although they were not statistically significant as shown in Table 10. WSG comparisons of presumed age groups along the two radii also showed no significant differences. The WSG formed at the same time are similar regardless of the side of the tree on which cambium is produced slowly or rapidly. This finding is consistent with the characterization of WSG changes per unit time rather than per unit size, as reported by Williamson and Wiemann (2011).

| Effect | Num DF | Den DF | *F* Value | Pr > *F* |
|---|---|---|---|---|
| Radii | 1 | 338 | 0.02 | 0.884 |
| RRD | 9 | 338 | 9.12 | <0.0001 |
| Radii*RRD | 9 | 338 | 1.03 | 0.4183 |

**Table 9**: Results of the fixed hypothesis test with AR(1)+RE structure (ANOVA *F*-tests) Radii is a purely spatial factor (no significance), RRD is a purely temporal factor (significant) and Radii*RRD is the space-time factor (no significance).

| Parameter | Estimate | Std Error | DF | *t* Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Radii 1-2 avg. over RRD 1-10 | 0.002417 | 0.01656 | 338 | 0.15 | 0.8840 |
| Radii 1-2 RRD 1 | -0.00122 | 0.02099 | 338 | -0.06 | 0.9536 |
| Radii 1-2 RRD 2 | -0.00400 | 0.02099 | 338 | -0.19 | 0.8490 |
| Radii 1-2 RRD 3 | 0.01911 | 0.02099 | 338 | 0.91 | 0.3633 |
| Radii 1-2 RRD 4 | 0.005222 | 0.02099 | 338 | 0.25 | 0.8037 |
| Radii 1-2 RRD 5 | 0.009333 | 0.02099 | 338 | 0.44 | 0.6569 |
| Radii 1-2 RRD 6 | -0.00217 | 0.02099 | 338 | -0.10 | 0.9179 |
| Radii 1-2 RRD 7 | -0.00444 | 0.02099 | 338 | -0.21 | 0.8325 |
| Radii 1-2 RRD 8 | 0.007722 | 0.02099 | 338 | 0.37 | 0.7132 |
| Radii 1-2 RRD 9 | 0.005611 | 0.02099 | 338 | 0.27 | 0.7894 |
| Radii 1-2 RRD 10 | -0.01100 | 0.02099 | 338 | -0.52 | 0.6007 |

DF: degree of freedom

**Table 10:** Between-subject comparison with AR(1)+RE structure. Differences in mean WSG between long radius (growing rapidly) and short radius (growing slowly) are almost same over time (RRD).

### *3.4.6 Modelling polynomial change over time*

Data from each aspect were combined to represent the specific growth rate, and polynomial modeling of the fixed effects of radius and presumed age was applied using the AR(1)+RE covariance structure. Correlation between errors from consecutive assumed ages on the same core was included in the model. The third-degree polynomials showed no significant evidence of third-degree age terms ($p = 0.827$, type 1 tests of fixed effects tests). The quadratic term was significant, implying that there is a quadratic age effect on the radial WSG in the selected teak. The results are shown are Table 11. The scaled residuals and the Q-Q plot of the residuals of the quadratic model is shown in Fig. 6. They appeared normal and well behaved.

The fitted polynomial equations are as follows:

R1: $\text{WSG} = 0.5691 + 0.3652\ \text{RRD} - 0.3112\ \text{RRD}^2$

R2: $\text{WSG} = 0.5831 + 0.3114\ \text{RRD} - 0.3051\ \text{RRD}^2$

Zobel and Sprague (1998) defined the core wood zone as the area of rapid property changes near the pith and the outer wood as more uniform towards the bark. The pith-to-bark profiles for each growth category yielded different but identical curves, particularly different starting points (intercepts) and slopes in the outer wood zone. The difference in the parameter $\beta_0$, which is the starting point (first-formed WSG) of the mean pith-to-bark profile was 0.014, corresponding to an approximately 2.5% increase in WSG on the short radius. The inflection point (shift from low to high WSG) was estimated from the first derivative of the quadratic polynomial. The maximum estimated of the quadratic function of the core wood part $x_0 = -\beta_1 / (2\beta_2)$ in WSG for R1 were 0.6 and 0.5 for R2 since this is the presumed age when WSG values tend to reach an asymptote (WSG levels at this point). These correspond to approximately eleven years and nine years in R1 and R2, respectively. The longer radius may have had a higher rate of cell production and therefore required more time to complete the wood formation process. The differential growth rate can affect the age of the transition from core wood to outer wood, with rapid growth increasing the proportion of core wood. Our working hypothesis seems to have been confirmed. The slope gradient on the slow-growing side is steeper and flatter on the fast-growing side. The shorter radius and long radius follow a fixed trajectory. The low WSG is larger in the fast-growing core, indicating that fast growth appears to be associated with a longer period of core wood content. This case suggests that maturation might be controlled by cambium age. This suggests that xylem maturation (production of higher WSG) begins after reaching a certain cambium age. The higher growth rate can result in cells having less time to expand as the cambium produces new cells faster, resulting in the long radius having more core wood (less WSG) than the short radius (Lachenbruch et al. 2011). It is evident that slowing young growth can reduce the low WSG (core wood) area. During the young phase, the low WSG averaged 0.619 with a CV of 3.7% on the long core and 0.619 with a CV of 2.6% on the short core. After maturity, the overall mean was 0.668 (CV: 1.2%) in the long core and 0.657 (CV: 0.99%) in the short core, a difference of 0.011. The overall mean WSG was 0.644 in the long core with a CV of 4.7% and 0.642 with a CV of 3.5%. The slow growing side has more consistent wood with a small WSG difference between young stage and adult stage WSG. The WSG increases by about 13% over the lifetime of the tree, which translates into an increase in modulus of rupture by about 245 kg/cm$^2$ (Mitchell 1963; Zobel and Jett 1995). This pattern could be driven by the greater need for hydraulic function before maturity (Domec and Gartner 2002; Schneider et al. 2008) and for mechanical strength after maturity to achieve stiffness (Schniewind 1962; Wiemann and Williamson 1989; Mosbrugger 1990; Fournier et al. 1991). During the early growing seasons, the total stem cross-section is small, and a large proportion of void volume is required, producing large-diameter and thin-walled fibers (Larson 1960,1962). As a stem increases in size, the percentage void volume required is reduced and WSG can increase to achieve maximum mechanical efficiency. Larson (1960) observed that as the cambium ages, the cell diameter decreases and the cell wall thickness increases. The same amount of material spread over a smaller area increases the WSG (O. Bouriaud, personal communication, September 16, 2021). From a physiological point of view, since the tree is taller, the water tension is much higher and the cell walls must therefore be thicker to withstand the pressure (O. Bouriaud, personal communication, September 16, 2021). Such effects may explain the steady increase in WSG observed in the outer forest region. In both cores, WSG in the outer wood differed significantly from the core wood. On the R1, $t(8) = -4.22$, $p = 0.0029$; and R2 $t(4.406) = -4.09$, $p = 0.0123$.

From Table 12, the WSG formed during youth differed significantly between the fast-growing side and the slow-growing side. WSG was significantly higher on the slow-growing side during the young phase of tree growth. After maturity, the WSG differences are the same in the two cores. This phenomenon is supported by the correlation structure. WSG exhibits compensatory the growth as growth in WSG of the first-formed wood decays to the WSG of later formed wood (Riska et al. 1984) and can be represented by this equation $\mathrm{WSG}(t) = 0.9452e^{-0.099t}$. The decreasing temporal correlation structure over time can be attributed to the decreasing crown effect on later formed wood, differential gene expression, radial morphogen (i.e., auxin) gradient, and changing microenvironmental conditions under which the trees evolved. The temporal correlation structure provides statistical evidence that young cambium differs from adult cambium in terms of physiology and epigenetics. We expect that there would be differences in early radial growth rate and WSG, but both sides of the same tree can achieve nearly similar WSG after maturity. This leads to a reduction of the variation in WSG in the later growth stages. These changes have been associated with changes in the physiological system and gene pattern and activity (Olesen 1978; Namkoong et al. 1988). Genes do not function simultaneously and vary with age i.e., a qualitative change (Olesen 1978) since genes on both sides of the same tree may not function optimally at the same time. By changes in gene activity is meant that active genes can be more or less active (gradual change with age), i.e., a quantitative change (Olesen 1978) since there is a different activity of genes at different ages. Maturation is related to genetic changes (Olesen 1978).

| *Fixed effects* | | | Estimate | S.E. | *T* |
|---|---|---|---|---|---|
| Radii | 1 | $\beta_{A0}$ | 0.5691 | 0.03113 | 18.28** |
| | 2 | $\beta_{B0}$ | 0.5831 | 0.03113 | 18.73** |
| Radii*RRD | 1 | $\beta_{A1}$ | 0.3652 | 0.00880 | 2.30* |
| | 2 | $\beta_{B1}$ | 0.3114 | 0.00880 | 1.97 |
| Radii*RRD$^2$ | 1 | $\beta_{A2}$ | -0.3112 | 0.00103 | -0.93 |
| | 2 | $\beta_{B2}$ | -0.3051 | 0.00103 | -0.92 |
| *Random effects* | | | | | |
| Level 2 “Tree” | | | Variance | S.E. | *Z* |
| | | bi | 0.001049 | 0.001615 | 0.87 |
| Level 1 “RRD” | | | | | |
| | AR(1) | ρ | 0.7481 | 0.03736 | 20.02** |
| | Residual | $e_{ij}$ | 0.003884 | 0.000577 | 6.73** |

SE = standard error of estimated parameters, $t$ = $t$-test *value,* $z$ = $z$-test-value, AR(1) = first-order autoregressive process. * $p < 0.05$, ** $p < 0.01$.

**Table 11**: Final nonlinear mixed-effects model. $\beta_{A0}$ - $\beta_{B2}$ correspond to the fixed effect regression model (intercept, linear, quadratic trend), the bi parameter is the corresponding random effects. AR(1) is the autocorrelation coefficient.

| Parameter | Estimate | Std Error | DF | *t* Value | Pr > \|t\| |
|---|---|---|---|---|---|
| Radii 1-2 RRD 1 | -0.01928 | 0.007871 | 348 | -2.45 | 0.0148 |
| Radii 1-2 RRD 2 | -0.01650 | 0.005214 | 348 | -3.16 | 0.0017 |
| Radii 1-2 RRD 3 | -0.01194 | 0.002324 | 348 | -5.14 | <0.0001 |
| Radii 1-2 RRD 4 | -0.00567 | 0.006265 | 348 | -0.90 | 0.3661 |
| Radii 1-2 RRD 5 | 0.002247 | 0.01327 | 348 | 0.17 | 0.8656 |
| Radii 1-2 RRD 6 | 0.01175 | 0.0215 | 348 | 0.55 | 0.5851 |
| Radii 1-2 RRD 7 | 0.02277 | 0.03065 | 348 | 0.74 | 0.4581 |
| Radii 1-2 RRD 8 | 0.03524 | 0.04049 | 348 | 0.87 | 0.3847 |
| Radii 1-2 RRD 9 | 0.04911 | 0.05083 | 348 | 0.97 | 0.3347 |
| Radii 1-2 RRD 10 | 0.0643 | 0.06148 | 348 | 1.05 | 0.2963 |

DF: degree of freedom

**Table 12**: Between-subject comparison for AR(1)+RE structure and polynomial model for RRD. The temporal heterogeneity of the mean WSG appears to be similar for both growth categories only after RRD 4. Both sides of the same tree may show a similar onset of intra-annual wood formation. However, exogenous and endogenous factors are likely to be reduced in the short radius at the beginning of wood formation. On the long radius, there may be a higher rate of cell production which may have reduced the bulk density.

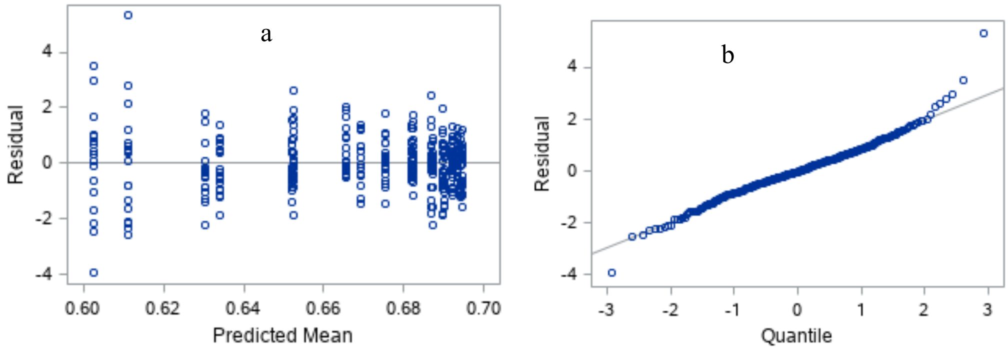


**Figure 5**: Profiles of the scaled residuals (a) and Q-Q plot of the residuals (b) of the quadratic model with AR(1)+RE correlation structure. Residuals examined for adequacy of the normal distribution model.

### *3.4.7 Application to an independent dataset*

The best model was introduced into the Bayesian framework, fitted using the Markov chain Monte Carlo (MCMC) approach, with the exact model structure on the same data. To prevent the posterior distribution from being influenced by the means chosen for the model's parameter values, we used weakly non-informative priors. The parameters estimated by the Bayesian framework are presented in Table 13. A focus was on examining the pattern of WSG variation between the two radii. For Radii 1 and 2, the predicted slopes were 0.00483 and 0.00543, respectively. The difference in slope was -0.00060 (95% Credible interval: -0.00385 to 0.00269). This suggests that the radial WSG variation may not be affected by the differential growth rate since the 95% credible interval contains zero. The steeper slope in the short radius may indicate that radial increases in WSG are age dependent, consistent with our working hypothesis. A significant difference between trees was found by the Bayesian model. It has been reported that random tree-level variation is a major source of variation in a population (Bouriaud et al. 2004; Zhang et al. 1994; Guilley et al. 2004; Jakola et al. 2005). The autoregressive correlation parameter was high and significant. Even after accounting for time trend, the typical assumption of a random structure over time is wrong since wood data are typically collected in time series and the wood data contain significant temporal autocorrelation. The independence assumption is satisfied by the residuals of a suitable AR(1) model, which can be put to the test. We should recognize that tree growth is a significant repository of the interactions between various environmental, molecular, cellular, developmental, and physiological elements. Only models that take growth process variability into account may explain these random fluctuations.

| Parameter | N | Mean | Standard Deviation | 95% HPD Interval | |
|---|---|---|---|---|---|
| Radii 1 | 5000 | 0.6061 | 0.0405 | 0.5300 | 0.6842 |
| Radii 2 | 5000 | 0.6010 | 0.0414 | 0.5235 | 0.6804 |
| RRD | 5000 | 0.00543 | 0.0012 | 0.00312 | 0.00788 |
| RRD*Radii 1 | 5000 | -0.00060 | 0.00167 | -0.00385 | 0.00269 |
| Residual Var | 5000 | 0.00468 | 0.000834 | 0.00319 | 0.0063 |
| Residual AR(1) | 5000 | 0.8521 | 0.0255 | 0.8022 | 0.9006 |
| Random Var | 5000 | 0.00426 | 0.0127 | 0.0001 | 0.0141 |

N: independent MCMC samples; HPD: highest posterior density which is defined by the 2.5th and 97.5th percentiles. Residual Var gives the within tree variance statistic. Residual AR(1) gives the first-order autocorrelation parameter. Random Var gives the between tree variance.

