LINKING ENVIRONMENTAL VARIABLES TO THE REGIONAL VARIATION IN LOBLOLLY PINE SPECIFIC GRAVITY IN THE SOUTHEASTERN UNITED STATES

by

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(Under the Direction of Joseph Dahlen)

ABSTRACT

Wood specific gravity (SG) is correlated with many physical and mechanical properties and hence is a widely-used indicator of wood quality. Since dry wood contains around 49% carbon, the role of wood SG has emerged in assessment of carbon sequestration potential. Within tree stems, SG shows radial and vertical patterns of variability that are related with tree age, climate and various site conditions. Our goal was to develop a model that estimates ring SG of loblolly pine (*Pinus taeda*) as a function of cambial age and environment variables as independent variables. Pith-to-bark SG density profiles were obtained on 12-mm increment cores collected from 269 trees from 13 stands across the Southeastern U.S. using X-ray densitometry. We used the spatial coordinates of the stands to obtain interpolated climate variables for each year corresponding to the year of each growth ring. A four-parameter logistic base model was used to predict SG with cambial age as the explanatory variable. The base model was updated and modified using environmental covariates including annual indices for temperature and water deficit, and soil characteristics including permeability and depth to water table. The inclusion of environmental covariates improved the prediction by reducing root mean square error by 3.5 percent and decrease in AIC by 2% compared with the base model. Temperature positively affected both the upper asymptote and the point of inflection in the SG model, and water deficit was negatively related to SG. The model developed can be used to predict SG under contrasting conditions of climate and soil.

INDEX WORDS: annual rings, carbon sequestration, climate, dendrochronology, wood density, wood quality

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A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2017

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August 2017

ACKNOWLEDGEMENTS

I would like to thank everyone who contributed to the completion of my thesis. Firstly, I want to thank my major professor Dr. Joseph Dahlen for all his continuous guidance and advice for my research and all the opportunities he has provided throughout my graduate study. I appreciate the flexibility you offered for the selection of classes, my research ideas and personal development. I want to thank my committee members- Dr. Cristian Montes and Dr. Bronson Bullock, who provided me with needed resources, were always patient and willing to help me through all the process. Thank you, Dr. Montes, for all the valuable time you gave me out of your busy schedules and your guidance and motivation.

I want to acknowledge the Wood Quality Consortium (WQC) at University of Georgia, Athens for funding my research. I want to heartily thank Dr. Pradip Saud, New Mexico State University for guiding me at numerous points in time during the process. Thank you for taking time to respond to many little queries I had. I want to thank my friend Hector Restrepo, UGA for guiding me with the analysis and for reviewing my thesis. I am also grateful to my friend Mukti Ram Subedi, Texas A&M University, for taking time to review my analysis and writing.

Thank you to all the known/unknown scholars and academicians who showed their interest and provided feedback for my research presentations during multiple conferences. I also want to thank all the UGA faculty and TAs for their support in my studies, and all Warnell staff for the logistics and administrative support. How can I forget acknowledging Arnett C. and Ruth Mace for providing me their scholarship and motivating me to perform even better! Thank you for your generous support. Thanks to all my loving, caring and fun-loving friends at Athens, with whom I shared so much of wonderful moments of my graduate life.

Thank you to the major contributor, Mr. Rajesh Bista, my husband for always being there for me. Thank you for taking care of everything and making sure I had nothing to worry about besides my studies and research. I always pretended to be ignoring your motivational speeches but I know how immensely you have contributed to boost my confidence. Also, I cannot thank God enough for giving me a wonderful family-my mother and my sisters who always want to see me grow and succeed. Thank you for all your love, care and support.

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CHAPTER 1

INTRODUCTION

Loblolly Pine

The Southeastern United States forests represents 40% of U.S. timberland (Wear and Greis 2012), 50% of which is hardwood forests and 34% is planted by pine (Allen et al. 1996). There are over 12.9 million hectares of Southeastern pine plantations which are principal sources of softwood products in the United States (Jokela et al. 2010). The four major southern pines are loblolly pine (*Pinus taeda*), longleaf pine (*Pinus palustris*), shortleaf pine (*Pinus echinata*), and slash pine (*Pinus elliotti*), with loblolly pine being the most widely planted (Fox et al. 2007). Currently loblolly pine is a major raw material source for lumber, composites, pulp and paper, and energy. Forest plantations have been established because an extensive amount of wood and fiber is consumed by society and the growth rates from natural forests are not sufficient to meet these demands (Fox 2000). The widespread planting of loblolly pine is due to its ability to grow well on a variety of soils (Baker and Balmer 1983), easy regeneration, rapid growth rate, and responsiveness to intensive silviculture (Fox et al. 2007). Faster growth results in merchantable timber at reduced rotation ages which allows landowners to increase their financial return (MacDonald and Hubert 2002). However, as stand growth rate accelerates, concerns arise regarding wood quality from short rotation plantations (Kennedy 1995).

Wood quality

Wood quality is a subjective term that depends on the end product being referenced; different products requiring different properties (MacDonald and Hubert 2002). Overall wood quality is an aggregate expression of the physical (e.g., SG, moisture content, color, knots), mechanical (e.g., modulus of elasticity (MOE), and modulus of rupture (MOR) or strength), and anatomical (e.g., microfibril angle, tracheid wall thickness, tracheid length) properties of wood (Megraw 1985). Wood quality is a function of different factors such as species, climate and site conditions in which tree grows (Cregg et al. 1988), position within a tree at which it is produced, genetics of the planting material used (Zobel and Jett 2012) and the management regime. Faster growth rates from young intensively managed plantation, though desirable from yield perspective, may be accompanied by greater proportion of juvenile wood, lower overall wood densities, higher microfibril angles, lower cellulose and a higher lignin content (Saucier et al. 1990), thus affecting stiffness, strength and dimensional stability of timber (Kennedy 1995, Dahlen et al. 2014).

Wood Formation

Secondary xylem (wood) is formed by the vascular cambium and the cells form through various phases of development: cell division, cell enlargement and cell wall thickening (Plomion et al. 2001). In softwoods two types of distinct wood are formed each year. Earlywood is formed in the beginning of the growing season and is characterized by tracheids that have large lumens and thin cell walls. Latewood is formed in the latter part of the growing season when abundant amounts of photosynthate are available for secondary cell wall thickening. Latewood tracheids have small lumens and thick cell walls. The combination of earlywood and latewood constitute an annual ring (Larson 1969). Figure 1 shows the alternating SG bands of earlywood and latewood on a loblolly pine sample prepared for X-ray densitometry analysis. Larson et al. (2001) considered the growth hormone auxin, which is high in concentration in the uppermost part of the active crown, as the physiological driver responsible for the formation of earlywood and latewood. As the distance from the active shoot increases, the proportion of large earlywood cells gradually decreases (Lindstrom 1996). In the upper part of the bole, auxin levels are usually high enough to maintain relatively higher proportion of earlywood cells (Megraw 1985).

Figure 1: Loblolly pine pith-to-bark sample showing SG earlywood and latewood bands

Within a mature conifer, the wood has traditionally been separated into three types of wood: juvenile, transition and mature wood. Juvenile wood, formed by the immature cambium within the active crown is associated with wider ring widths that contain a low proportion of latewood, higher microfibril angles (MFA) and lower specific gravities. Mature wood is formed within the bole after canopy closure and within the regions not contained within the green crown (Clark III et al. 2006). Between the juvenile and mature wood zones is a region where wood properties are changing rapidly from juvenile to mature wood and is called transition wood (Burdon et al. 2004). While the distinction between juvenile and mature wood is based on phenomenon of ageing or maturation, Burdon et al. (2004) argues about the need of another categorization of wood i.e. corewood and outerwood. This characterization is based on radial variation of wood properties. Per Mora et al. (2007), the butt section of a tree contains juvenile corewood surrounded by juvenile outerwood. Going up the stem, there is an inner corewood of mature crown-formed wood that integrates into mature outerwood. The different types of wood produced by conifers results in considerable variation in the wood properties and wood quality (Burdon, et al. 2004, Jordan et al. 2008, Antony et al. 2011).