**Table 13**: Posterior summary and intervals

### *3.4.8 Maturation mechanism in teak*

Previous studies have identified the transition from core wood to outer wood after 8-10 years (Kedharnath et al. 1963; Sanwo 1987; Kokutse et al. 2010; Nocetti et al. 2011) which is consistent with our results. However, Bhat et al. (2001) reported that teak in India starts maturing at around 15-25 years, and Hidayati et al. (2014) reported that teak from Indonesia starts maturing at 12 years. The differences in the maturation time of teak planted worldwide can be attributed to proximity to the equator and several other factors including genetic control, breed selection, soil conditions and traits considered (Kojima et al. 2009). In tropical latitudes, changes in day length are large enough to affect plant development around the equinox (Borchert et al. 2005). The transition from core wood to outer wood in teak is characterized by (1) an increase in fiber length of about 50% (Kedharnath et al. 1963; Bhat et al. 2001; Hidayati et al. 2014), (2) a decrease in microfibril angle of about 100% from the pith to the bark (Bhat et al. 2001) and (3) from large annual rings to narrow rings (Bhat et al. 2001; Rugmini and Jayaraman 2009; Kokutse et al. 2010; Miranda et al. 2011)**.** These disclosures support the relative stability in the correlation structure of WSG later in tree life (referred to herein as xylem maturity). Aging of the cambium plays an important role in the radial variation of WSG. This leads to systematic variations in the secondary tissues that affect both the anatomical and physical properties of wood. At a young age, short fibers are produced, these cells have a large diameter and a thin wall (Larson 1960,1962), which explains the initially wide rings, high MFA, low WSG. As the cambium ages, the fibers increase in size, cell diameter decreases, and cell wall thickness increases (Larson 1960). This leads to a reduction in ring width and a lower MFA, which also explains the steady increase in WSG observed in the outer wood portion.

Radial increases in WSG have been studied in several tropical pioneering species. It has been linked to the mechanical reinforcement of the trunk that would result from stiffer/stronger wood at the periphery (Wiemann and Williamson 1989a,b;1988). Tropical pioneers exhibit rapid growth in height and diameter by producing a low WSG as juveniles but require greater stability later in tree development. Given this phenomenon, as de Castro et al. (1993) noted, one would expect WSG to be spatially rather than temporally controlled. However, ecologically pioneering species are shade intolerant and therefore require electromagnetic energy from light to grow in space, making them more sensitive to time; thus, the development of pioneer species is controlled by time (Kärenlampi and Riekkinen 2004). The age effect indicates an intrinsic control of wood development limiting the younger and often shorter cambium cells in the size of cells they can produce (Rungwattana and Hietz 2018).

### 3.5 Conclusion

The influence of the different growth rate on the WSG is studied using a linear mixed modeling technique. Overall, the linear mixed model method fits our data better. It has been found that models that account for serial correlation in the data tend to perform better than models with independent and identically distributed (simple) structure. This should serve as a warning to wood technologists who ignore serial correlations as unworthy. The serial correlation provides important background knowledge to understand a complex system like the tree and its growth process. We have also made suggestions for choosing an appropriate covariance structure. The models presented here could serve as a prototype for wood technologists who wish to clarify the response of trees to different growth rates over time, even in the absence of annual rings, particularly in tropical timber species, and to understand the physiological differences in the tree growth process. It only requires that the data be collected in a repeated measures design, so that the statistical analysis can account for the time series nature of the data, taking into account the variance function and autocorrelation between repeated measures. Analysis of wood properties in time series format can help us to understand the underlying wood formation process and the pattern of variation of wood properties over time. Despite the data limitations in the current analysis, the model we developed provides a novel way to study WSG variation in response to random fluctuations during tree growth. The data collection process in future work could be assisted by the Bayesian model that we give here. Using Bayesian model and posterior summary we can test our predictions on future observations.

# CHAPTER 4

# SPACE-TIME ANALYSIS OF THE LONGITUDINAL VARIATION IN TEAK WOOD SPECIFIC GRAVITY AND ITS EFFECT ON TREE GROWTH AND DEVELOPMENT

## 4.1 Abstract

The space-time structure of a teak wood specific gravity (WSG) dataset was analyzed using a mixed-effects model. Spatial correlation increased in space, a phenomenon attributable to the maturation of apical meristems, while the temporal correlation of vascular meristems decreased over time. The decay of autocorrelation over time can be attributed to a diminishing crown effect on the later wood that forms further from the pith, morphogen gradient, and probably changing microenvironmental conditions. The Kronecker product was used to collect spatiotemporal data on the intricate dynamic process of the evolution of the apical and lateral meristems. By jointly modeling the mean and variance structure, the results of the analysis show that height and relative radial distance (RRD) (i.e., the flow of time with wood formation) were statistically significant factors, with their interaction showing no significance. Our results confirm the usefulness of using the space-time approach to elucidate the interaction between the apical and lateral meristems, two major inherent biological systems that control tree growth and wood formation dynamics. To understand the origins of patterns that vary both temporally and spatially in the tree, we should describe the variation in WSG within the tree due to increasing height (space) and diameter (age) as a matrix; then we can model the correlation function jointly.

**Keywords** Teak, Space-time dynamics, Stochastic processes, Tree growth, Mixed-effects model, Kronecker product, Maturation, Juvenility, Wood specific gravity.

## 4.1 Introduction

Teak (*Tectona grandis* L.f) is a highly valued tropical timber species that is widely grown in regions within its native habitat in Southeast Asia, specifically India, Laos, Myanmar, and Thailand, as well as in Latin America, Africa, and Oceania (Gaitan-Alvarez *et al.* 2019; Moya and Tenorio 2021; Sasidharan 2021). There has been a significant amount of research on the radial properties of teak wood, while the longitudinal variations have received relatively little attention, as recently summarized by Moya and Tenorio (2021). In the context of the above information, the growth pattens of teak in both spatial (height) and temporal (diameter/radial) dimensions are characterized jointly, i.e., the organization of growth pattens in both space and time into a hierarchical system, using tensor and vector calculus principles. This approach involves understanding the complex dynamics of tree growth and development processes and using this information to predict how the tree will change over its life cycle.

The growth mechanism of a tree is a spatial and temporal process; that is, a tree grows simultaneously in space and time. One can visualize the stem form as being the space field, and time as the initiation, evolution, and ending in wood formation (Ashtekar 2006). Thus, tree construct is a domain of space and time. To coordinate this space-time field during development, the primary apical meristem (*responsible for vertical growth*) and the secondary vascular meristem (*responsible for diameter growth*) are unified by a signalling system (Uggla et al. 1998). The secondary growth units follow each primary unit (Thibaut et al. 2001), causing the expansion of the space-time. This explains the relationship between primary and secondary growth (Huang et al. 2014; Olesen 1982). Consequently, wood property exhibits complex heterogeneity in both space and time.

This biological coordination of cambial action generates dependencies in both space and time (Manceur et al. 2012), as the cambial initials are always formed in the prior growing season (Fritts 1976), resulting in complex patterns in wood formation. Capturing these dependencies is an extremely important task, as they reveal the physiological gradients in the tree (Larson 1969) and reflect how various wood properties in growth increments interact with one another. Wood locations in a tree that are separated spatially and temporally are correlated based on the shared environment (Richardson 1964; Larson 1964; van der Maaten et al. 2003), physiology, genetics, and morphology (Larson 1969; Fritts 1976; Savidge 2003). In the process of wood formation, specific genes and proteins are differentially expressed in various ways that contribute to wood plasticity (Déjardin et al. 2010). The correlation pattern in space and time may partially explain the variations in the expression of specific genes and physiological processes (i.e., polar transport of hormones and photosynthetic foods) during wood formation. If we want to be able to deduce the beginning of wood development from later observations, we should better understand how relationships change as trees grow. This information will clarify the basic physics of wood formation.

By analysing the properties of the wood at a macrolevel, it is possible to gain insight into the spatial and temporal distribution of the cambial cells within the stem. Wood specific gravity (WSG), a critical property, is believed to depend on cell composition and structural organization (Wang and Aitken 2001; Wimmer and Grabner 2000; Elliot 1970), giving a biomass estimate, the history of tree functioning, genetic expression, and ecological character (Morel et al. 2018). A direct connection between WSG and tree growth is expected (Williamson and Wiemann 2011; Bouriaud et al. 2004).

The variation of WSG on the vertical axis has been less explored than the variation on the radial axis. Typically, vertical variation has been assumed to be negligible (Kellison 1981) and similar to a radial pattern (Lachenbruch et al. 2011) due to the same physiological age of the cambium at the tree base and at the treetop. However, vertical variations can have an actual effect on a tree's mean WSG that can differ significantly from that at breast height, a spatial standard point for sampling (Wiemann and Williamson 2014; Nogueira et al. 2008). Vertical WSG variations are critical for reconciling biomass estimates with carbon accounting (Billard et al. 2021; Rueda and Williamson 1992). A more accurate assessment of wood quantity and quality depends on the spatial location along the stem (Kimberley et al. 2015; Tian et al. 1995). By describing the wood resources in this way, it should be possible to optimize them for different end uses.

An increase in tree size with time, thus altering the physiological stem gradients, introduces variability in wood properties that is of interest to wood technologists. According to Larson (1973), age and physiological stem gradient are primarily responsible for the plasticity in wood properties, in particular wood specific gravity. But the two factors alone cannot explain the plasticity in wood formation, as there exists a major "dark" element that is not yet understood. The molecular, cellular, developmental, physiological, and environmental aspects—each fascinating in and of themselves—interact to produce the tree structure that we see. These processes occur at various spatiotemporal scales and organizational levels of complexity. All that can be seen are the results of these processes, which take the shape of intricate patterns of connection (Shipley 2016). A stochastic description that takes into account the statistical behavior of the processes is therefore necessary.

In addition to analyzing this variation, it is also important to consider the spatial and temporal dependencies of wood formation (Gartner et al. 2002; Larson 1969). The correlation structure is important because it is of interest in understanding the physiology of wood formation (Larson 1969). Also, modelling the interaction in the space-time field can reveal the underlying tree growth process (Borders and Bailey 1986) and provide explanatory patterns for a complicated biological system as the tree (Longuetaud et al. 2017). In a complex biological system as the tree, there is much information on how fluctuations proceed around the mean values of the physical quantity especially WSG, which are structured in space and time (Grigeria 2021). The observed fluctuations are mainly the product of stochastic meristem activity and changing environmental conditions. According to Lachaud (1989), hormonal expression, cambium activity, and wood property response are all correlated. It has been shown (Fortin et al. 2013) that the occurrence of autocorrelation generates correlated error terms that can affect statistical conclusions. Consequently, they would require accurate modelling of the correlation pattern for valid statistical analysis.

To understand the origins of the WSG patterns, which vary both axially and radially, a unified framework is proposed here by modelling the evolution of the apical meristem (height) and lateral meristem (time) jointly. Jointly modelling axial and radial WSG can address these questions of interest – the overall relationship between apical and lateral meristems and the influence of factors especially aging on them. The authors expect that this approach will reveal hidden knowledge of the space-time structure of the tree. The main goal of this work was to analyze the space-time structure of longitudinal WSG datasets to better understand the physics of tree growth. The following questions were considered:

1). How do spatial and temporal heterogeneities affect WSG variability?

2). Are there correlation patterns with the spatial structures and how does this affect the overall correlation pattern within the stem?

3). What does the two-dimensional covariation of the tree look like? How clear and distinct are these patterns?

To clarify the space-time effects, the rate of longitudinal change in the WSG was also determined using linear regressions performed at all available heights for each relative radial distance. This approach allows for a direct comparison of the overall changes in longitudinal patterns across relative radial distance (RRD) for WSG. It is important to understand random fluctuations that arise during tree growth process due to incomplete knowledge of the factors affecting tree evolution or our inability to measure them accurately enough. The concept of correlation has been used in statistical physics to understand biological systems of high complexity (Villegas et al. 2021).

## 4.2 Materials and methods

### *4.2.1 Wood sampling*

Three trees were randomly selected from an even-aged, monoculture teak plantation in Ghana under a 3 by 3 $m^2$ spacing regime. The plantation was 18 years old; at this age Ghanaian teak is believed to be suitable for harvesting (Adu-Bredu et al. 2018). In each tree, disks 5 cm thick were taken at every meter from 0.3 m ground level until 5.3 m. Two opposing radial strips were taken in 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 obtained 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 20ºC and 65% relative humidity for more than two weeks using a bench-top temperature and humidity chamber (SH-222, Espec Corp., Osaka, Japan).

### *4.2.2 Gravimetric density determination*

The gravimetric density was measured using an electronic densimeter MD-300S (ALFA MIRAGE Co. Ltd, Osaka, Japan) with a density resolution of 0.01g/cm$^3$. The device was calibrated to compensate for water temperature (as water is 1 g/cm$^3$ at 4 ºC). This device measures air-dry density and in our case at 12% equilibrium moisture content. It is measured according to the Archimedes principle. The densimeter can measure the specific gravity of floating samples, such as wood, in water instantaneously. Each disc was analyzed as two separate halves, separated by the pith. Each disc was then divided into 10 consistent parts over the radius and the mean value for each fraction was calculated using the relative distance approach (Chowdhury et al. 2009). Using this approach, the different lengths of wood strips were standardized. The WSG values for the entire disc were determined by taking the average of the WSG values for the two halves of the disk at each height (i.e., *separation in space*), while the SG values for each time point for the two halves of the disc were averaged for each RRD (i.e., *separation in time*). A total of 360 observations were used in this analysis (3 trees × 2 aspects × 6 height levels × 10 RRD).

### *4.2.3 Statistical analysis*

### *4.2.3.1 The linear mixed model*

Repeated measurements for the same tree are correlated in time and space. Wood traits on related trees and specific height are subject to correlations at any time point due to some shared genetic, physiological, and co-annual environmental influences. Additionally, the wood properties of related trees at different points in time also correlate due to the above factors. Height-time data consist of two components i.e., both axial and radial elements, which are repeated both in time and space (doubly repeated measures). By jointly modelling the height-time data, the dependency between the two factors is considered in two ways: firstly, for that among the height levels (i.e., *purely spatial dependence*) and secondly for the correlation of the time factor (i.e., *purely temporal dependence*). This modelling approach shows the underlying process of WSG for longitudinal and radial dynamics in wood formation.

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

$y = X\beta + Zb + \varepsilon,$ (1)

$b \sim N(0, G)$

$\varepsilon \sim N(0, R)$

where $y$ is the vector of observations, $\beta$ is a $p \times 1$ vector of fixed effects $X$, $b$ is a $q \times 1$ dimensional vector of random effects with corresponding design matrix $Z$, and the random effects covariance matrix $G$. The expected value and variances are $E[y] = X\beta$, $var[b] = G = \sigma_b^2 A$ and $var[e] = R = \sigma_e^2 I$ for the A the numerator relationship matrix and I an identity matrix.

*Multivariate case*

In the multivariate case, Eq. 1 was expanded to accommodate WSG values for each height level by stacking up the vectors in such a way that $\beta,\ b\ and\ \varepsilon$ now contain the values for each height/spatial point. The multivariate linear mixed model can be expressed as the following:

$$\begin{pmatrix} y_1 \\ \vdots \\ y_n \end{pmatrix} = \begin{pmatrix} X_1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & X_n \end{pmatrix} \begin{pmatrix} \beta_1 \\ \vdots \\ \beta_n \end{pmatrix} + \begin{pmatrix} Z_1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & Z_n \end{pmatrix} \begin{pmatrix} b_1 \\ \vdots \\ b_n \end{pmatrix} + \begin{pmatrix} \varepsilon_1 \\ \vdots \\ \varepsilon_n \end{pmatrix} \qquad (2)$$

where $\beta$, b, and $\varepsilon$ are vectors of fixed effects, random effects, and random residuals, respectively.

$$G = A \otimes G_0;\ R = I \otimes R_0 \qquad (3)$$

In Eq. 2, the symbol ⊗ is the Kronecker product. The distribution of the random effects and error terms are assumed to be normal with mean zero and variance-covariance matrix:

$$G_0 = \begin{pmatrix} \sigma_1^2 & \cdots & \sigma_{1,n} \\ \vdots & \ddots & \vdots \\ \sigma_{1,n} & \cdots & \sigma_n^2 \end{pmatrix};\ R_0 = \begin{pmatrix} \sigma_{\varepsilon_1}^2 & \cdots & \sigma_{\varepsilon_{1,n}} \\ \vdots & \ddots & \vdots \\ \sigma_{\varepsilon_{1,n}} & \cdots & \sigma_{\varepsilon_n}^2 \end{pmatrix}, \qquad (4)$$

Where $G_0$ and $R_0$ are the spatial and temporal variance-covariance matrices, respectively. The variances are printed diagonally and the covariances are elsewhere. The height factor is treated as a random effect with the correlation among height levels modeled in the random effects covariance matrix *G* and the correlation among years (time) is modeled in the residual covariance matrix *R*.

One method for integrating variable-specific correlation structures into an overall correlation model involves modelling the correlation pattern for space and time separately. With the Kronecker product, factor-specific correlation structures are combined into an overall correlation pattern. Once the spatial and temporal model is defined, separable space-time models are easy to obtain. The separable space-time process can be written as the product of the purely spatial and purely temporal covariances at a finite set of space-time locations.

For instance, if there are two spatial locations and three repeated measures across time from a tree, then we assume a covariance matrix with the following structure UN⊗AR(1):

$$\begin{bmatrix} \sigma_{b_1}^2 & \sigma_{b_{12}} \\ \sigma_{b_{21}} & \sigma_{b_2}^2 \end{bmatrix} \otimes \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} = \begin{bmatrix} \sigma_{b_1}^2 * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} & \sigma_{b_{12}} * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} \\ \sigma_{b_{21}} * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} & \sigma_{b_2}^2 * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} \end{bmatrix} \qquad (5)$$

Here, the UN is a 2x2 symmetric matrix with the variances of the spatial structure as the diagonal elements and the covariances as the off-diagonal element. It is assumed that the longitudinal measurements of the same tree have an AR(1) structure, that remains the same over time for all spatial structures.

The models in this document were implemented in SAS 9.04 PROC MIXED (SAS Institute, Cary NC) and solved using restricted maximum likelihood (REML). In the modelling, the Kenward-Roger method was used to determine the degrees of freedom (Kenward and Roger 1997). The REML variance components were estimated. The homogeneity and normality of the residuals were checked to ensure that the assumptions according to Schabenberger (2004) were fulfilled and appropriate. An F test was used to determine the statistical significance of fixed effects ($\alpha = 0.05$).

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

$$Y_{ijk} = m + T_k + h_i + r_j + (h \times r)_{ij} + \varepsilon_{ijk}. \qquad (6)$$

Where $Y_{ijk}$ denotes the WSG for tree $k = 1, \ldots, 3$ in relative radial position $r_j = 0.1, \ldots, 1$ at height level $h_i = 0.3, \ldots, 5.3$, $m$ is the overall mean, and $(h \times r)_{ij}$ is the interaction of height and relative radial position. The fixed effects were height, RRD, and their interaction. The experimental error is denoted by $\varepsilon_{ijk}$. The spatial and temporal variation in WSG, within and between trees was statistically assessed using an ANOVA approach. Large-scale and small-scale spatial heterogeneities were considered by the tree and height factors, respectively, while the relative radial position factor accounted for temporal heterogeneity.

## 4.3 Results

The mean and standard deviations for each height level are presented in Table 1. The distribution of WSG across space-time is shown in Fig. 1. The overall mean WSG was 0.666±0.027. The model fit estimates and the REML estimates of the variance-covariance matrix of the purely spatial factor (height) are presented in Tables 2 and 3, respectively. From Table 2, the unstructured (UN) covariance structure imposed on the spatial factor estimates 6 distinct variances and 15 covariances for the 6 height levels (6 by 7 divided by 2). One parameter is estimated for the first order autoregressive (AR(1)) structure, which is imposed on the temporal factor. This was done to reduce the number of unknown parameters in the temporal factor (10 by 11 divided by 2). It models the association among the set of repeated measurements in the radial direction (the flow of time). The other parameter is the variance between the trees, which indicates how much variation there is between trees. The AIC and BIC provide measures of model performance accounting for model complexity.

Table 3 can be viewed as the evolutionary variance-covariance of the apical meristem. The multivariate approach has shown the existence of covariation among height levels. This information is lost in the traditional regression model. The variance-covariance matrix of the apical meristems may reveal the changes probably due to hormonal balance, gene pattern, and gene activity (Olesen 1978; Luo and Li 2022). No clear pattern was found in the spatial variation of WSG. However, the variation was highest at 3.3 m and lowest at 2.3 m.

Table 4 gives the correlation matrix of the purely spatial factor. The correlations describe the strength and direction of the linear association among the spatial structures. The spatial correlation matrix can be viewed as a developmental and functional correlation according to Emerson and Hastings (1998) or as genetic linkages and pleiotropy (Cheverud 1996, 2000). The spatial correlation function suggests some interesting relationships among WSG of height in the tree. It appears that there is generally a positive association among the residuals, while residuals separated at great distances have low linear association. As expected from the spatial patterns, the response of the WSG at a lower height level is more strongly correlated than that of WSG separated by greater distances (Table 4). In other words, the size of the correlations between two spatial points in the tree is larger than the size of the correlations between three or more spatial points. The increasing spatial dependence with increasing height can be attributed to the maturation mechanism of the apical meristem (from bottom to top) and the decreasing longitudinal hormonal gradient (from top to bottom). The total growth behind the apical meristems is smaller in lower spatial positions (far below the crown at 0.3 m), maturation is said to have progressed furthest in the apical meristem at 5.3 m and to have had the greatest growth behind it (Olesen 1978). This means that the similarity index in the WSG increases with increasing height. The correlation structure suggests several facets of the biology of the tree, so while choosing a model, it is important to take these facets into account. The dependencies may reflect how the tree adds height as it grows. According to Duff and Nolan (1953), longitudinal correlation is influenced by climatic conditions of the previous season, since the food supply is then being stored and made available for new tissue growth in the current year. The spatial correlation pattern can then reveal the physiological process involved in the distribution and usage of tree's photosynthate, i.e., increasing the biomass allocation to cell walls (Kozlowski 1992; Larson 1969).

The correlation matrix of the purely spatial factor was simulated five thousand (5000) times to evaluate the uncertainty in the correlation matrix (Table 5). Probabilities of significance are printed below the diagonal; all but one structural correlation (0.3 m and 3.3 m) are statistically significant at the 0.05 level. This implies that in all but one case there are significant spatial dependencies and interactions of the apical meristem. There was almost no correlation between 0.3 and 3.3 m, suggesting that the genetic, physiological memory of the first formed wood at 0.3 m is lost at 3.3 m spatial location in the tree. This point could represent the vertical transition zone for the formation of juvenile to mature apical meristems. It can be inferred that at the transition point, there may be no genetic correlation between the termination spatial position and the prior spatial position. Furthermore, the correlation between 1.3 and 3.3 m was negative but was of low order. The weak correlation between 3.3 m and the two prior height levels indicates that WSG evolution at the two prior height levels is independent of wood evolution at 3.3 m. Correlation values above 0.3 observed from 3.3 m upwards indicate a strong local spatial trend. This local trend may reveal the intrinsic fact that the apical meristem forms a more ordered wood with time.

Based on Fig. 2 (representing how WSG varies averagely in a vertical series of annual height-growth), the WSG decreases rapidly from 0.3 m to 2.3 m and then increases at a nearly constant rate from 3.3 m to 5.3 m altitude. Interestingly, the mean WSG and variance were lowest at 2.3 m. WSG increased approximately 4.6% from the base at 0.3 m to the peak at 5.3 m. Miranda et al. (2011), Bailleres and Durand (2000), and Moya (2000) have also found that the radial WSG increases with time. The WSG was found to be lower in the lower stem and higher in the upper stem. According to Moya (2000), the dry density of teak falls from the base of the tree to a certain height (50 percent of total height) and then increases with increasing height (up to 75% of total height). For teak plantations grown in India, Sekhar and Negi (1996) showed an inconsistent behavior of dry density with increasing height level. Miranda et al. (2011) and

Perez and Kaninen (2003) discovered that the density at the base of teak trees was lower than at a distance near the canopy. Tondjo et al. (2015) discovered unusually low densities for teak growing in Togo at the height level thought to be between 2.3 and 3.3 meters for Togolese and Tanzanian provenances.

The correlation matrix for the purely temporal factor (RRD) is presented in Table 6. The temporal correlation decreased over time. This phenomenon can be attributed to evolutionary changes in the anatomy, as well as differential gene expression of the wood produced with the maturation of the initials of the cambium. Also, the decay could be attributed to the diminishing crown effect on the vascular meristem as wood is formed further away from the pith. Similarly, the random fluctuations acting on the tree growth are nonconstant in time. One explanation for the decreasing correlation, for instance, is that the microenvironment the trees evolved in changed with time. The stress related to the competition for resources changes as stems grow over time. The conditions are more similar when there is less time between measurements. However, these conditions could alter and affect the correlation among the within-tree errors in time. The autoregressive parameter estimate (Table 6) suggests that the within-tree correlation decreases from 0.823 one RRD apart to 0.458 for four lags (RRD) apart.

The correlation between the unstructured random effect (purely spatial) was low (*averaging $r = 0.30$*) whereas the correlation between the temporally structured random effect was high ($r = 0.823$) for a time lag. This may be due to the relatively short distances in the temporal distances measured in centimeters with the spatial structure measured in meters. Both the spatial and temporal autocorrelations can be interpreted as axially, the first formed wood (at 0.3 m) could only account for 2% of the variation in the WSG of the wood at 5.3 m, whereas radially, only 3% of the variation in the WSG of the later formed wood (1% RRD) could be attributed to the first formed wood (0.1% RRD). This reveals the relationships with spatial and temporal scales with changing growth process.

WSG increases with cambial age (Fig. 3). From 1 to 5% RRD, WSG increased linearly and relatively stabilized at 6 to 10% RRD. From 1 to 5% RRD, the wood formed at this stage can be considered as juvenile core wood, while mature core wood is formed from 6 to 10% RRD. Overall, WSG increased by 14% from near the pith at 1% to near the cambium at 10% RRD. This consistent pattern of change in WSG can be attributed to inherent ageing processes in the cambium, which specifically reflect the elongation of fiber length (Hidayati et al. 2014; Bhat et al. 2001; Kedharnath et al. 1963), increasing fiber wall thickness and smaller vessel diameter (Dié et al. 2012) in teak. The exponential increase in WSG from 1 to 5% RRD can account for a larger portion of the variation in teak quality. The effects of tree size and age on the stem gradients are simply reflected by variations in the radial direction (flow of time) of a stem (Larson 1973).

There were temporal patterns of WSG variation across spatial structures (see Fig. 4a,b). From 0.1 to 0.5% RRD, the WSG averaged 0.645 with a CV of 5.50%. From 0.6 to 1% RRD, the mean WSG was 0.687 with a CV of 0.81%. This represents an approximately 6.5% increase in WSG in the wood formed at a later stage of tree growth. With increasing WSG, the variation is reduced, thus increasing uniformity. A desirable trait of planted trees. The WSG formed in the early phase of tree growth (0.1 to 0.5% RRD) showed greater variation throughout the trunk. From 0.6 to 1% RRD, which corresponds to a later growth stage, a greater value was found. The crown-formed wood of older tree (at 5.3 m) even though is structurally and physiologically similar to the juvenile wood when the tree was young (at 0.3 m) is not identical in terms of mean WSG. Larson (1973) suggested that because the crown of the older tree is larger, the fibers of the crown-formed wood are larger in diameter and thick-walled than those of the juvenile wood produced by the same tree when it was young.