Specific gravity

Specific gravity is one of the most important wood quality traits due to its correlation with mechanical properties (e.g. modulus of elasticity (MOE), modulus of rupture (MOR), and hardness) and papermaking attributes (Panshin and Zeeuw 1980). SG is the total amount of woody material (cellulose, lignin, and hemicellulose) present in a given volume of wood compared to the density of pure water at 4° C (Smith 1954). In softwoods, there is a uniform and predictable variation in SG within a tree, the greatest of which lies within each annual ring. For loblolly pine, specific gravities as low as 0.25 are found in the earlywood while maximum values as high as 0.8 to 0.9 are found in the latewood (Megraw 1985, Antony et al. 2015). Going outward from the pith, latewood rapidly increases in proportion at all heights. For any given ring position from the pith, SG values are distinctly higher near the base of the tree and decreases with tree height. When factoring in this, average SG is a function of tree age, ring position from the pith, and height within the stem (Megraw 1985). Antony et al. (2010) found that disk SG follows a non-linear decreasing trend with relative height in conventionally managed loblolly stands without fertilization and weed control.

Megraw (1985) states that SG is a genetically controlled trait and in loblolly pine, a variation of approximately 0.15 to 0.25 units in heritability can be expected. Cumbie (2003) also found high heritability of 0.10 to 0.43 in loblolly pine full-sib seedling. Antony et al. (2013) estimated individual-tree clonal repeatability of 0.31 for whole-core SG, 0.31 for latewood SG, 0.28 for earlywood SG and 0.26 for latewood proportions for loblolly pine. They also found that SG was higher for clonal lines than full-sib and open-pollinated seedlings. Researches have looked at the variation in SG within the Southeast region (Megraw 1985, Jordan, et al. 2008). Jordan et al. found that the South Atlantic whole-core SG was significantly higher (0.486) with significantly higher latewood proportion (40.1%) compared to other regions. Megraw (1985) found that within the Southeastern pine range, SG is highest in the Southern and Atlantic coastal areas, that gradually decreases going inland to higher elevations. Researchers speculate that greater latewood formation due to extended growing seasons, higher summer precipitation and higher mean annual temperature in the southernmost latitudes to higher SG (Jordan, et al. 2008, Antony et al. 2010, Samuelson et al. 2013). These environmental factors along with available site nutrition influence the number and size of cells produced, thus affecting SG.

X-Ray Densitometry

X-ray densitometry is one of the technical innovations that has seen wide application in forestry research (Cown and Clement 1983, Jacquin et al. 2017). The underlying principle of X-ray densitometry is to measure the variation in the intensity of X-ray radiation as it passes through a wood sample and is then detected by a digital radiation sensor or exposed on a film. The amount of radiation received by the sensor or film depends on the density of wood and the thickness of the sample (Polge 1978, Jacquin, et al. 2017). Major components of this system consist of a radiation source, scintillator detector, sample carriage, pulse rate counter and a computer. It is a fast and non-destructive method of determining density of wood (Pagotto et al. 2017) and it has been widely applied for the generation of various wood quality data i.e., information on -ring SG, proportions of early/latewood, and ring-widths of many conifers. These information have been used to determine the transition age of SG from juvenile to mature wood (Clark III, et al. 2006, Mora, et al. 2007). Many studies have used densitometry to predict variation in different wood properties (Antony, et al. 2013, Auty et al. 2014, Moore et al. 2014, Eberhardt and Samuelson 2015, McLean et al. 2016). Densitometer data have been used to determine density responses to various silvicultural treatments (Antony et al. 2009, Love-Myers et al. 2009, Antony et al. 2011, Antony et al. 2012), use in dendroclimatic research to measure the climatic influence on conifer tree ring properties (Cleaveland 1983, Adams 2014, Sattler and Stewart 2016).

The process of preparing samples for running through densitometer differs by laboratories, species of interest, and age of material. Typically, material is dried and then depending on the objectives of the research the samples can be resin extracted. Eberhardt and Samuelson (2015) found that extraction did not have much impact on the individual ring profiles in three southern pines: loblolly (*Pinus taeda L.*), longleaf (*Pinus palustris Mill.*), and slash (*Pinus elliottii Engelm.*). The samples are machined to approximately 2 mm thickness on the radial or transverse surface by using a twin-blade saw.

The mass attenuation coefficient (MAC) is an important concept in X-ray densitometry. It is a measure of the absorption between the sample and the electromagnetic radiation source; which depends on the sample species, thickness, moisture content and its SG. Laboratory practices differ, some laboratories calculate the MAC for every sample, whereas others run the same MAC value for a given species. Changing the MAC also allows for adjusting the SG value to different SG values at differing moisture contents. The most common calibrations are air dry density (air dry weight / air dry volume), bone dry SG (oven dry weight / oven dry volume), and basic SG (oven dry weight / green volume). As wood passes through the scanner, the machine identifies the growth ring boundaries based on changes in SG and then assigns ring numbers and years to each ring. Data collected from X-ray densitometer include a) ring width information - start and end of ring, width of the latewood, percentage of latewood and width of the whole ring, and b) SG information - SG for earlywood, latewood and whole ring. After the sample is scanned and the rings marked by the computer, an operator analyzes the data by removing any false rings or inserting rings where density resolution was insufficient to trigger a boundary identification, which occurs frequently near the pith (Cown and Clement 1983).

Relation between climate and growth

Many researches have shown the relation between climate and forest growth (Toledo et al. 2011, Alvarez et al. 2012, Adams 2014). Tree growth varies with resource availability which vary over spatial and temporal scales, particularly with variation in temperature, solar radiation, and moisture. Temperature has a major impact on plant growth. The temperatures at which physiological processes go on normally in plants range from approximately 0°C to 40°C above and below which can cause disruption of physiological processes of plants and inhibit growth (Went 1953). Higher summer temperatures can result in higher evapotranspiration resulting in less amount of water available to plants, creating moisture-related stress in plants (Fritts 1976, Adams 2014). Cregg et al. (1988) in a study on 10 year old loblolly pine stand found that temperature was related to growth rate, low temperatures limited growth during spring and high temperatures limited growth in the summer.

Water availability is an important factor determining growth and quality. Precipitation and evapotranspiration determines the amount of water available in soil that can be extracted by plants. Water deficit conditions, especially during high summer temperature can be detrimental to plant growth (Nath et al. 2006). Tree responds to water stress by suppressing photosynthesis to avoid water loss during transpiration (Puritch 1973). A study by concluded that water availability during the growing season was major factor determining productivity of P. radiata in Chile and found that sites with low water deficits were more productive. On the other hand, excess water can also cause negative effect on plant growth due to the increase of respiration rate in water-logged condition (Pallardy 2010).

Solar radiation has been tied to forest productivity (Linder 1987, Cannell 1989, McCrady and Jokela 1998). Per Cannell (1989), wood production is determined by the efficiency of solar radiation interception and that extreme temperatures and severe draught can reduce light-use efficiency and hence biomass production. Water and nutrition availability is governed by the climatic and soil conditions and their effect is seen in growth (Rojas 2005) through their effects on photosynthetic efficiency (Linder 1987).