Between 0.1 and 0.5% RRD, the tree can be said to have undergone rigorous growth typical of tropical pioneers, with a longitudinal change rate (LCR) of 1.1% (see Fig. 5). The age-related decrease in forest productivity may probably explain the decrease in the LCR from 0.6 to 1%, which corresponds to 0.5%. As forest productivity declines, trees can be expected to produce wood with high WSG. It is inferred that the trees may have reached their final height at 0.5% RRD, which corresponds to nine years of the sampled trees (Burdon et al. 2004). Water conduction is restricted to increasing gravitational and frictional forces to the top as the tree grows taller. The rise in WSG at the top may be caused by this, as cells must be thicker to withstand the pressure. According to Dié et al. (2012), WSG, which is characterized by narrow lumen and thick-walled fibers, is initiated in teak under declining precipitation levels. The high variation exhibited in the core wood area can be controlled by slowing down growth at the early stage.

The residuals from the model appeared normal and well behaved (see Fig. 6). The quantile plot shows that the assumption of normality was reasonable.

To assess the effects of space and time on WSG, Type 3 fixed effects tests were applied, and the results are presented in Table 7. The between-subjects effects of height (i.e., the purely spatial main effects) are statistically significant. The mean values were statistically different at 0.3 and 2.3 m, 2.3 and 4.3 m, and 2.3 and 5.3 m. The difference between putative yearly means is significant in terms of temporal heterogeneity of the WSG mean (i.e., within-subjects effects), but the product of height x time (RRD) is not statistically significant. Teak is sensitive to light, which is a characteristic of pioneer species, as indicated by the significance of time (RRD) effects (Kårenlampi and Riekkinen 2004). Due to high light requirement of pioneering species, their cambial activity is influenced by time-related factors, including the cycle of daylight and darkness experienced.

Xylem formation can be modelled as a function of cambium activity and apical activity (Huang et al. 2014), and based on this assumption, the Kronecker product between the height factor and the time factor was applied (see Fig 7 and Table 8).

The typical temporal patterns of wood formation dynamics at different spatial distances. Correlations show larger variations between 0.1 and 0.5% RRD along the tree stem. In other words, the wood formed in that year along the height is different. Later, similar correlations appear in the outer wood along the trunk, meaning that the wood formed in that same time is typically uniform. The wood formed at 0.3 m may consist of a typical juvenile apical meristem, more distinct from other spatial distances. The trend at 1.3 to 5.3 m from 0.1 to 0.5% RRD may indicate a maturing apical meristem. Genetically, it can be concluded that they are different. Greater similarity was shown from 0.6 to 1% RRD at 1.3 m to 5.3 m indicating that cambium may have common genes. It can be inferred that the mature apical meristem can still produce relatively variable wood, whereas the mature lateral meristem is stable across the spatial structures (see Fig 7). At 0.3 m, there is a rapid change in wood formation, whereas from 2.3 to 5.3 m, there is progressively slower change up the stem. In the stem, wood formed below 0.3 m can be thought of as being in a random condition, whereas wood formed higher up (2.3 to 5.3 m) is in a more ordered state (Fujimoto 2022). In other words, growth by the younger trees can be most sensitive to random environmental perturbations while growth by the older trees would be less affected.

The distribution chart (Table 7) depicts the latent, unobservable process underlying wood formation and the sources of variability in WSG. These processes are stochastic in nature and influence dynamics of wood formation on a temporal and spatial level, for example the diffusion and polar transport of morphogen (i.e., auxin) (Hartmann et al. 2017). The Kronecker product describes the two types of maturation processes to which the vascular cambium is subjected, namely those that are transmitted from the apical meristem to the lateral meristem as it forms, and those that the lateral meristem undergoes after its initiation (Olesen 1982). The correlation function (see Table 7) can be viewed as a measure of order in the biological system, describing how wood formed at differential spatial positions from time to time relates to each other (spatiotemporal interaction of the apical and lateral meristems). In particular, it describes and quantifies how wood increments, on average, covary with each other over space and time. The Kronecker tensor product revealed the intrinsic fact that trees form a more ordered wood both in time and space, attributable to both apical and lateral meristem ageing. Typically, the wood at 0.3 m height level, consists of juvenile core wood and juvenile outer wood close to the pith and close to the bark, respectively. The juvenile outer wood is similar to the mature core wood formed at upper height levels in the stem. This is called superimposition. As the tree grows into vertical space, the point at which core wood fuses into mature wood gradually moves upward in each consecutive yearly increment that is added to the stem by the cambium (Larson 1973). This has the implication that the inner wood that is produced at higher height levels (1.3 ~ 5.3 m) can be accurately predicted by the outer wood that is formed at lower height (0.3 m). The mature outer wood is formed close to the bark in the upper height levels of the stem (Burdon et al. 2004). Within the tissues of mature outer wood, one can speculate that there is an almost stationary concentration level of morphogen in both space and time (Hartmann et al. 2017). Accordingly, the correlations can be placed into three categories as high, intermediate, and low auxin concentrations (Bhalero and Fischer 2014). High auxin concentrations can be regarded as a signal for cell differentiation, which correlates to high cambial activity of the juvenile apical meristems, resulting in large variation in wood structure and, consequently, in wood properties. The intermediate auxin concentration levels could encourage cell elongation. Bioactive gibberellin peaks at this stage. The apical meristems are maturing at this time, resulting in the development of mature apical meristem and thus mature core wood. Low auxin levels could be a signal that causes deposition of secondary cell walls. This concentration level may ensure the steady growth in the mature outer wood zone. The meristem is thus considered to be fully mature. Additionally, important details can be learned about gene expression during tree growth from the correlation structure. It is possible to say that each of the three phases is regulated by a different set of genes that drive the growth of xylem cells at the cellular and molecular levels (Luo and Li 2002). The variation in WSG within a tree is therefore largely associated with crown-formed wood compared with mature wood in the bole of the stems.

| Height, M | Mean | StdDev |
|---|---|---|
| 0.3 | 0.673 | 0.048 |
| 1.3 | 0.663 | 0.082 |
| 2.3 | 0.625 | 0.067 |
| 3.3 | 0.651 | 0.061 |
| 4.3 | 0.680 | 0.087 |
| 5.3 | 0.704 | 0.076 |

**Table 1**: Descriptive Statistics of WSG distribution

| Number of Parameters | -2LogLike | AIC | BIC |
|---|---|---|---|
| 23 | -1090.8 | -1044.8 | -1065.5 |

AIC: Akaike information criterion; BIC: Bayesian Information Criterion

**Table 2**: Model Fit Statistics

|  | Height Levels, m |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  | 0.3 | 1.3 | 2.3 | 3.3 | 4.3 | 5.3 |
| 0.3 | 0.003368 | 0.00077 | 0.00046 | 0.001367 | 0.000609 | 0.000474 |
| 1.3 | 0.00077 | 0.003885 | 0.000716 | 0.000641 | 0.00054 | 0.000602 |
| 2.3 | 0.00046 | 0.000716 | 0.002478 | 0.001006 | 0.001013 | 0.000737 |
| 3.3 | 0.001367 | 0.000641 | 0.001006 | 0.005104 | 0.001282 | 0.000681 |
| 4.3 | 0.000609 | 0.00054 | 0.001013 | 0.001282 | 0.002611 | 0.001241 |
| 5.3 | 0.000474 | 0.000602 | 0.000737 | 0.000681 | 0.001241 | 0.003422 |

Variances on the diagonals; covariances off the diagonals

**Table 3**: REML estimates of the variance-covariance matrix of the purely spatial factor

|  | Height levels, m |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  | 0.3 | 1.3 | 2.3 | 3.3 | 4.3 | 5.3 |
| 0.3 | 1 | 0.213 | 0.159 | 0.033 | 0.205 | 0.14 |
| 1.3 | 0.213 | 1 | 0.231 | -0.047 | 0.17 | 0.165 |
| 2.3 | 0.159 | 0.231 | 1 | 0.283 | 0.398 | 0.253 |
| 3.3 | 0.033 | -0.047 | 0.283 | 1 | 0.351 | 0.163 |
| 4.3 | 0.205 | 0.17 | 0.398 | 0.351 | 1 | 0.415 |
| 5.3 | 0.14 | 0.165 | 0.253 | 0.163 | 0.415 | 1 |

**Table 4**: Correlation matrix of the purely spatial factor (height level)

|  | 0.3 | 1.3 | 2.3 | 3.3 | 4.3 | 5.3 |
|---|---|---|---|---|---|---|
| 0.3 | 1 | 0.22054 | 0.16716 | 0.0106 | 0.19 | 0.13099 |
| 1.3 | <0.0001 | 1 | 0.21231 | -0.03312 | 0.16818 | 0.15002 |
| 2.3 | <0.0001 | <0.0001 | 1 | 0.30325 | 0.37814 | 0.24663 |
| 3.3 | 0.4538 | 0.0192 | <0.0001 | 1 | 0.37117 | 0.17664 |
| 4.3 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | 1 | 0.41298 |
| 5.3 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | 1 |

**Table 5**: Simulated correlated matrix (5000 times) of the purely spatial factor

| RRD 0.1 | RRD 0.2 | RRD 0.3 | RRD 0.4 | RRD 0.5 | RRD 0.6 | RRD 0.7 | RRD 0.8 | RRD 0.9 | RRD 1 |
|---|---|---|---|---|---|---|---|---|---|
| 1.000 | 0.823 | 0.677 | 0.557 | 0.458 | 0.377 | 0.310 | 0.255 | 0.210 | 0.173 |
| 0.823 | 1.000 | 0.823 | 0.677 | 0.557 | 0.458 | 0.377 | 0.310 | 0.255 | 0.210 |
| 0.677 | 0.823 | 1.000 | 0.823 | 0.677 | 0.557 | 0.458 | 0.377 | 0.310 | 0.255 |
| 0.557 | 0.677 | 0.823 | 1.000 | 0.823 | 0.677 | 0.557 | 0.458 | 0.377 | 0.310 |
| 0.458 | 0.557 | 0.677 | 0.823 | 1.000 | 0.823 | 0.677 | 0.557 | 0.458 | 0.377 |
| 0.377 | 0.458 | 0.557 | 0.677 | 0.823 | 1.000 | 0.823 | 0.677 | 0.557 | 0.458 |
| 0.310 | 0.377 | 0.458 | 0.557 | 0.677 | 0.823 | 1.000 | 0.823 | 0.677 | 0.557 |
| 0.255 | 0.310 | 0.377 | 0.458 | 0.557 | 0.677 | 0.823 | 1.000 | 0.823 | 0.677 |
| 0.210 | 0.255 | 0.310 | 0.377 | 0.458 | 0.557 | 0.677 | 0.823 | 1.000 | 0.823 |
| 0.173 | 0.210 | 0.255 | 0.310 | 0.377 | 0.458 | 0.557 | 0.677 | 0.823 | 1.000 |

**Table 6**: Correlation matrix of the purely temporal factor (RRD $\times$ $100, \%$)

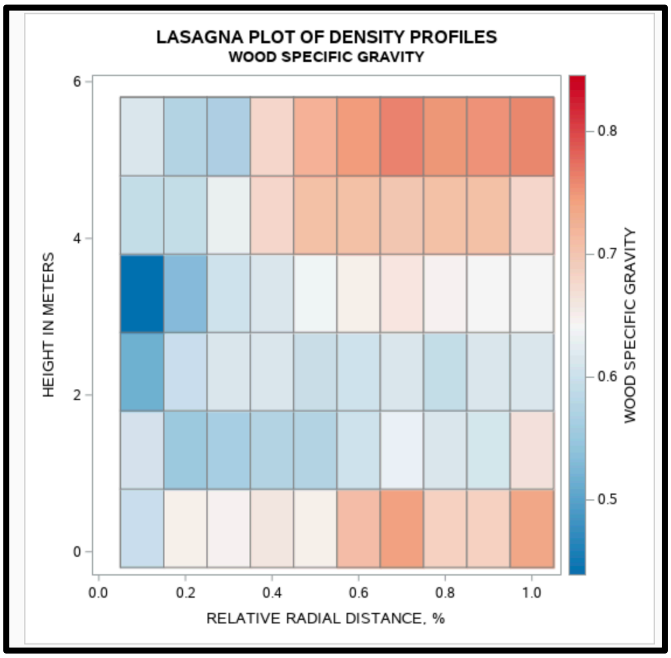


**Figure 1**: Heatmap of Height-Time WSG data. This represents both the temporal evolution of spatial structures and the spatial structure of temporal dynamics of WSG within the tree.

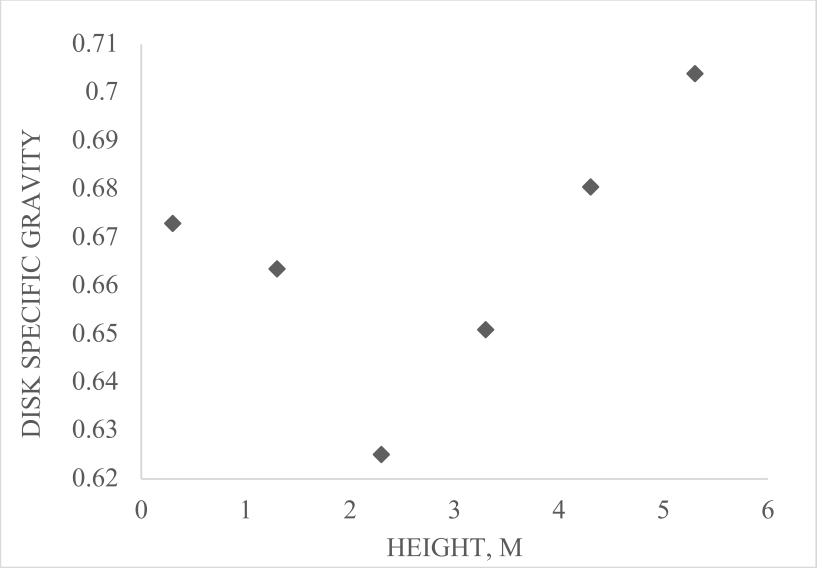


**Figure 2**: Disk WSG as a function of height (Spatial variability in WSG). This represents how WSG varies in a vertical series of annual height-growth.

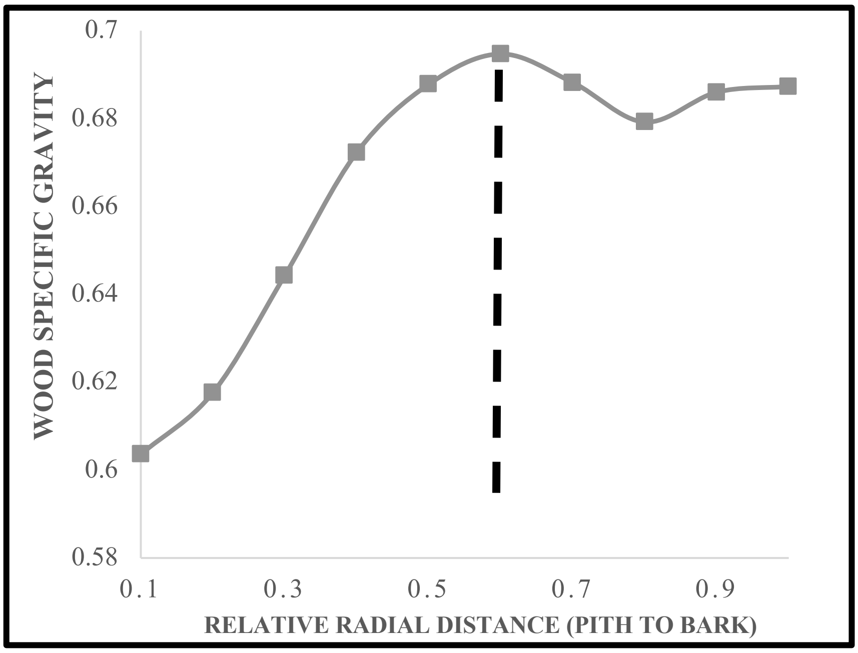


**Figure 3**: Temporal Effect on WSG (WSG versus relative radial distance × 100 (%)). This represents on average how WSG varies radially in successive increments from pith to bark.

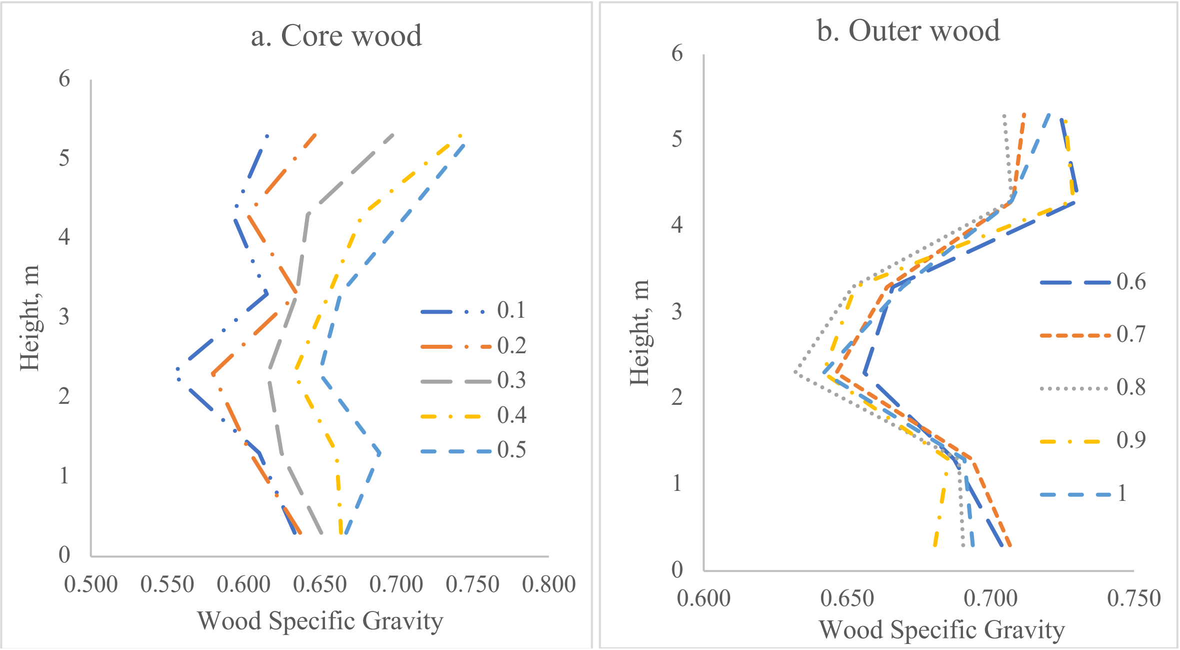


**Figure 4**: Longitudinal patterns of WSG variation per RRD a. core wood b. outer wood

Type 3 Tests of Fixed Effects

| Effect | Num DF | Den DF | Chi-Square | F Value | Pr > ChiSq | Pr > F |
|---|---|---|---|---|---|---|
| Height | 5 | 19 | 17.47 | 3.23 | 0.0037 | 0.0282 |
| RRD | 9 | 46.4 | 39.77 | 4.41 | <0.0001 | 0.0003 |
| Height*RRD | 45 | 114 | 60.2 | 1.19 | 0.0644 | 0.2242 |

**Table 7**: Repeated measures ANOVA showing the effects of space (height), time (RRD), and space-time interaction (height-time) factors on WSG

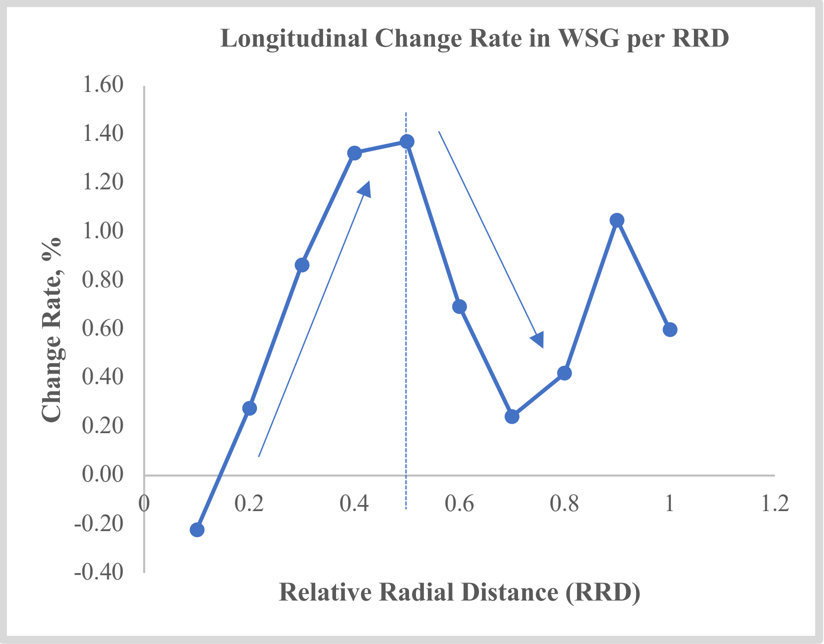
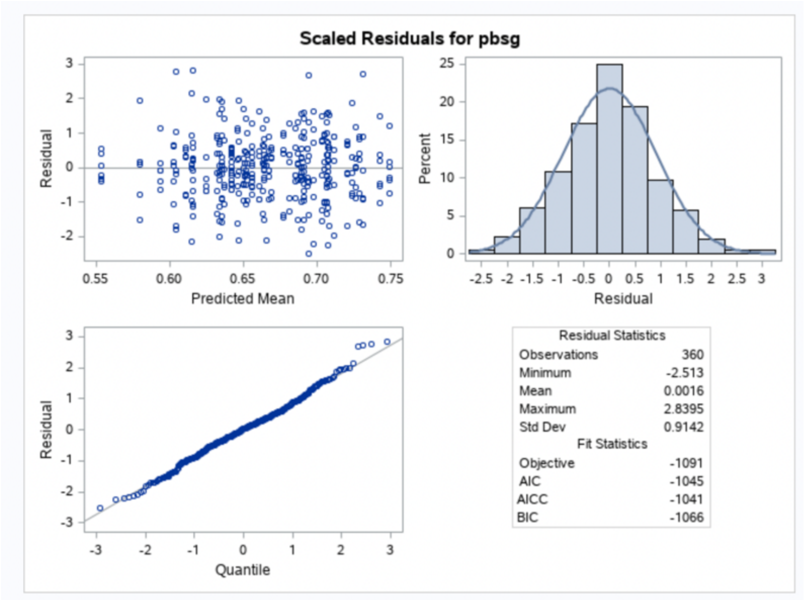


**Figure 5**: Longitudinal change rate (%) in WSG: representing the vertical gradient of wood formation, i.e., rate of axial growth. The slopes of the linear regressions performed for all height levels for each RRD.



| Residual Statistics | |
|---|---|
| Observations | 360 |
| Minimum | -2.513 |
| Mean | 0.0016 |
| Maximum | 2.8395 |
| Std Dev | 0.9142 |
| **Fit Statistics** | |
| Objective | -1091 |
| AIC | -1045 |
| AICC | -1041 |
| BIC | -1066 |

**Figure 6**: Scaled residual plot from the model

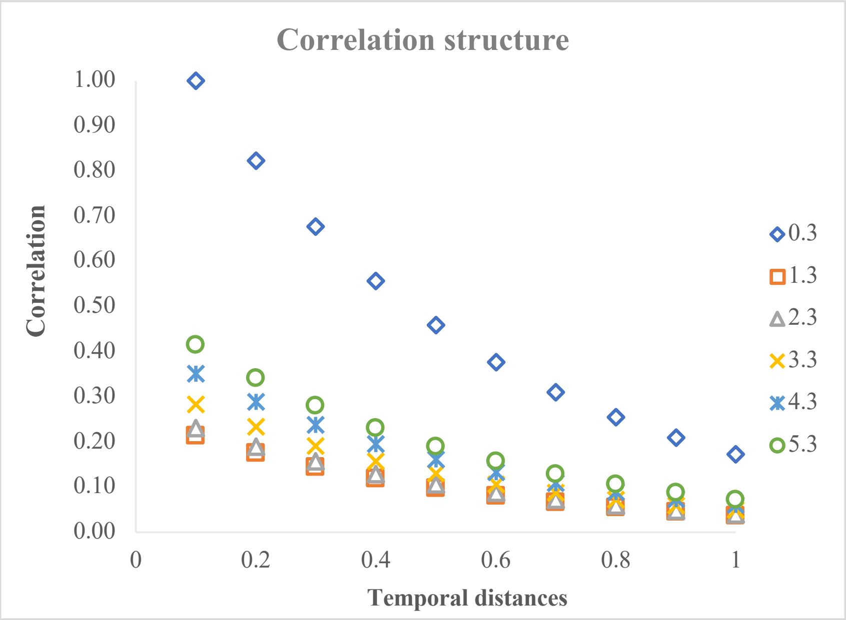


**Figure 7**: Kronecker product of the space-time correlation (Height ⊗ RRD)

| | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1 |
|---|---|---|---|---|---|---|---|---|---|---|
| *r (0.3)* | 1.00 | 0.82 | 0.68 | 0.56 | 0.46 | 0.38 | 0.31 | 0.26 | 0.21 | 0.17 |
| *r (0.3,1.3)* | 0.21 | 0.18 | 0.14 | 0.12 | 0.10 | 0.08 | 0.07 | 0.05 | 0.04 | 0.04 |
| *r (1.3,2.3)* | 0.23 | 0.19 | 0.16 | 0.13 | 0.11 | 0.09 | 0.07 | 0.06 | 0.05 | 0.04 |
| *r (2.3,3.3)* | 0.28 | 0.23 | 0.19 | 0.16 | 0.13 | 0.11 | 0.09 | 0.07 | 0.06 | 0.05 |
| *r (3.3,4.3)* | 0.35 | 0.29 | 0.24 | 0.20 | 0.16 | 0.13 | 0.11 | 0.09 | 0.07 | 0.06 |
| *r (4.3,5.3)* | 0.42 | 0.34 | 0.28 | 0.23 | 0.19 | 0.16 | 0.13 | 0.11 | 0.09 | 0.07 |

This chart can serve as a guide for sorting wood parts during processing.

**Table 8**: Distribution chart of the Kronecker product of space-time correlation (Height ⊗ RRD). The correlations increased in space across time.

## 4.4 Discussion

In the space-time analysis, the WSG increased approximately with time, which correlates with the spatial dimensions in the radial (14%) and vertical (~ 5%) variations. The CV of WSG in the spatial structure was 4%, and in the temporal structure it was 5%. The WSG of the core wood produced by the juvenile apical meristem (0.607 to 0.651 between 0.3 and 2.3 m) was significantly lower than that of the outer wood (0.644 to 0.695 between 0.3 and 2.3 m). Further up in the trunk, core wood produced by the more mature apical meristem (at 5.3 m, WSG = 0.690) did not show much difference from the outer wood (at 4.3 and 5.3m, WSG = 0.720). Generally, WSG increased from base to the top across all timescales. For example, at RRD 3% it grew by 0.87 $m^{-1}$, resulting in WSG increase of 0.046 or 7% from 0.3 to 5.3 m. The longitudinal rate of change in the core wood area increased steadily over time (Fig. 5). This stage can correspond to the early growth stage of teak trees. As a fast-growing pioneer, teak can produce wood with reduced density (Fig. 3), allowing a faster mass growth rate for light absorption. This corresponds to the formation of wider rings (Rugmini and Jayaraman 2009; Kokutse et al. 2010) and higher nutrient levels in the tree trunk (Fernandez-Moya et al. 2013). After RRD 0.5%, WSG increased from 0.3 to 5.3 m at almost the same rate with a decreasing rate of longitudinal change (Fig. 5), reflecting age-related decline. It is likely that the phase of increased WSG occurs concurrently with canopy closure, i.e., as the competition for space and light begins (Paul 1957), the ring width narrows (Bhat et al. 2001; Rugmini and Jayaraman 2009; Kokutse et al. 2010; Miranda et al. 2011), along with an increase in fiber length, fiber wall thickness, and narrowing of vessel diameter (Dié et al. 2012), thus confirming the cambium aging mechanism (Larson 1960). The age-related decline phase corresponds to the stabilization of WSG as the tree produced wood with increased WSG. This phase occurred at 9 years in the studied trees. Moya et al. (2013) and Gaitan-Alvarez et al. (2019) discovered that WSG of fast-growing teak stabilizes at 6 years of age.

Xylem formation can be modelled as a function of lateral meristem activity and apical meristem activity (Huang et al. 2014). Also, the lateral meristem is a derivative of the apical meristem (Olesen 1982). Thus, it may seem logical to assume that the Kronecker product of the spatial and temporal correlation structure (Table 7) represents the underlying mechanism of the interaction between the apical and lateral meristems. Since the apical and lateral meristems can develop in dependency, this is a first step in understanding the implications of such dependency. This coordination decreases exponentially with time/age at a given height level. The decay reflects the intrinsic maturation of the lateral meristem as the effect of the crown reduces on the wood formed further from the pith.