Effect of climate on SG

Physical, chemical and mechanical characteristics of wood vary across scale from within tree to regional level. At the tree scale, various tree characteristics and site conditions influence wood properties (Zobel and Van Buijtenen 2012) while at the regional level, climate has been identified as a key determinant of wood quality (Larson et al. 2001; Jordan et al. 2008; Zhang et al. 2011). Several studies have found a relationship of rainfall with wood density and ring width. Sarris et al. (2007) found that a decline in rainfall was associated with reduced tree-ring width in Pinus brutia. Filipescu et al. (2014) examined intensively managed Douglas-fir and found that ring SG slightly increased with increases in temperature and decreases in precipitation of some months during the growing season. Many studies have found variation in SG with latitude, longitude and elevation (Megraw 1985; Wiemann and Williamson 2002), which influence temperature, precipitation, solar radiation and soil water balance. Seasonal changes in the growing environment affect cambial activity thus affecting the duration and timing of secondary growth that in turn determines the duration and timing of earlywood and latewood formation and distribution of fiber properties within stem (Downes and Drew 2008). Schweingruber et al. (1978) in their study on different Swiss alpine trees including fir, beech, spruce, larch and pine, found that the maximum density was directly correlated to temperature during the growing season. Antony et al. (2010) determined that stands in the southern Atlantic Plain and Gulf Coastal Plain have the highest SG within the loblolly pine range and they speculate it is because of higher summer precipitation, higher mean annual temperature and a longer growing season. Wiemann & Williamson (2002) found that wood density was negatively correlated with mean annual precipitation and positively with mean annual temperature in their study of regional variation in SG in different angiosperms. Samuelson et al. (2013) found that the ring width was significantly related to precipitation during the dry season (May–September) in their study of wood properties of mature loblolly pine in Hawaii while also found positive correlation of SG with February to July temperatures and annual temperatures in northernmost sites of the Southeast. Initiation of latewood, which is a major determinant of SG, is promoted by moisture stress, causing presence of false rings in many conifers including loblolly pine (Cregg, et al. 1988). Gonzalez et al. (2010) showed that an increase in soil water availability was associated with an increase in whole-core SG by 0.036 and latewood proportion by 7% in 11-year-old loblolly pine in the Southeastern US.

CHAPTER 2

SIGNIFICANCE

Climate is one of the major factors that regulates forest growth. Potential climate change and the associated changes in temperature and precipitation may cause changes in growth rate, wood quantity and quality (Toledo, et al. 2011). In the face of global climate change, understanding the relationship between climate and wood density is needed for loblolly pine (*Pinus taeda*) , which is an important commercial species in the Southeastern United States (Baker and Balmer 1983). Knowledge on the response of wood quality to varying environmental conditions is useful in understanding the factors limiting quality at different locations.

Geographic variation in wood properties of southern pine plantation is known to exist (Wiemann and Williamson 2002, Bhuta et al. 2009, Antony, et al. 2010, Samuelson, et al. 2013). Among various factors impacting wood quality at the tree to landscape level, the environment is one of the major source of variation due to their effect on tree growth and stem wood production (Alvarez, et al. 2012). In studies of wood quality, climatic effects have mostly been overlooked. Despite the economic and ecological importance of the loblolly pine plantations in Southeast region, few studies have developed models to explain the observed variability in within tree loblolly pine SG. However, those models do not hold for all locations. We hypothesize that the spatial distribution of climatic and soil conditions accounts for much of the variation in the ring SG across regions.

This study used the geographic coordinates of the stands to obtain climate and soil information to understand the influence of environmental variables in loblolly pine individual-tree SG model for the Southeast. The objectives of this study are: (1) To characterize the variation in annual ring SG with cambial age and environmental variables; and (2) To develop a nonlinear mixed-effects model integrating environmental variables that can account for the regional variation in SG. This research matches annual variation in SG, measured temporally with variation in environmental factors measured spatially, as in research by (Downes and Drew 2008).

Climate predictions show that temperature will increase by almost 2°C in the Southeastern United States at the end of this century (Meehl et al. 2007). Physiological processes like respiration, photosynthesis and translocation are temperature and moisture dependent. On one hand, climate change impacts favoring higher productivity such as higher temperature and higher concentration of atmospheric carbon dioxide enhances radial growth at the expense of decline in the average wood density, on the other hand, irregular weather events may trigger tree mortality, slow growth and production of low quality wood. On the other hand, decrease in wood density, which is an important parameter for forest carbon estimation can cause a huge reduction in carbon storage due to its effects on decomposition rate of biomass (Zhang et al. 2011), and can potentially lead to climate change (Telewski et al. 1999). Since loblolly pine is an important economic resource for the Southeast, the ability to assess climate-SG relationships and predict future wood SG for sustainable management of loblolly pine in the face of increasing global climate change is hence very much desirable.

CHAPTER 3

METHODOLOGY

Study sites and sample preparation

The Wood Quality Consortium (WQC) at the University of Georgia (UGA), in collaboration with the United States Forest Service, industrial partners, and other research cooperatives, collected extensive wood samples from loblolly pine plantations growing across the Southeastern United States (Jordan, et al. 2008). The sites covered the 6 physiographic regions where loblolly pine is typically planted. The plantations received no silvicultural management except phosphorus in phosphorus deficient sites. This study uses data collected from 13 of the randomly selected baseline study stands (Figure 2). Details on the average tree characteristics of these stands are presented in Table 1. Mean stand DBH ranged from 19 to 30 cm and mean total height ranged from 14 to 24 m. The stands ages ranged from 18 to 25.