The spatial correlation decreased from the highest height level at 5.3 m to the stem base at 0.3 m, whereas the temporal correlation pattern decreased from pith to bark. These patterns reflect the distinct dynamics of the wood structure of the lateral and apical meristems. A bottom-up spatial correlation may be evident as the apical meristem matures at higher tree heights (Burdon et al. 2004; Olesen 1982,1978). The variation in the wood structure decreases, thereby increasing similarity among higher spatial structures. The pattern can give us an indication of the secondary wall thickening typical of "latewood", which according to Larson (1964) starts at the base of the trunk and progresses upwards. Increasing similarity can thus be explained by narrow-diameter fiber cells that can appear progressively at higher height levels (Larson 1964). For the so-called "earlywood" density component, we found a spatial autocorrelation of 0.04, while the "latewood" density component was 0.460 (data not shown). This gives us an indication that the spatial correlation is driven by the wood formed in the late growing season. Reduction in cell division activity and both radial and axial expansion of xylem cells may increase the correlations among spatial structures thereby increasing uniformity in space.

The longitudinal hormonal and nutritional gradients from the active crown could be represented by a top-down spatial correlation (Larson 1969) because xylem development has been shown to be a useful proxy for auxin transport (Huang et al. 2014). Aloni (2007, 2001) and Aloni and Zimmerman (1983) found that a downward gradient in indole-3-acetic acid (IAA) levels in young leaves and gradually increasing effects of gibberellin in mature leaves regulated the transition from the juvenile phase to the mature phase. This could be the case in the present analysis. The results from 5.3 to 3.3 m could represent the polar transport of gibberellin, whereas the results from 2.3 to 0.3 m track the polar transport of IAA. The lack of correlation between 3.3 m and the prior lower height levels (0.3 and 1.3 m) may be due to the increasing effect of gibberellin at the 3.3 m on wood cell formation dynamics. At the lower height levels, it can be inferred that the wood cells formation may be controlled by IAA. It is suspected that the influence of high nutritional and hormonal (IAA) levels on physiological age strongly affects the expression of juvenile characteristics in the core wood zone. A vigorous crown likely produces more IAA in their young leaves when phosphorus is optimally supplied, which would yield numerous cells that remain small due to their rapid differentiation, thereby increasing tree size radially and axially at the young stage.

Recent tree physiology studies have shown that tree size may be the primary reason for age-related decline due to increasing environmental constraints on water transport, nutrition, and respiration (Binkley et al. 2002). It can be hypothesized that physiological constraints, particularly conduction needs (Dié et al. 2012) and food supply (Fernandez-Moya et al. 2013; Drechsel and Zech 1994), increased as trees reached their predetermined maximum height growth (Fig 4). Increasing WSG at 5.3 m was observed for both core and outer wood, which was associated with the production of narrow lumens and thick-walled fiber cells. Fernandez-Moya et al. (2013) and Drechsel and Zech (1994) observed decreasing concentrations of nitrogen and phosphorus concentrations over time, in the foliage. In the tree trunk, Fernandez-Moya et al. (2013) observed that nitrogen, potassium, and magnesium decreased over time in teak plantations from Costa Rica and Panama. Phosphorus deficiency is known to slow down cell division and elongation (Thomas et al. 2005). It can be speculated that as nitrogen, phosphorus and IAA concentrations decreased, the biomass allocated to the apical meristem was preferentially used for secondary wall thickening rather than to produce additional cells, thereby increasing WSG as wood material spread over small area. It was found that the low-density/earlywood components increased by about 8% (data not shown) from base to top, which may reflect the gross anatomical changes. The shift from low WSG to high WSG has been associated with mechanical reinforcement after the tree has reached the canopy (Wiemann and Williamson 1989, 1988).

Finally, apical meristem maturation appears to have a significant impact on wood produced near the pith with height. However, after about nine years, its influence may diminish as cambium maturation becomes increasingly influenced by cyclophysis and physiological limits. Cyclophysis, according to Olesen (1982), is the maturation of the apical meristems. This view is supported by the biological argumentation of the two-dimensional characterization of maturation in trees (Burdon et al. 2004; Olesen 1982; Larson 1973).

The model used in this study will usher in a time when the relationships between axial and radial variance structure in wood properties can be quantified jointly. For example, one can account for the statistical connection by considering correlations and patterns between wood formation in space and time when viewing the tree as a space-time continuum (Gartner et al. 2002; Larson 1969). This should also inspire us to create better tools and observables to understand the mechanisms underlying the patterns we see.

In conclusion, the present work highlights a clear direction for future research: wood scientists should make the necessary investments to compute both spatial and temporal correlations in their wood quality assessments, depending on the data collection design. There are numerous processes that affect the tree throughout its life cycle and contribute to variation in WSG (a physical quantity of interest). These additional sources of variations i.e., the drivers of variability (“process” error) and modifications of the basic physiological processes that ultimately contribute to WSG need to be recognized (Larson 1973). The variation in wood properties can be wholly understood as a function of tree growth and development if we incorporate these complexities into our models.

## 4.5 Conclusion

The space-time analysis of wood specific gravity (WSG) has been studied. At any given inferred age (RRD) in the core wood, WSG generally increased with trunk height, but in the outer wood WSG remained nearly constant. Height and RRD were found to be significant factors controlling WSG. Their interaction did not show statistical significance. When assessing the impacts of growth acceleration on WSG, it is important to keep in mind that WSG variation predominantly occurs in the so-called core wood.

The space-time approach chosen in this study could describe the pattern in the dynamics of wood formation. The mixed effect modelling approach used in this study was able to capture the physiological mechanism underlying tree growth dynamics over time both radially and axially in the stem and for the variations in WSG. It can be concluded that the apical and cambium meristems over time contribute to the increase in WSG. The Low spatial correlation can imply that a spatial point used to estimate a representative WSG value for the whole tree may be erratic. This has implications for estimating biomass.

With the Kronecker product correlation model, it is possible to mode and understand the radial and axial physiological correlation patterns of wood production. This model could be useful in growth and physiological models for plants. We are optimistic that elucidating this underlying correlation structure will provide insights into the evolution of wood formation. The correlation function provides information about how large the fluctuations in the wood formation and thus the WSG during tree growth and development.

# CHAPTER 5

# SPATIOTEMPORAL VARIATION AND COVARIATION OF HEARTWOOD COLOR IN PLANTED TEAK FROM GHANA

## 5.1 Abstract

Heartwood color is a complex trait that affects the economic and aesthetic value of the wood but is highly variable. How the color of the heartwood varies spatially and temporally is poorly understood. To illustrate how heartwood color varies within a tree, two opposite sides of the same tree, representing differential growth rate, were used to model the long-short axis system jointly. The color of the heartwood on the long and the short axis was considered to be two different traits. By jointly modeling the long-short axis, we examined the correlation between aspect (spatial) and contemporaneous correlations (within aspect). Spatial and temporal correlations and their interactions describe the indirect physiological, genetic, and environmental changes in wood formation with time and position in the trunk. Spatial correlations were consistently lower than temporal correlations but were positive and significant. Between the heartwood color parameters, $b^*$ showed a relatively higher spatial correlation. The results suggest that there is a spatial correlation in the long-short axis for all color parameters and in the two surfaces. Variations between aspects were not statistically significant for any color parameter. The bivariate mixed model method reveals the hidden physics behind heartwood color formation. Models need to be developed to account for both spatial and temporal dependence in studies of wood property change.

**Keywords:** Bivariate mixed models; CIE L*a*b*; Dependencies; Spatiotemporal process; Teak; Wood quality

## 5.2 Introduction

Wood formation in a tree occurs in a spatiotemporal sequence (Fayle 1973) involving the space element (radial or axial position in the tree) and the time element (age: beginning, yearly changes, and the end of wood formation). Wood layers increase in the quantity and quality around and along the tree stem, increasing variability and dependency over time. These two elements are integrated to form a shape/continuum as a tree by sharing some common functions *e.g.*, physiology and genetics that create correlations during growth. These correlations according to Fritts (1976) and Larson (1969) are physiological correlations and or genetic correlations (Savidge 2003). The correlation function between the spatial and temporal elements of tree growth determines the spatiotemporal structure of tree development. To gain insight into the growth process of the tree, an analysis of changes in wood properties evaluated across the wood core should be able to model changes in variance and covariance over time. The environment is the main cause of fluctuations in wood quantity and quality, as environmental conditions are not constant over time or space (Larson 1964; Burdon 1977; Bell and Lechowicz 1994).

Trees exhibit an intriguingly complex plasticity in adapting to their environment because of their sessile fate (Larson 1964; Bell and Lechowicz 1994; Friml 2003). One of these plasticities is the differential wood production around and along the trunk known as eccentricity. Eccentric radial growth induces pronounced growth in one direction than in others occurring mostly in stems and branches. Trees correct imbalance mechanical loading induced by asymmetrical distribution of crown weight which may lead to differential tension stresses and differences in illumination (Williamson and Wiemann 2011). According to Cote and Day (1965), the longer-axis lignification occurs least or not at all in hardwoods. Eccentricity can be viewed as an inherent evolutionary mechanism of tree’s response to environmental heterogeneity (Bell and Lechowicz 1994; Pruyn *et al.* 2000). A wood trait in eccentric stems may vary, although the cambium genotype is thought to be constant throughout the stem (Taylor 1968; Savidge 2003). The variations are the nature of gene expression in different physical and chemical environments to which the cambial cells are exposed (Pruyn *et al.* 2000; Savidge 2003). Eccentricity presents an interesting possibility to clarify the effect of environment on cambium genotype. Correlation between the two sides of the same tree can represent the extent to which a given trait shares the same genetic basis when measured in different aspects/environments (Via 1984; Via 1991). The effects of environmental variability on genetic covariation of traits are poorly understood in tropical tree species. The evolution of wood traits depends not only on the extent of variation of individual traits, but also on the pattern of covariation (Lande 1979; Lande and Arnold 1983). When we recognize trees as a space-time continuum, we must consider these sources of variation (Larson 1969).

Teak is a prime exotic species in Ghana, reportedly planted on approximately 250,000 ha (FAO 2010; Apertorgbor and Roux 2015). It is valued for its texture and aesthetic trait, especially that of the heartwood. Heartwood in teak is believed to initiate at between 4 to 6 years (Moya *et al.* 2014) after the living functional cells die (Hillis 1987). Two main chemical constituents, namely tectoquinones and anthraquinines, in heartwood play an important role in the biological resistance of the wood (Rudman and Gay 1961; Sumthong *et al.* 2006; Lukmandaru and Takahashi 2009; Niamke *et al.* 2011; Gasparik *et al.* 2019). Wood color like any other trait can vary widely within the tree. The drivers of these variations are known to be either spatial factor (position in the tree; height, radius), the growth rate of the tree, and the age of the tree (Rink 1987; Klumpers *et al.* 1993).

Little is known about the variation of heartwood, the effect of spatial variation in environment on heartwood color, and its pattern of change. This is particularly an issue for teak grown in Ghana, where more research is needed. It is the purpose of this paper to describe such variations using mixed modeling techniques. A mixed bivariate model is developed for heartwood color variations representing two opposite sides of the same tree. The approach allows assessing the association between the two sides for a trait that can provide better insight into wood biology. Specific questions were: (1) Does spatial autocorrelation exist in eccentric heartwood color data? (2) How strong is the spatial autocorrelation? We strongly believe that this approach is key to understanding heartwood color variation within-stem variation and would serve as a starting point to improve heartwood color uniformity, which is a fundamental requirement for suitable wood, particularly of planted trees. This study focuses on the correlation analysis between the two opposite sides of the same tree and its evolution over time. This approach may be able to capture both genetic and environmental factors affecting heartwood color variations.

## 5.3 Materials and Methods

### *5.3.1 Sampling*

All samples were collected from a private teak plantation with a spacing of 3 m × 3 m near Dormaa Ahenkro in the Bono region of Ghana. Three trees were selected at 18 years of age. 10 cm thick discs were prepared from each tree at 1.0 m intervals starting at 0.3 m above ground level until 5.3 m height level. Two opposite sides were randomly selected from these discs. The selected sides were eccentric by a factor of at least 1.3. The two orthogonal radii represent the long and short axis of the tree at a given height. A radial strip (2 cm in the tangential direction and 3 cm thick in the longitudinal direction) was cut from each radius for analysis of the wood properties. The strips were air-dried at 20°C and 65% relative humidity for several weeks to a dry-base moisture content of 12%.

### *5.3.2 Wood color measurement*

The colorimeter used to evaluate the color of the wood was a Nippon Denshoku NR-3300 (Tokyo, Japan) with a measuring aperture diameter of 10 mm. The instrument was placed to record a sample representative of the strip surface from the pith outward at 1.0 cm intervals. A D56 standard illuminant and the 2° standard observer (daylight observation at 6500 K) parameters were also used. The color coordinates $L^*$, $a^*$, and $b^*$ were recorded. A total of 230 and 231 measurements were recorded for the cross-sectional (CS) and longitudinal-radial (LR) surfaces, respectively. Here, $L^*$ refers to lightness, $a^*$ refers to redness, and $b^*$ refers to yellowness. The color difference denoted as $\Delta E^*$, expressed as the distance between two points in the color coordinate system, was used to assess the uniformity of the color between the two opposite sides (aspects) and between the two surfaces. The equation for the total color difference $\Delta E^*$ is given by Eq. 1 according to Tappi (1994):

$$\Delta E^* = (\Delta L^{*2} + \Delta a^{*2} + \Delta b^{*2})^{0.5} \quad (1)$$

Where:

$\Delta L$ is the difference in the lightness

$\Delta a$ is the difference in the $a^*$ coordinate

$\Delta b$ is the difference in the $b^*$ coordinate

### *5.3.3 Statistical analysis*

#### *5.3.3.1 The linear mixed-effects model*

Heartwood color data represent a spatiotemporal repeated measurement on a tree. The properties on related trees and aspects are subject to correlations at any time due to shared genetic, physiological, and environmental effects. In addition, the wood properties of related trees at different points in time are also correlated due to the above factors. The long-short-axis data consists of two components representing spatial and temporal dependencies. By modelling the long-short axis data together, 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 process of heartwood color formation for the two aspects.