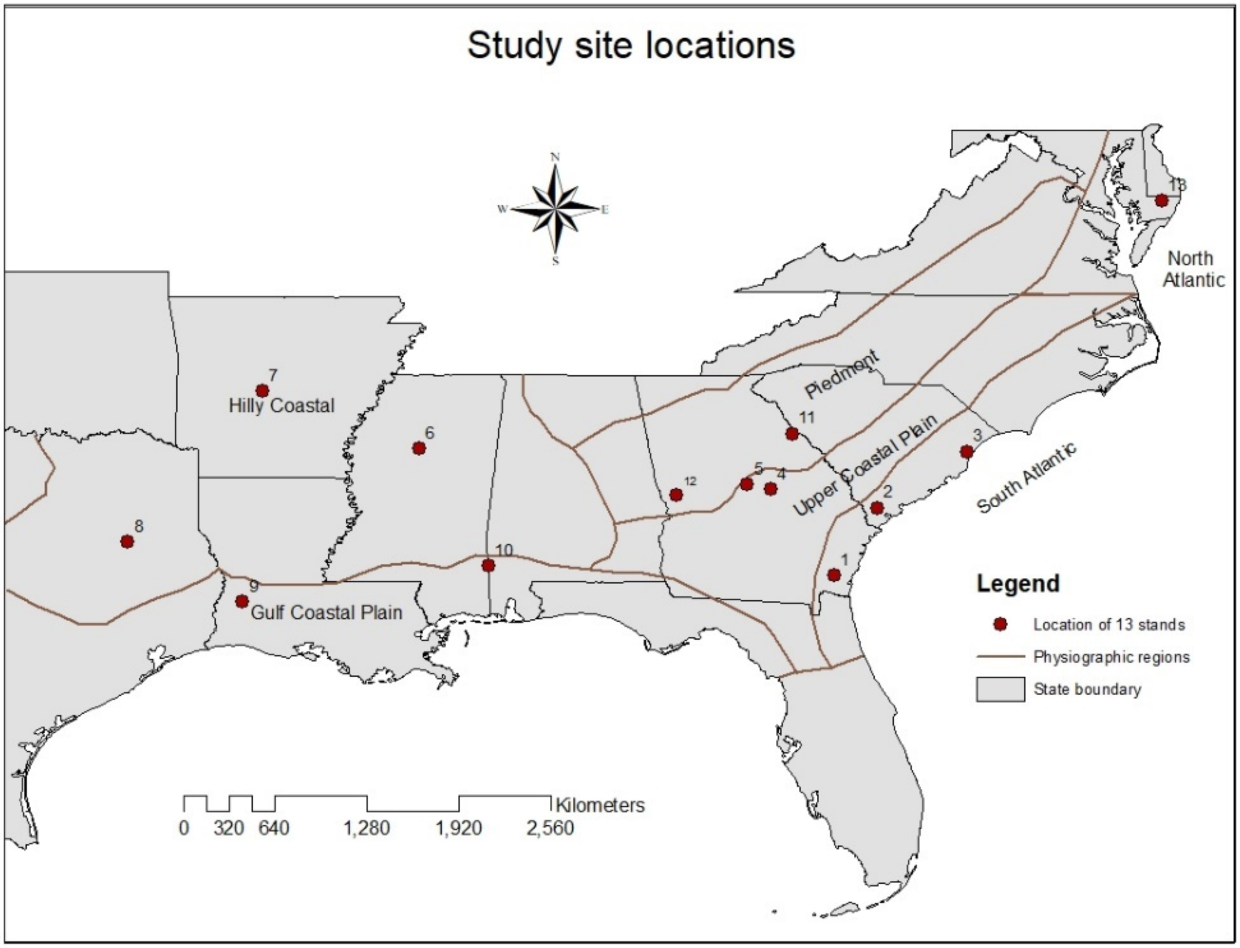

Figure 2: Location of 13 stands and physiographic regions in the Southeastern US.

Table 1:Average tree characteristics from 13 stands

Stand	Physiographic region	No. of trees sampled	DBH (cm) ± SD	Height (m) ± SD	Age
1	South Atlantic Coastal	23	20.68 ± 4.18	16.16 ± 1.86	25
2	South Atlantic Coastal	18	20.75 ± 4.13	14.61 ± 1.38	21
3	South Atlantic Coastal	22	28.68 ± 6.14	20.9 ± 2.1	20
4	Upper Coastal	25	21.92 ± 3.84	18.56 ± 1.63	25
5	Upper Coastal	18	20.68 ± 5.67	24.41 ± 2.29	24
6	Hilly Coastal	12	30.3 ± 6.3	21.61 ± 2.8	21
7	Hilly Coastal	19	28.19 ± 6.34	22.11 ± 2.33	23
8	Hilly Coastal	22	21.08 ± 4.46	21.83 ± 2.63	21
9	Gulf Coastal	14	19.53 ± 2.86	17.13 ± 1.99	22
10	Gulf Coastal	25	21.06 ± 4.93	19.44 ± 2.8	18
11	Piedmont	24	29.95 ± 2.92	21.07 ± 1.22	21
12	Piedmont	28	19.66 ± 3.84	15.63 ± 1.2	21
13	North Atlantic Coastal	19	23.29 ± 3.91	21.54 ± 1.76	25

DBH = diameter at breast height

At each study site, core specimens, measuring 12-mm in diameter, were collected at breast height (1.37 m). The samples were transported to the laboratory, dried to a moisture content of 8% and glued into poplar core holders. Thin radial strips of 2 mm were cut from these sections using a twin-blade circular saw. The samples were scanned on the transverse face along the radial direction from bark to pith on a Quintek Measurement Systems (QMS) densitometer using a step resolution of 0.06 mm to obtain ring-by-ring profiles of latewood percentage, ring width and SG. A SG transition value of 0.48 was assigned for distinction between earlywood and latewood as consistent with prior studies on loblolly pine (Clark III et al. 2004, Antony, et al. 2009, Antony et al. 2012, Eberhardt and Samuelson 2015).

Ring SG was calculated by considering SG values and area of latewood and earlywood within the ring as follows:

$$\mathrm{SG_{ij}} = \frac{\mathrm{SGearly_{ij}} \times \mathrm{EArea_{ij}} + \mathrm{SGlate_{ij}} \times \mathrm{LArea_{ij}}}{\mathrm{EArea_{ij}} + \mathrm{LArea_{ij}}} \qquad (1)$$

where, i and j are the values for the j^{th} ring in the i^{th} tree; SGearly and SGlate are SG for earlywood and latewood respectively; EArea and LArea are an area of earlywood and latewood respectively.

Ring width and SG values were normalized and detrended to get ring width index (RWI) and SG index respectively. The 'dplR' package in the dendrochronology program library in R (Bunn 2008) was used for detrending the effect of age on ring width and SG respectively. The chronologies were built on the detrended raw ring width and raw SG values for each site using a spline function with a frequency response of 50% at a wavelength of 0.67 of the series length.

Statistical analysis

All non-linear models, mixed-effects models and extended form of those models with climatic covariates were fitted using 'nls' and 'nlme' functions contained in the 'nlme' library (Pinheiro and Bates 2000) of the R statistical programming environment (R Development Core Team 2017) and using the RStudio interface (RStudio Team 2015). Nested models were compared based on likelihood ratio test. Parameter estimates were obtained using the maximum likelihood method, and only significant parameters ($p<0.05$) were retained in the models. Model fit was assessed through a combination of visual analysis of plots of standardized residuals against explanatory variables and fitted values, and different fit statistics including RMSE, RSE and Akaike information criterion (AIC) statistics (Aho et al. 2014). The RMSE is the squared root of sum of squared prediction error and RSE is the positive squared root of the error sum of squares divided by the error degree of freedom, lower values of both indicating better fit. AIC measures the relative adequacy of different nested models fitted to the same dataset and the model with the lower AIC is better.

Environmental data

Climate data were obtained from the database maintained by the University of East Anglia Climatic Research Unit that uses a climate model to generate a suite of monthly data based on latitude, longitude, and elevation (CRU 1982). These datasets have been developed from data acquired from weather stations around the world. The mean monthly climate values were predicted at each stand location for all the years corresponding to years in which each annual ring was produced. This was done by interpolating the CRU data using 'thin plate spline' using 'Tps' function in 'fields' package in R (Nychka et al. 2015). The thin plate spline is a method of interpolating a surface through available data points. Climatic inputs used were monthly averages of maximum temperature and minimum temperature, total precipitation, potential evapotranspiration and water deficit. Potential radiation was obtained using digital elevation model (DEM) in ArcMap. Stand level soil information were also collected from NRCS soil database. Table 2 presents the location information, climatic and edaphic characteristics of selected stands.

Table 2 Soil and long term mean annual climate characteristics for the 13 stands

Stand	Latitude	Longitude	Mean annual temp (^{0}**C**)	Mean monthly ppt (mm)	Radiation (MJ m^{-2})	Soil type	Soil texture	Drainage	SS	Soil PH	Perm	SHW (m)
1	31.1	-81.7	19.3	108.3	223.2	Bladen	SL	PD	MOD	4.6	SLOW	1
2	32.4	-80.9	19.0	102.7	753.0	Argent	C	PD	MOD	4.8	SLOW	0.5
3	33.5	-79.2	18.0	113.3	544.7	Chisolm	FS	WD	LOW	5.2	MOD	4
4	32.8	-83.0	18.0	97.2	179.2	Mascotte	FS	PD	LOW	4.5	HIGH	1
5	32.9	-83.4	17.7	96.8	712.8	Orangeburg	LS	WD	LOW	5.2	MOD	6
6	33.6	-89.8	16.4	120.1	0.0	Smithdale	SL	WD	LOW	5	MOD	4
7	34.7	-92.8	16.4	115.1	606.9	Carnasaw	CL	WD	LOW	4.8	SLOW	6
8	31.8	-95.4	18.9	98.8	756.6	Kenny	FS	WD	LOW	5.5	MOD	6
9	30.6	-93.2	19.4	125.7	791.1	Kolin	SL	PD	MOD	5.2	SLOW	2
10	31.3	-88.4	18.5	129.1	236.9	Poarch	L	MD	LOW	5	MOD	2
11	33.9	-82.6	16.4	95.1	342.2	Mecklenburg	L	WD	LOW	6.4	SLOW	6
12	32.7	-84.8	17.4	102.4	607.7	Lloyd	L	WD	LOW	5.5	SLOW	6
13	38.4	-75.4	13.8	95.1	856.8	Runclint	S	WD	LOW	4.6	HIGH	4.5

Note: temp=temperature, ppt=precipitation, SS=soil shrink swell property, Perm=soil permeability, SL = Sandy loam; C = Clay; FS = Fine Sand; LS = Loamy sand; SL = Sandy loam; CL = Clay loam; L = Loam; S = Sand; WD = Well drained; PD = Poorly drained; MD = Moderately drained, MOD=moderate

The 13 stands have considerable differences in climate and soil characteristics. Climate monthly data were integrated to provide indices of annual climate. These indices combine one or more hydro-meteorological variables such as precipitation, temperature, evapotranspiration, radiation etc. into a single quantitative value, which is more readily usable than raw hydro-meteorological data (Subedi 2016). Water deficit (WD) was calculated monthly and an annual average was calculated by:

$$\mathrm{WD} = -\sum_{\mathrm{n}=1}^{12} [\mathrm{pet} \geq \mathrm{pre}] * (\mathrm{pet} - \mathrm{pre}) \tag{2}$$

where, n is the set of months from January to December, 'pre' is precipitation and 'pet' is potential evapotranspiration. The first expression after the summation term returns 1 if pet ≥ pre, 0 otherwise. WD, which is a non-positive continuous value, is an important simple index of water balance and is associated with biologically important effects of precipitation and evapotranspiration(Lagacherie et al. 2006).

Likewise, Excess water (EW) was calculated similarly using the following formula:

$$\mathrm{EW} = \sum_{\mathrm{n}=1}^{12} [\mathrm{pre} \geq \mathrm{pet}] * (\mathrm{pre} - \mathrm{pet}) \tag{3}$$

where, n is the set of months from January to December. The first expression after the summation term returns 1 if pre ≥pet, 0 otherwise.

An index of monthly temperature was calculated using a temperature modifier, which is a nonlinear function of temperature and summed to calculate annual temperature index (TempI). The TempI variable considers the notion that productivity or growth increases with increasing temperature up to some optimum value and then declines (Landsberg and Sands 2011). It is calculated using this equation:

$$\text{Temperature Index} = \sum_{n=1}^{12}\left(\left(\frac{\text{Ta}-\text{tmn}}{\text{topt}-\text{tmn}}\right)*\left(\frac{\text{tmx}-\text{Ta}}{\text{tmx}-\text{topt}}\right)^{\left(\frac{\text{tmx}-\text{topt}}{\text{topt}-\text{tmn}}\right)}\right) \quad (4)$$

where, Ta is the monthly temperature, topt = optimum temperature for loblolly pine growth (15^{o}C), tmx = maximum temperature (35^{o}C) and tmn = minimum temperature (7.5^{o}C). The use of using this index is to give more weightage to those months which have more influence on growth and hence linked to SG formation. If the temperature falls below 7.5 ^{o}C there is no growth. Likewise, temperatures above 35^{o}C have the consequence of higher respiration cost, and hence is higher than optimum for carbon gain in loblolly pine (Teskey and Will 1999). A representation of temperature modifier is shown in Figure 3.

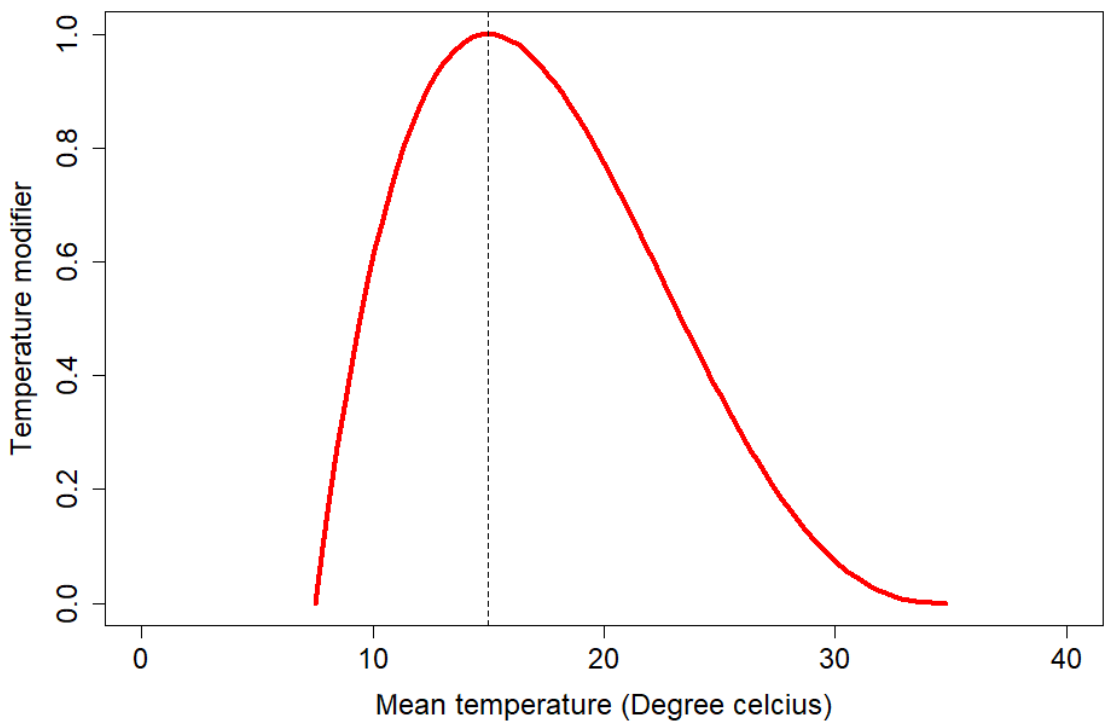

Figure 3: Graph showing temperature modifier as a function of mean monthly temperature

Monthly potential solar radiation data was obtained from DEM in ArcGIS using ‘area solar radiation’ tool that is used to calculate the insolation across an entire landscape. This tool uses the input topographic surface at each point to produce insolation maps for an entire geographic area, using transmittivity value of 1 and diffuse proportion of 0.3. Actual radiation was calculated using Hargreaves equation (Hargreaves and Samani 1982) as shown below and monthly radiation was then summed to get an annual index of solar radiation.:

$$\text{Actual radiation} = 0.16 \text{ x potential solar radiation x} \sqrt{(\text{tmx} - \text{tmn})} \tag{5}$$

We calculated Pearson's product-moment correlation, which is a measure of the strength of a linear association between two variables, between different monthly environmental variables and ring SG and ring width index. The first ring at the pith in all samples were removed from the analysis because some samples did not include the complete pith due to errors in coring which missed the center of the tree and SG errors related to ring curvature. Within-site (across year) and between-site variations in SG were examined. Based on a sigmoidal pattern of ring SG variation as a function of cambial age, a four-parameter logistic model was chosen out of five different candidate models to best fit the variation in ring SG. This base model has the following form:

$$\mathrm{SG_{ij}} = f\left(\mathrm{ring_{ij}}, \beta_{\mathrm{i}}\right) + \varepsilon_{\mathrm{ij}} \tag{6}$$

where,

$$\mathrm{f}(\mathrm{ring_{ij}}, \beta_{\mathrm{i}}) = \beta_{0\mathrm{i}} + \frac{\beta_{1\mathrm{i}}}{1 + \exp\left(\frac{\beta_{2\mathrm{i}} - \mathrm{ring_{ij}}}{\beta_{3\mathrm{i}}}\right)} \tag{7}$$