A general linear mixed model has the form (Laird and Ware 1982; Henderson 1984; Searle *et al.* 1992) as shown by Eq. 2:

$$y = X\beta + Zb + \varepsilon, \quad (2)$$

$$b \sim N(0, G)$$

$$\varepsilon \sim N(0, R)$$

where $y$ is the vector of observations, $\beta$ is a $p \times 1$ vector of fixed effects, $X$, $b$ is a $q \times 1$ 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[$y$] = $X\beta$, var[$b$] = $G = \sigma_b^2 A$ and var[$e$] = $R = \sigma_e^2 I$ for A the numerator relationship matrix and I an identity matrix.

### 5.3.3.2 Bivariate analysis

In the bivariate case, the Eq. 2 was expanded to accommodate color trait values in the two aspects (stacking up the vectors), in such a way that β, b, and ε now contain the values for both radii (aspects).

$$\mathrm{z} = \begin{bmatrix} \mathrm{Z}_1 & 0 \\ 0 & \mathrm{Z}_2 \end{bmatrix};\ \mathrm{b} = \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix};\ G = A \otimes G_0;\ R = \mathrm{I} \otimes \mathrm{R}_0 \tag{3}$$

(The symbol ⊗ 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.

$$\mathrm{G}_0 = \begin{bmatrix} \sigma_{\mathrm{b}_1}^2 & \sigma_{\mathrm{b}_{12}} \\ \sigma_{\mathrm{b}_{21}} & \sigma_{\mathrm{b}_2}^2 \end{bmatrix};\ \mathrm{R}_0 = \begin{bmatrix} \sigma_{\varepsilon_1}^2 & \sigma_{\varepsilon_{12}} \\ \sigma_{\varepsilon_{21}} & \sigma_{\varepsilon_2}^2 \end{bmatrix}, \tag{4}$$

where $\sigma_{\mathrm{b}_1}^2$ and $\sigma_{\mathrm{b}_2}^2$: variances of the aspects 1 and 2, respectively.

$\sigma_{\mathrm{b}_{12}}$: random treatment effects of covariance between aspects 1 and 2.

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

Note that the two aspects are independent under joint normality if $\mathrm{G}_0 = \begin{bmatrix} \sigma_{\mathrm{b}_1}^2 & 0 \\ 0 & \sigma_{\mathrm{b}_2}^2 \end{bmatrix}$. This implies there is no correlation at all between means of the trait in the two aspects.

The Pearson correlation ($\mathrm{r}_{12}$) between the two aspects were estimated using the standard formula from the long-short axis variances and covariance components as:

$$\mathrm{r}_{12} = \frac{\mathrm{Cov}(\mathrm{b}_1,\mathrm{b}_2)}{\sqrt{\mathrm{var}(\mathrm{b}_1)\mathrm{x}\mathrm{var}(\mathrm{b}_2)}} = \frac{\sigma_{\mathrm{b}12}}{\sqrt{\sigma_{\mathrm{b}_1}^2 \mathrm{x}\, \sigma_{\mathrm{b}_2}^2}} \tag{5}$$

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.

The coefficient of variation (CV) is given $CV = \sqrt{\sigma^2}/_{\mu} \text{ x } 100$ (6)

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

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

$$\begin{bmatrix} \sigma_{b_1}^2 & \sigma_{b_{12}} \\ \sigma_{b_{21}} & \sigma_{b_2}^2 \end{bmatrix} \otimes \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} = \begin{bmatrix} \sigma_{b_1}^2 * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} & \sigma_{b_{12}} * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} \\ \sigma_{b_{21}} * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} & \sigma_{b_2}^2 * \begin{bmatrix} 1 & \rho & \rho^2 \\ \rho & 1 & \rho \\ \rho^2 & \rho & 1 \end{bmatrix} \end{bmatrix} \quad (7)$$

The models in this paper were implemented in PROC MIXED from SAS 9.04 (SAS Institute, Cary NC) and solved using Restricted Maximum Likelihood (REML). In the modelling, the Kenward-Roger method (Kenward and Roger 1997) was used to determine degrees of freedom. The REML variance components were estimated. The homogeneity and normality of the residuals were checked to ensure that the assumptions were met by visual inspection, as per Schabenberger (2004). The F-test was used to determine the statistical significance of fixed effects ($\alpha = 0.05$). Repeated measures ANOVA in which three types of heterogeneity (*i.e.*, mean, variance, autocorrelation) are considered as follows:

$$Y_{ijk} = m + a_i + r_j + (a \text{ x } r)_{ij} + \varepsilon_{ijk} \quad (8)$$

Where $Y_{ijk}$ denotes individual color parameters ($L^*$, $a^*$, $b^*$) for a tree k = 1, …, 3 at a distance from the pith (DFP) $r_j = 1, \ldots, 10$ along aspect $a_i = 1{,}2$ at a given height level, $m$ is the overall mean and $(a \text{ x } r)_{ij}$ is the interaction of aspect and distance from the pith. The experimental error is denoted by $\varepsilon_{ijk}$. The spatial and temporal variations of the color parameter within and between trees was statistically evaluated using an ANOVA approach. Spatial heterogeneity was explained by aspect factor, while the distance from the pith factor accounted for temporal heterogeneity. After fitting the model, we simulated the bivariate data to create plots using the Eigen decomposition method. Aspect 2 (short axis) trait values were plotted against Aspect 1 (long axis). A regression line of aspect 2 against aspect 1, included in the bivariate variance structure for the evolution effects was drawn. The slope is given by Eq. 9

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

## 5.4 Results and discussion

### *5.4.1 Differences in Heartwood Color Between Surfaces and Aspects*

The mean color values and their standard deviations are presented in Table 1. These values compare with those reported from teak grown in Ghana (Derkyi *et al.* 2010) and elsewhere (Thulasidas *et al.* 2006; Moya and Calvo-Alvarado 2012). The two radii and surfaces were not identical, but the differences are neither significant statistically. The REML estimates of the variances of heartwood color traits for the two aspects are shown in Table 2. The variances for aspect 1 were almost as large as that for aspect 2 for $L*$ in the LR surface, $a*$ and $b*$ in the CS surface. The covariance estimates were positive for all color parameters indicating the relationship between the aspects may be positive. Color can change more in one spatial dimension than the other illustrating how plastic color traits are. Coefficients of variation (CV) were consistently larger for $a*$, particularly in the LR surface (>30%) and in the CS surface (about 18%). The color parameter $L*$ showed the lowest CV (8% to 10%). The CV was about 9% to 14% for $b*$. The luminance index ($L*$) was higher on the fast-growing axis than on the slow-growing side of the LR surface, while the opposite was true on the CS. This is consistent with the assumption that fast-growing side may be lower in lignin content. Lignin is known to absorb visible light (Hon and Minemura 2001). Luminance variability (*i.e.*, darkness or lightness) may be the primary source of variability in teak heartwood (Phelps *et al.* 1983). The color difference between the two radii can be attributed to the differential growth rate of cambium around the axes. This is consistent with Rink's (1987) findings on black walnut that growth rate can affect heartwood color. The wood color difference between aspects on the LR surface was 0.46 and 2.88 in the CS. On the LR surface, the difference means little or no color difference, while on the CS a color difference is perceived rarely accepted (Buchelt and Wagenfuhr 2012). The wood color difference between the LR surface and CS surface was $\Delta E*$ = 4.65, which means the difference is significant (Buchelt and Wagenfuhr 2012). In this regard, teak heartwood surfaces may need to be graded in applications where a homogeneous color is desired. The color non-uniformity observed between the surfaces may be attributed to the pattern of wood cell arrangement in the two surfaces (Hon and Minemura 2012) and the variation in the quality and quantity of extractives (Keey 2005).

### *5.4.2 Spatial and Temporal Relationships*

The association of traits in the two opposite sides is determined by correlations at two different levels: between- and within- aspect correlations. The underlying drivers of these correlations are physiological, genetic, chemical, and environmental mechanisms. The correlations between the aspects (*i.e.*, *purely spatial*) were 0.18, 0.04, 0.33 for $L^*$, $a^*$, $b^*$, respectively in the LR plane and 0.16, 0.22 and 0.36 for $L^*$, $a^*$, $b^*$, respectively in the CS plane. These associations represent the mean values of the characteristics in the two aspects. These correlations were highly significant (see Table 3). The $b^*$ color parameter showed a relatively stronger spatial correlation in both wood surfaces *i.e.*, 0.33 and 0.36 for LR and CS. The positive correlation means that two characteristics are usually associated with each other, *i.e.*, they move together. Also, the positive spatial correlation implies that the growth rate may not have an adverse impact on the color of the heartwood in teak. The contemporaneous correlations (*i.e.*, *purely temporal*) or the correlations within an aspect measure the strength of the association between the change in one aspect between time lags and the corresponding change over the same time in the opposite aspect. The within-aspect correlations were 0.70, 0.67, 0.69 for $L^*$, $a^*$, $b^*$ in the LR plane and 0.71, 0.75 and 0.78 for $L^*$, $a^*$, $b^*$ in the CS plane. These correlations were highly significant. These correlations clarify the physiological basis for tree growth and development (Larson 1969; Fritts 1976). The wood color formed at the same presumed time on the opposite sides shows a stronger similarity or resemblance as opposed to wood color being poorly correlated with distance (between aspect). This may give an indication that the wood color can be controlled temporally in teak. The spatial and temporal autocorrelations indicate the spatiotemporal nature of wood formation. The two autocorrelations and their interactions show that the development of wood features is more complex. Spatial correlations can be employed to predict changes in color traits when selecting one aspect.

### *5.4.3 Measurement Associations of Heartwood Color Traits Between Aspects*

The degree of association between two heartwood color parameters was measured by the regression coefficient. This expresses the change in trait 2 (aspect 2), in units of measurement, for each unit change in trait 1 (aspect 1). The estimated slopes were 0.15, 0.19, 0.30 for $L^*$, $a^*$, $b^*$, respectively on the CS surface (see Figs. 1a, b, c). On the LR surface, the gradients were 0.17, 0.04, 0.26 for $L^*$, $a^*$, and $b^*$, respectively (see Figs. 2a, b, c). The coefficients of determination were 3%, 0.15%, 10.7% for $L^*$, $a^*$ and $b^*$, respectively for LR surface. For the CS surface, coefficients of determination were 2.7%, 4.9%, 13.2% for $L^*$, $a^*$, and $b^*$, respectively. The slope was consistently similar for $L^*$ on both surfaces. The color parameter $b^*$ recorded the highest slopes. This is likely to have resulted from the soil chemical constituents.

### *5.4.4 Effects of Growth Rate on Wood Color Parameters*

To assess the effect of growth rate on color parameters, Type 3 fixed effects were applied, and the results are presented in Table 4. Differences between the aspects can be viewed as effects caused by differential growth rate (Taylor 1968; Williamson and Wiemann 2011). For all color parameters, the effect caused by aspect was not significant. This gives us an indication that growth rate may not be a statistically important factor in controlling teak heartwood color. Distance from the pith (DFP) was a significant factor for $a^*$ and $b^*$ in the LR surface and $L^*$ in the CS surface. The DFP as a factor controlling pith outwards variation of color parameters can be explained by the temporal degradation of previously formed extractives (Hillis 1987).

### *5.4.5 Overall Findings*

The answers to the two questions from this study are: (1) spatial correlation exists in heartwood color data from trees exhibiting eccentric growth and (2) spatial correlation was significant statistically but of low order ($< r = 0.5$) in all color parameters measured in the two surfaces. The bivariate analysis allows us to assess the variations and covariations in the two aspects jointly. In our analysis, the variances for both aspects were non-zero for all traits (see Table 2). Variations in the color of the heartwood showed strong plasticity, implying that the color of the heartwood can change more in one aspect than in the other. The correlations between the two aspects were positive but of low order, less than 0.5 (Sokal and Oden 1978) for all color parameters in the two surfaces. This indicates that the color of the heartwood in teak can be affected by the environment and that they can have some degree of independent evolution which can be judged by the relatively lower slopes. This can be attributed to the differential rate of cambium production in the two aspects. The discs showed an average factor of 1.3 in eccentricity. Positive spatial autocorrelation can be attributed to microsite influences (Matern, 1947). The microsite effect creates a positive spatial dependency because opposite sides of the same tree are subject to similar environmental conditions. From the purely spatial correlations, we can infer that the $L*$ and $a*$ color indices are more influenced by the heterogeneity of environmental conditions, which is consistent with Derkyi *et al.* (2010). The heartwood color parameter $b*$ can show a stronger microsite effect than the others. This agrees with the results of Moya and Calvo-Alvarado (2012). Teak yellowness ($b*$) is reported to correlate positively with soil pH, calcium, magnesium but negatively with potassium, iron, and phosphorus (Derkyi *et al.* 2010; Moya and Calvo-Alvarado 2012) although the brightness parameter $L*$ is known a better indicator of the durability of teakwood (Niamke *et al.* 2021). We found an interesting pattern in the brightness parameter; it was lower in the LR and CS surfaces for slow-growing and fast-growing sides, respectively. Because the color of the heartwood in teak is affected by secondary metabolites and the extractive chemical composition, we expect the proportion of the durability of the heartwood to be different even in the same tree at a specific height level. Also, some genes change gradually over time (Olesen 1978; Namkoong et al. 1988). In our case, it can be assumed that 'genetic' correlations are due to pleiotropy rather than linkage equilibrium (Falconer 1952). Pleiotropy is simply the property of a gene, whereby it affects two or more traits, while linkage is more applicable to crosses between different strains (Falconer 1989), which should not be applicable in this study. When breeding for heartwood color in teak in Ghana there may be a relatively higher tendency towards heritability in the $b^*$ color index. The positive correlations can be interpreted to mean that, at the spatial level, environmental conditions that enhance a color trait in one aspect enhance the opposite aspect. Heartwood may be under heavy environmental control. The existence of significant spatial correlations raises an important problem with respect to the widely used traditional analysis method, namely regression analysis, which assumes error independence. This should be a warning to wood technologists who dismiss spatial and temporal dependencies as unworthy. It is important to realize that all assessments of wood quality are statistical and can be confusing unless the biological sources of variability are accounted for and explained (Larson 1969).

| | Longitudinal Radial Surface | | | Transverse Surface | | |
|---|---|---|---|---|---|---|
| Aspect | *L** | *a** | *b** | *L** | *a** | *b** |
| 1. Long | 50.43±5.20 | 9.70±3.39 | 17.56±1.85 | 49.43±4.93 | 14.77±2.74 | 16.98±2.38 |
| 2. Short | 49.59±4.77 | 9.97±3.81 | 17.51±1.85 | 49.85±4.46 | 14.32±2.51 | 17.43±2.28 |

**Table 1:** Heartwood Color Parameters in the Long and Short Axis for Longitudinal Radial and Transverse Surfaces *(Average ± Standard Deviation)*

| | | Error Variance | | | Autocorrelation | |
|---|---|---|---|---|---|---|
| Surface | Color Parameter | Aspect 1 | Aspect 2 | Covariance | Spatial Between-Aspect | Temporal Within-Aspect |
| LR | L* | 24.43 | 25.90 | 4.65 | 0.18 | 0.70 |
| LR | a* | 11.18 | 13.03 | 0.47 | 0.04 | 0.67 |
| LR | b* | 4.05 | 2.84 | 1.11 | 0.33 | 0.69 |
| CS | L* | 16.95 | 18.29 | 2.88 | 0.16 | 0.71 |
| CS | a* | 6.65 | 6.14 | 1.41 | 0.22 | 0.75 |
| CS | b* | 5.99 | 5.54 | 2.10 | 0.36 | 0.78 |

**Table 2:** The REML Estimates of the Model Parameters

| Surface | Color Parameter | Correlation | *P value* | 95% Confidence Interval | |
|---|---|---|---|---|---|
| LR | L* | 0.17 | <0.0001 | 0.14 | 0.19 |
| LR | a* | 0.03 | 0.0151 | 0.01 | 0.06 |
| LR | b* | 0.32 | <0.0001 | 0.28 | 0.33 |
| CS | L* | 0.14 | <0.0001 | 0.12 | 0.17 |
| CS | a* | 0.20 | <0.0001 | 0.17 | 0.23 |
| CS | b* | 0.34 | <0.0001 | 0.32 | 0.37 |

The 95% confidence interval evaluates the uncertainty in the correlation parameter. Spatial correlations are significant because none contains 0.