where, SG_{ij} is the SG of j^{th} ring of the i^{th} tree, $ring_{ij}$ represents the j^{th} ring in the i^{th} tree, β_{0i} is the lower asymptote corresponding to the limit as $ring_{ij}$ approaches 0, β_{1i} is the difference between upper asymptote of $ring_{ij}$ corresponding to the maximum value of $ring_{ij}$ that can be attained and lower asymptote, β_{2i} is the $ring_{ij}$ at the inflection point of the curve, β_{3i} is a scale parameter and ε_{ij} is the random error and $\varepsilon_{ij} \sim N(0, \sigma^2)$. Because of the nested nature of the data, mixed-effects model with different combinations of random and fixed effects were employed to account for the distinct source of group variability. Mixed-effects models have been the most commonly applied method for longitudinal data analysis (Pinheiro and Bates 2000) as they accommodate between-subject variability. Several researches have used mixed-effects modeling techniques for SG analysis (He 2004, Mora, et al. 2007, Franceschini et al. 2010). Different possible environmental covariates that could explain the random variation were then examined and models were updated with environmental variables, beginning with the variable that displayed highest correlation with ring SG. For each of the models screened, the temporal autocorrelation was addressed by using a first order autoregressive function AR (1). Models were also updated to address heteroskedasticity, which is the change in the variance of the residuals with time, using a power variance function. Models including power variance function and autoregressive structure were fitted separately and in combination (Pinheiro and Bates 2000).

CHAPTER 4

RESULTS

Descriptive statistics

Mean SG of South Atlantic Coastal stands were relatively higher (0.52) compared to others, while Hilly Coastal had the lowest SG (0.46-0.48). Similarly, average stand level ring width and latewood percentage was also found to be highest in South Atlantic stands. Mean minimum SG ranged from 0.3 to 0.34 and maximum ring SG ranged from 0.64 to 0.84 while latewood percentage ranged from 36 to 49%. Mean ring width of stands in South Atlantic Coastal area was higher while low ring width were found in North Atlantic Coastal stands. Minimum ring width ranged from 0.06 mm in Upper Coastal Plain to 1.2 mm in Piedmont and South Atlantic Coastal area. Maximum ring width ranged from 12 mm to 18 mm, the highest standard deviation being 3.93 in South Atlantic stands.

Table 3: Descriptive statistics of ring properties of 13 stands

Stand	Physiographic region	Ring width (mm)				Latewood %	SG			
		Min	Max	Mean	SD		Min	Max	Mean	SD
1	South Atlantic Coastal	1.02	18.48	5.67	2.66	46.62	0.33	0.71	0.52	0.08
2	South Atlantic Coastal	0.48	21.6	6.79	3.93	48.64	0.31	0.84	0.52	0.08
3	South Atlantic Coastal	1.2	14.58	6.6	2.58	46.95	0.33	0.73	0.51	0.08
4	Upper Coastal Plain	0.06	15.3	5.34	2.9	40.8	0.3	0.72	0.48	0.08
5	Upper Coastal Plain	0.36	12.18	4.33	2.28	44.28	0.32	0.72	0.51	0.09
6	Hilly Coastal	0.9	12.78	4.49	2.45	40.3	0.31	0.69	0.48	0.08
7	Hilly Coastal	0.24	16.38	4.59	2.89	36.25	0.32	0.64	0.46	0.06
8	Hilly Coastal	0.48	17.4	5.53	3.45	39.97	0.31	0.66	0.48	0.08
9	Gulf Coastal	0.3	15.84	4.1	2.61	47.64	0.32	0.7	0.52	0.08
10	Gulf Coastal	0.84	14.28	4.77	2.89	42.31	0.3	0.74	0.5	0.09
11	Piedmont	1.2	14.46	4.6	2.29	37.55	0.32	0.76	0.48	0.08
12	Piedmont	0.6	13.8	4.34	2.1	42.43	0.34	0.69	0.51	0.07
13	North Atlantic Coastal	0.36	13.44	3.62	1.98	39.46	0.3	0.7	0.49	0.08

Pearson correlation between tree-ring variables and climate

Table 4 shows the correlation of different tree ring attributes with monthly combination and growing season-wise climate as well as annual indices of climatic parameters. It shows that the densitometric variables are significantly correlated with climatic variables. The WD seems to be the variable significantly correlated with all the SG and ring width variables and so is the temperature index, except its correlation with ring width. Figure 4 shows the correlation coefficient for ring SG index with different monthly climatic data. It shows that precipitation, potential evapotranspiration and water deficit are the most correlated variables, especially during two growing seasons, although the degree of correlation is not strong.

Table 4: Correlation between SG and ring width variables and different climatic variables

	pre56789	pre45678	def_67	gs_tmn	gs_tmx	gs_pet	gs_def	gs_pre	gs_rad	RadI	EW	WD	TempI
EW SG	0.05	-	-	-	-0.08	0.04	0.04	-	-0.03	0.17	-0.03	0.04	-0.11
LW SG	-	-	-0.10	-	-	-0.17	-0.12	-0.05	0.10	-0.04	0.05	-0.14	0.18
Ring SG	0.15	0.07	-0.19	0.15	-	-0.21	-0.19	0.08	0.03	0.04	0.10	-0.10	0.24
Ring width	0.14	0.12	-	0.10	0.14	0.17	0.06	0.09	-0.07	-	-0.04	0.09	-
LW %	0.19	0.09	-0.19	0.20	0.03	-0.20	-0.20	0.11	-	0.03	0.11	-0.09	0.26

Note: EW=earlywood, LW=latewood, pre56789=mean precipitation from May to September, pre45678= total precipitation from April to August, def_67=water deficit in June and July, gs=growing season climate (March to October), tmn=minimum temperature, tmx=maximum temperature, pet=potential evapotranspiration, def=water deficit, rad=radiation, pre=precipitation, -=no significant correlation, all other variables significant at $p<0.05$.

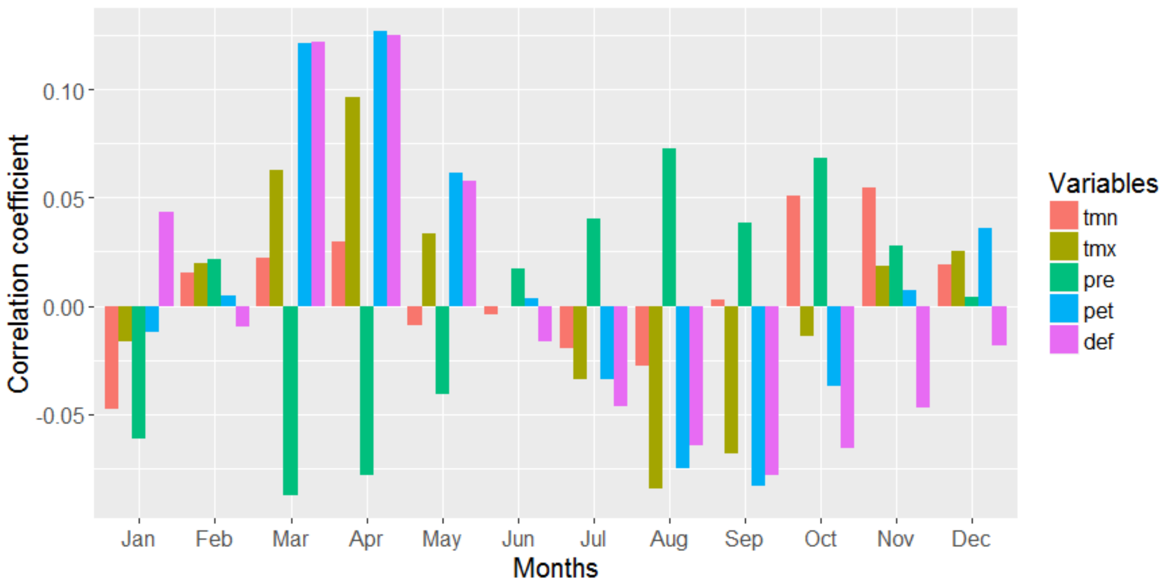

Figure 4: Correlation coefficient between ring SG index and monthly climate data

Since monthly climate data are highly correlated with each other, we decided to use climatic indices to avoid multicollinearity in model fitting. We also looked at the correlation between index variables to be used in modeling (Table 5). There was relatively high correlation between EW and WD ($r = 0.50$, $p<0.05$). Also, the correlation between soil PH and depth to seasonal high water (SHW) was relatively high ($r = 0.61$, $p<0.05$).

Table 5:Correlation matrix of climatic and soil predictors of SG

	EW	WD	TempI	PH	SHW
RadI	-0.27	-0.09	-0.20	-	0.23
EW		0.50	0.17	-	-0.16
WD			-	-0.05	-0.18
TempI				0.17	-0.32
PH					0.61

All correlations are significant at 0.05 unless denoted as -

Ring SG variation

The initial plot of ring SG based on cambial age (Figure 5) shows that ring SG follows a sigmoidal curve with an increase in SG rapidly towards the pith, followed by a decline in the rate of increase after which going further towards the bark it either reaches an asymptote or continues to decrease.

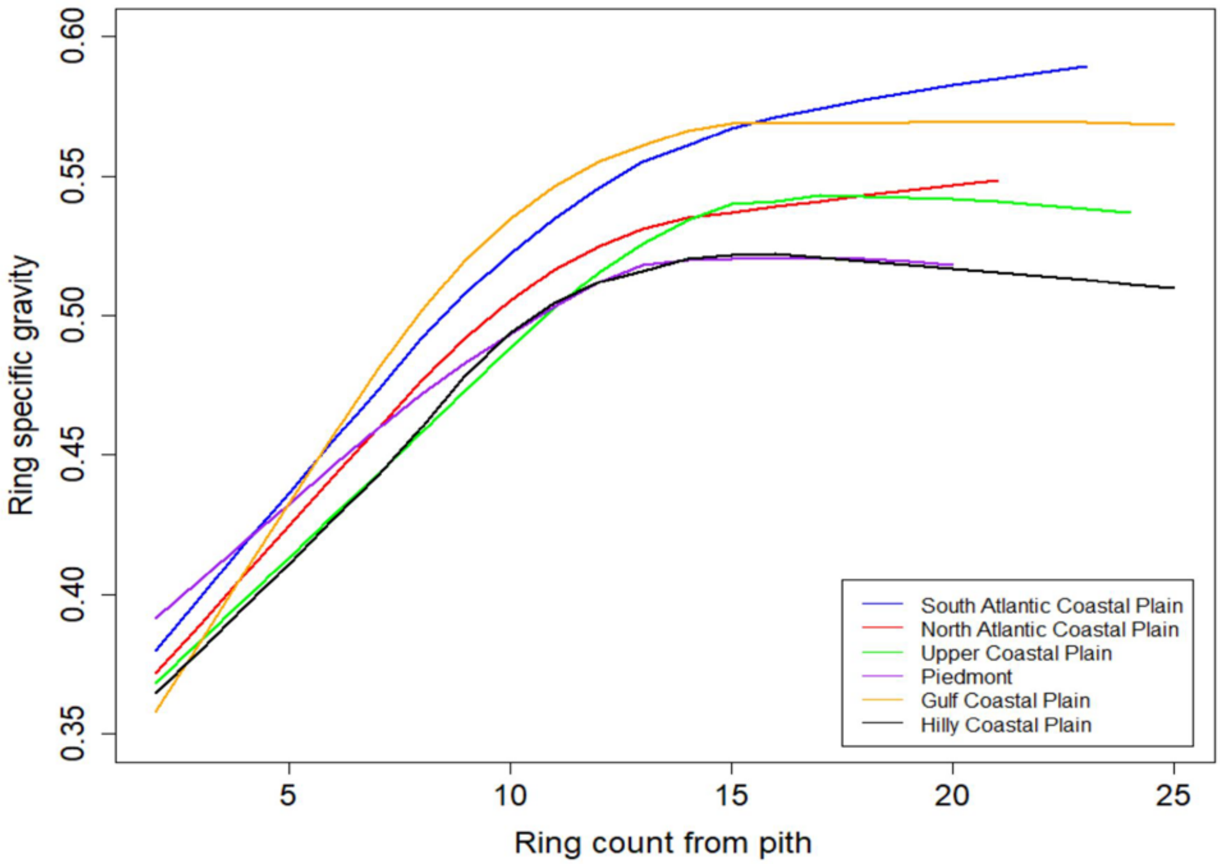

Figure 5:Variation of ring SG with cambial age for 13 stands from 6 regions. Each line represents smoothed loess curve fitted to data from each region.

Several nonlinear candidate models (Table 6) were compared during the preliminary analysis, and the four-parameter logistic model was selected as most suitable to represent the within tree variation in SG based on AIC, RMSE and adjusted coefficient of determination (R^2). Four-parameter logistic model with lowest value of RMSE (0.057), highest value of R^2 (51%) and lowest value of AIC (-14056) was chosen as the base model for incorporation of environmental variables. The four-parameter logistic model have been used in many other researches examining ring SG (Mora et al. 2007; Kantavichai et al. 2010).

Table 6:Candidate models and their fit statistics for base model selection

Model name	Equation	Fit statistics		
		RMSE	R^2	AIC
Michaelis - Menten	SG(age)= $\frac{\beta_0 * age}{1+\beta_1 * age}$ +ε	0.06	0.46	-13595
Chapman-Richards	SG(age) = β_0 [1-exp(-β_1*age)] β_2 +ε	0.059	0.48	-13806
Asymptotic exponential	SG(age) = β_0 [1-exp(-exp*(β_1)*age] +ε	0.064	0.38	-12936
Three-parameter logistic exponential	SG(age)= $\frac{\beta_0}{1+\exp\left(\frac{\beta_1-age}{\beta_2}\right)}$ +ε	0.058	0.49	-13943
Four-parameter logistic model	SG(age)= $\frac{\beta_1}{1+\exp\left(\frac{\beta_2-age}{\beta_3}\right)}$ + β_0 +ε	0.057	0.51	-14056

Note: age refers to cambial age.

Table 6 depicts the fit statistics of different models that predicts annual ring SG as a function of cambial age. The best model was the four-parameter logistic model. This model was hence selected for further development. While fitting the model for each individual tree, tree to tree variability of SG was found and hence individual tree effect was represented as a random effect to estimate its contribution to the overall variance of SG. At first, all the parameters of the logistic function were considered as random effects. The logistic model was fit for each of the tree and the plots of intervals of parameter estimates were made (Pinheiro and Bates 2000). Based on reduced AIC values, the β_1 and β_2 parameters were considered to have random components. The β_0 and β_3 parameters were treated as a pure fixed effect. The modeling process started with fitting 'NLME' model to explain the between-tree random-effects variation. The form of the resulting mixed effect model is:

$$SG_{ij} = \beta_{0i} + \frac{\beta_{1i} + b_{i,1}}{1 + \exp\left(\frac{(\beta_{2i} + b_{i,2}) - ring_{ij}}{\beta_{3i}}\right)} + \varepsilon_{ij} \qquad (7)$$

where, β_{0i}, β_{1i}, β_{2i} and β_{3i} are fixed effects parameters; $b_{i,1}$ and $b_{i,2}$ are the random effect parameter associated with β_{1i} and β_{2i}, specific to i^{th} tree and ε_{ij} is residual standard error. The random effects bi and within-tree errors ε_{ij} are assumed to be independent for different groups and to be independent of each other for the same group and normally distributed with mean 0, such that $\varepsilon_{ij} \sim N(0, \sigma^2)$ and bi ~ $N(0, \Psi)$ for each group, Ψ being the variance–covariance matrix of random effects (Pinheiro and Bates 2000).