**Table 3:** Pure Spatial Correlation (Simulated 5000 times)

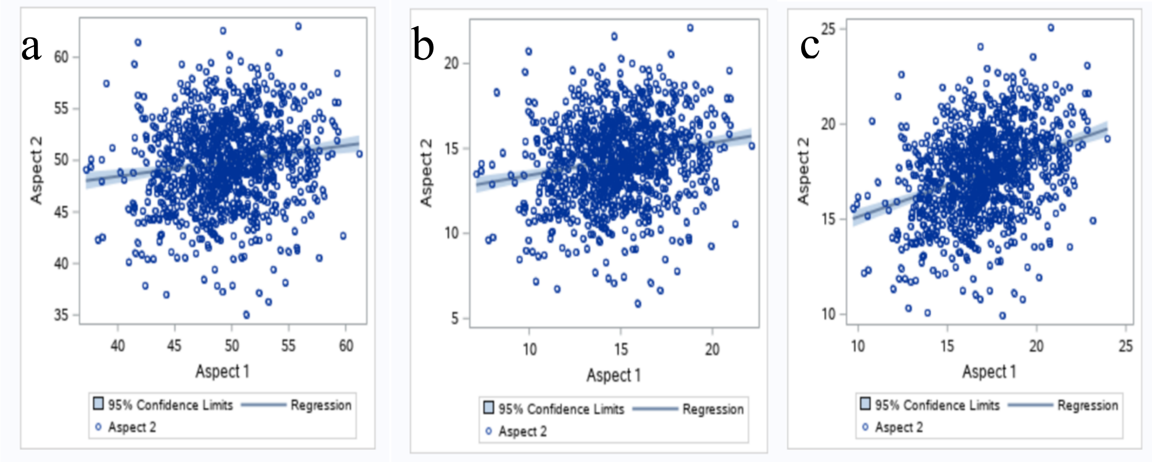


**Figure 1:** Scatter plot illustrating the association between Aspect 1 and Aspect 2 (a) *L**, (b) *b**, and (c) *a** in the CS surface.

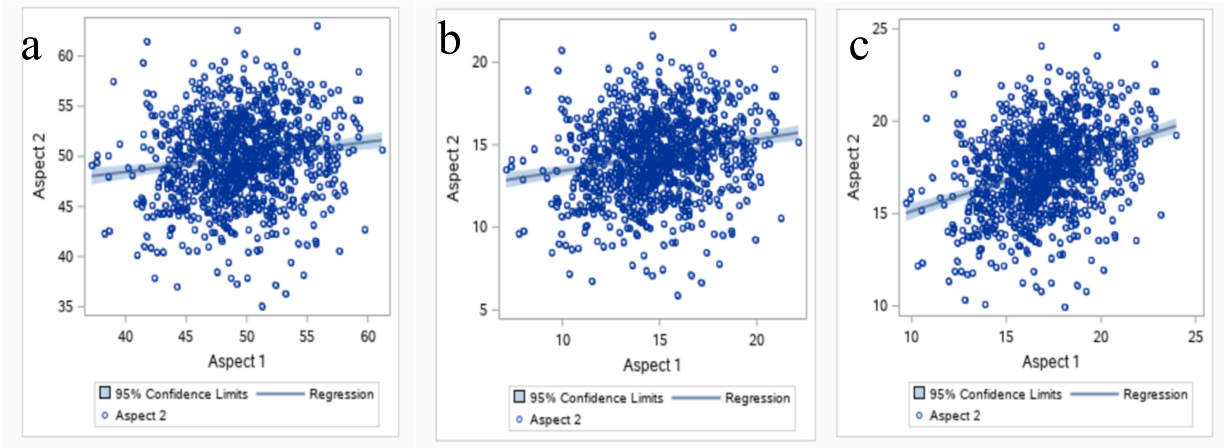


**Figure 2:** Scatter plot illustrating the association between Aspect 1 and Aspect 2 (a) *L**, (b) *b**, and (c) *a** in the LR surface.

## 5.6 Conclusions

1. A bivariate approach to test associations of wood traits measured over time from the same tree exhibiting eccentric growth could be a useful approach to clarify the variation and correlation structure of wood traits between the long-short axis at a time and over time.
2. The bivariate modelling approach employed in this study is an attractive method of linking information both in space and time. Variations in spatial factors present no problems in this approach and could be a very useful follow up for detailed interpretation of wood formation pattern.
3. The correlation between aspects and the error correlation reveals the underlying physiological mechanism in wood formation. The within-subject error correlation was relatively higher than the between-subject correlations. Considering both spatial and temporal autocorrelations can improve models and avoid biased results and misinterpretations.
4. Heartwood color measured on opposite sides of the same tree shows a positive but low correlation (average $r \sim 0.22$). These results indicate that it may not be appropriate to use a core to determine heartwood color for the whole disc sampled at a specific height.
5. The color parameter $b^*$ can have relatively low to moderate heritability and can be better than $L^*$ and $a^*$. The presented results are preliminary and need to be evaluated in future studies with a larger sample size.

# CHAPTER 6

# GENERAL DISCUSSIONS, CONCLUSIONS AND FUTURE WORK

## 6.1 General discussions and conclusions

This thesis represents the first comprehensive attempt to develop models for wood properties and to describe the patterns within individual trees from stump to top and from pith to bark.

I conclude this work by highlighting its major contributions arising from a combination of different fields of knowledge, including statistics, tree physiology, and wood science. I will also offer some thoughts on future research directions based on the main limitations.

Forestry and wood-related datasets are often multi-dimensional and non-stationary i.e., mostly collected in space i.e., aspect and/or height levels and over time and the variability evolves over time and its relativity according to position in the tree trunk. In this thesis, a dataset with properties of teak in two directions (radii), at six height levels and in ten relative radial positions was collected. Direction and height are spatial factors, with relative radial positions considered as a temporal factor. Consequently, the tree was viewed as a spacetime continuum to estimate the extent of variation within trees. The concept of spacetime continuum is relevant to understanding the statistical relationships with wood formation. It has long been known that variability in wood formation results from physiological gradients down the stem from the crown (Larson 1969) and that there is a correlation between hormonal expression, cambium activity and wood property response (Lachaud 1989). They are a source of variation that is largely ignored in the wood quality literature. Random effects were introduced to capture these hidden sources of variation termed “physiological growth correlations” by Larson (1969).

Chapter 3 modelled the serial correlation (within-tree error) in the WSG data and provided insight into the selection of an appropriate correlation structure. A variety of correlation structures were tested to account for autocorrelation within the tree i.e., temporal correlation function. First order autoregressive with random tree effect was the best correlation structure. The random tree effect incorporates inter-tree spatial correlation into the model, which significantly improved model performance. It is therefore logical to assume that environmental influences can have some influence on teak WSG. The serial correlation was significant. This serial correlation can be viewed as the evolution and maturation mechanism of the vascular meristem. The vascular cambium is known to undergo modes of maturation, namely (1) those transmitted from the apical meristem to the cambium as it forms, and (2) those which the cambium undergoes after formation (Olesen 1982). The difference in growth rate was not statistically significant. Teak WSG is largely controlled by the temporal factor (tree age) rather than growth rate. The WSG profile pattern was the same between the slow and fast-growing sides of the same tree. However, the time to reach the mature (outer) wood phase was shorter on the slow-growing side and thus the volume of core (juvenile) wood was relatively smaller. Increased growth rates in the young stage can lead to a large volume of core wood formation and deterioration in product quality.

In Chapter 4, I proposed a novel spacetime model for the analysis of longitudinal WSG variation. In this model, temporal autocorrelation captures vascular meristem dynamics, and the 'Unstructured' correlation structure accounts for the spatial inter-relationships of apical meristem activity (height levels). The relationship between apical and vascular meristems was modelled as a Kronecker tensor product. This model can capture the various morphological and physiological properties that change with both height and diameter in the tree during wood formation. When sampling wood along the trunk, it cannot be assumed that the height levels are independent. It is relevant to provide a dependency structure that assumes that the correlation occurs as measurements that are distant in space or time. The dependencies may relate to the way the tree increases in height as it grows. To the best of my knowledge, this model is the first mixed-effects model capable of capturing and providing insight into both spatial and temporal information from WSG data. The model presented in Chapter 4 provides insight into the biology or physiology of primary growth by describing the relationships between height/primary growth sites. The model takes much better account of the growth and physiology of the tree. The model can be used to make predictions about the biomass at height at the top of the trunk, the predictions suing knowledge about the biomass at the lower height levels, particularly at 1.3 m. Importantly, an age-related decline was observed as the tree began to produce high WSG, which were thought to correlate with a decrease in tree vigor over the tree's lifetime. Therefore, the observed decline leads to some potential impacts on (1) forest management, as silvicultural interventions (e.g., commercial thinning, pruning) could mitigate the impacts of decline by stimulating growth, and (2) estimates of above-ground biomass under or overestimated for teak if WSG is introduced as a constant value in allometric equations.

In Chapter 5, I presented an approach to elucidate the effect of eccentricity on heartwood color by capturing the spatial autocorrelation between the two radii and the contemporaneous correlation between the two radii in the model was accounted for by defining an appropriate within tree error.

It was observed that there are significant spatial and temporal autocorrelations in the residuals. Models should be developed in order to be able to capture these sources of error in wood quality assessment. The spatial autocorrelation was relatively smaller than the temporal autocorrelation for all color parameters. This implies that the color between the two opposite sides of the same tree is not strongly connected. This affects the wood sampling strategies. Sampling one side of the tree cannot be considered representative of the disk or entire tree. Importantly, growth rate had no significant impact on heartwood color variation in teak. A positive spatial autocorrelation implies that heartwood color is subject to a strong microenvironment effect.

These three main chapters gave insights into the physiological aspects of wood formation and thus WSG and heartwood color when modelling the wood properties and their intra- and inter-dynamics across the tree trunk.

## 6.2 Physiological basis for teak wood specific gravity

Specific gravity (SG) is affected by changes in dry matter allocation. High SG is formed at later stage with loss of vigor (age-related decline). High SG in teak is associated with an increase in fiber wall thickness and narrow cell diameter at the anatomical level and decreasing levels of precipitation (Dié et al 2012). Plant size and nutrient concentration are closely related during plant growth. Drechsel and Zech (1994) observed a decrease over time in nitrogen and phosphorus in the leaves of teak planted throughout West Africa and Fernandez-Moya et al. (2013) found decreased levels of nitrogen and phosphorus over time in teak trunks grown in Costa Rica. We might be tempted to think that the loss of vigor is caused by declining levels of these macronutrients especially, phosphorus. The declining nutrient content in the foliage could be attributed to the leaf maturation (Aloni 2011). Gibberellin from mature leaves promotes vascular cell elongation, which contributes to the gradual increase in xylem cell dimensions. Aloni (2011) further noted that mature leaves are also a major source of photosynthetic assimilate needed for increasing secondary cell wall deposition typical to mature wood. For these reasons we can believe that hormones, nutrients, and water conduction needs may be the main underlying drivers of changes in cell dimensions and hence wood specific gravity. When young, high levels of auxin and phosphorus promote cell division and differentiation, which keeps cells small due to rapid differentiation or division, as new cells require phosphorus for nucleic acids, membranes, and energy supply during formation. This leads to the formation of fibers with thin-walls and large lumen diameter. When the tree loses its vigor, as the phosphorus becomes limited, cell differentiation slows down, they incorporate assimilates into the cell walls of new and old cells to produce cellulose microfibrils, resulting in fewer but thick-walled fibers.

## 6.3 Future work

The above work provides informative knowledge to unravel the confounding sources of variation and clarify the physiological aspects of wood formation. However, there are still several sources of variation that are not fully understood. To help us better understand the relationship between wood physiological processes and WSG, more efforts need to be made in the future as suggested below:

1. Model confirmation. The models developed in this study should be tested for their applicability to the wider cultivation of teak in West Africa. Cross-validation of all models can provide a measure of their universality and an indication of the similarity of teak cultivation response in different parts of West Africa to determine whether the same pattern of change in correlations is observed or not in other planted teak trees, under the same or different conditions.
2. At the height level of 2.3 m, a significantly lower WSG was determined. Future studies should be conducted to investigate the possible cause of this phenomenon and how carbon is allocated to the height level.
3. The data set was 3-dimensional, however, the analyses used in this study were 1-dimensional and 2-dimensional. Future studies should focus on 3-dimensional modeling of wood properties.
4. The need to test the influence of environmental variables such as macronutrients, temperature, soil moisture and precipitation on tree growth and timber quality. This will allow explicit connections to climate models to estimate the impact of future climate on teak wood quality for the rest of the century.

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# APPENDIX

Articles submitted to science citation index journals:

Chapter 3 submitted to Journal of Wood Science (Impact Factor: 2.658)

Chapter 4 submitted to Bioresources (Impact Factor: 1.747)

Chapter 5 submitted to Bioresources (Impact Factor: 1.747)