The data involved repeated measurements from the same individual and hence involved temporal autocorrelation. Repeated measures on the same individual likely have non-independent errors (Crawley 2013) and non-constant error variance. To address the correlation issue, the error term ε_{ij} is broken down into error terms that apply at chosen grouping level i.e. between trees. Based on the plots of the autocorrelation function and short lag period of one year, an autocorrelation structure of order 1 was chosen. Also, the plots of fit and residuals indicated evidence of heteroskedasticity with variance increasing with increasing predicted value. To resolve the problem of heteroskedasticity of model residuals, a within-tree variance power function with ring number was also applied to the models. Different fit statistics of models without environmental covariates are given in Table 7. Based on the AIC, BIC, RSE and LRT values, model 12, with power variance function and AR (1) was found to be the best model.

Table 7: Fit statistics of different forms of the selected base model

Model	Equation	Df	RMSE	RSE	R^2	AIC	BIC	LRT
8	$SG_{ij} = \beta_{0i} + \frac{\beta_{1i}}{1 + \exp\left(\frac{\beta_{2i} - x_{ij}}{\beta_{3i}}\right)}$	5	0.057	0.057	0.51	-14056	-14023	
9	$SG_{ij} = \beta_{0i} + \frac{\beta_{1i} + b_{i,1}}{1 + \exp\left(\frac{(\beta_{2i} + b_{i,2}) - x_{ij}}{\beta_{3i}}\right)}$	8	0.057	0.042	0.51	-16199	-16147	
10	Equation 7+AR (1)	9	0.057	0.042	0.51	-16275	-16216	77.5 ($p<0.0001$)
11	Equation 7+power variance function	9	0.057	0.025	0.51	-16351	-16293	154.2 ($p<0.0001$)
12	Equation 7+power variance function + AR (1)	10	0.057	0.025	0.51	-16447	-16382	251.6 ($p<0.0001$)

LRT = Likelihood Ratio Test, Df = degree of freedom

Next possible covariates that could explain the random variation were examined. Plots of estimated random effects versus candidate covariates were made to identify any linear association. Covariates with most promising covariate-coefficient relation were introduced in the models one at a time. Environmental variables that were both significant and improved model fit were selected. Starting with fitting model shown in model 9, climatic and soil variables were gradually incorporated into the base model. Table 8 gives the fit statistics of different forms of models with environmental covariates.

Table 8: Fit statistics of models showing improvement with inclusion of different environmental variables

Model	Equation	Df	RMSE	RSE	R^2_{adj}	AIC	LRT
Including water deficit (WD)							
13	$SG_{ij} = \beta_0 + \frac{\beta_1 + b_1}{1 + \exp\left(\frac{(\beta_{20} + \beta_{21} * WD + b_2) - x_{ij}}{\beta_3}\right)}$	9	0.057	0.041	0.51	-16202	
14	Equation 11+AR (1)	10	0.0573	0.042	0.507	-16276	75.79 (p<0.0001)
15	Equation 11+power variance function	10	0.0574	0.025	0.506	-16359	158.9 (p <0.0001)
16	Equation 11+power variance function + AR (1)	11	0.0573	0.025	0.507	-16452	253.4 (p<0.0001)
Including index for temperature (TempI)							
17	$SG_{ij} = \beta_0 + \frac{\beta_{10} + \beta_{11} * TempI + b_1}{1 + \exp\left(\frac{(\beta_{20} + \beta_{21} * WD + \beta_{22} * TempI + b_2) - x_{ij}}{\beta_3}\right)}$	11	0.0568	0.041	0.516	-16220	
18	Equation 15+AR (1)	12	0.0567	0.042	0.517	-16296	78.2 (p<0.0001)
19	Equation 15+power variance function	12	0.0568	0.025	0.516	-16381	163 (p<0.0001)
20	Equation 15+power variance function + AR (1)	13	0.0518	0.025	0.518	-16473	256.6 (p<0.0001)
Including depth to seasonal high water table (SHW)							
21	$SG_{ij} = \beta_0 + \frac{\beta_{10} + \beta_{11} * SHW + \beta_{12} * TempI + b_1}{1 + \exp\left(\frac{(\beta_{20} + \beta_{21} * WD + \beta_{22} * TempI + b_2) - x_{ij}}{\beta_3}\right)}$	12	0.0567	0.041	0.518	-16152	

22	Equation 19+AR (1)	13	0.0566	0.042	0.52	-16306	77.16 ($p<0.0001$)
23	Equation 19+power variance function	13	0.0567	0.025	0.52	-16391	163 ($p<0.0001$)
24	Equation 19+power variance function + AR (1)	14	0.0566	0.0248	0.52	-16482	255.8 ($p<0.0001$)
Including permeability (Perm)							
25	$SG_{ij} = \beta_0 + \frac{\beta_{10} + \beta_{11} * SHW + \beta_{12} * TempI + b_1}{1 + \exp\left(\frac{(\beta_{20} + \beta_{21} * WD + \beta_{22} * TempI + \beta_{23} * Perm + b_2) - x_{ij}}{\beta_3}\right)}$	14	0.0558	0.041	0.53	-16278	
26	Equation 23+AR (1)	15	0.0557	0.042	0.53	-16354	78.7 ($p<0.0001$)
27	Equation 23+power variance function	15	0.0558	0.025	0.53	-16442	165.7 ($p<0.0001$)
28	Equation 23+power variance function + AR (1)	16	0.0557	0.025	0.53	-16535	261.3 ($p<0.0001$)

Based on fit statistics of different nonlinear mixed models and extended models with autocorrelation and heteroskedasticity correction, the final model for ring SG has the form:

$$SG_{ij} = \beta_0 + \frac{(\beta_{10} + \beta_{11} * SHW + \beta_{12} * TempI) + b_{i,1}}{1 + \exp\left(\frac{\left(\beta_{20} + \beta_{21} * WD + \beta_{22} * TempI + \beta_{23} * PermMOD + \beta_{24} * PermSLOW + b_{i,2}\right) - ring_{ij}}{\beta_3}\right)} + eij \qquad (28)$$

The description and summary statistics of the explanatory variables of the final model are given in Table 9. When all the parameters were random effects, it was found that the random effect of parameter β_0 had near-zero estimate for the standard deviation and hence β_0 was considered as a fixed effect. Based on fit of the models and considering different parameters as random, only β_1 and β_2 were included in the model as having random effects. Parameter β_{i1} is comprised of a random tree effect and covariates consisting of temperature and depth to seasonal high water or SHW. The parameter β_1 is the range of SG between age zero and age infinity. The estimated coefficient of temperature index is positive, indicating that the SG increases as the temperature increases. On the other hand, as the depth to water table increases, SG tends to decrease. Parameter β_{i2} is comprised of a random tree effect and covariates consisting of water deficit, temperature and soil permeability. Water deficit and temperature also affected positively to the inflection point of the SG model.

Table 9: Statistics of the environmental variables incorporated into the n=4873 rings from the 269 sample trees

Variable	Variable description	Mean	SD	Min	Max
SG_{ij}	specific gravity of ring j of tree i	0.49	0.082	0.3	0.84
WD	Water deficit Index (mm)	-320.48	124.51	-641.6	-28.63
TempI	Temperature Index	5.58	2.39	-4.04	8.11
SHW	Seasonal high water table (m)	3.75	2.16	0.5	6
Perm	Water permeability through soil surface: High (PermHIGH), Moderate (PermMOD), Slow (PermSLOW) (m^2)				

Differences in SG were expressed by lower inflection points for slow permeability followed by moderate permeability, and high permeability showed a higher inflection point. These differences between permeability are illustrated in figure 6.

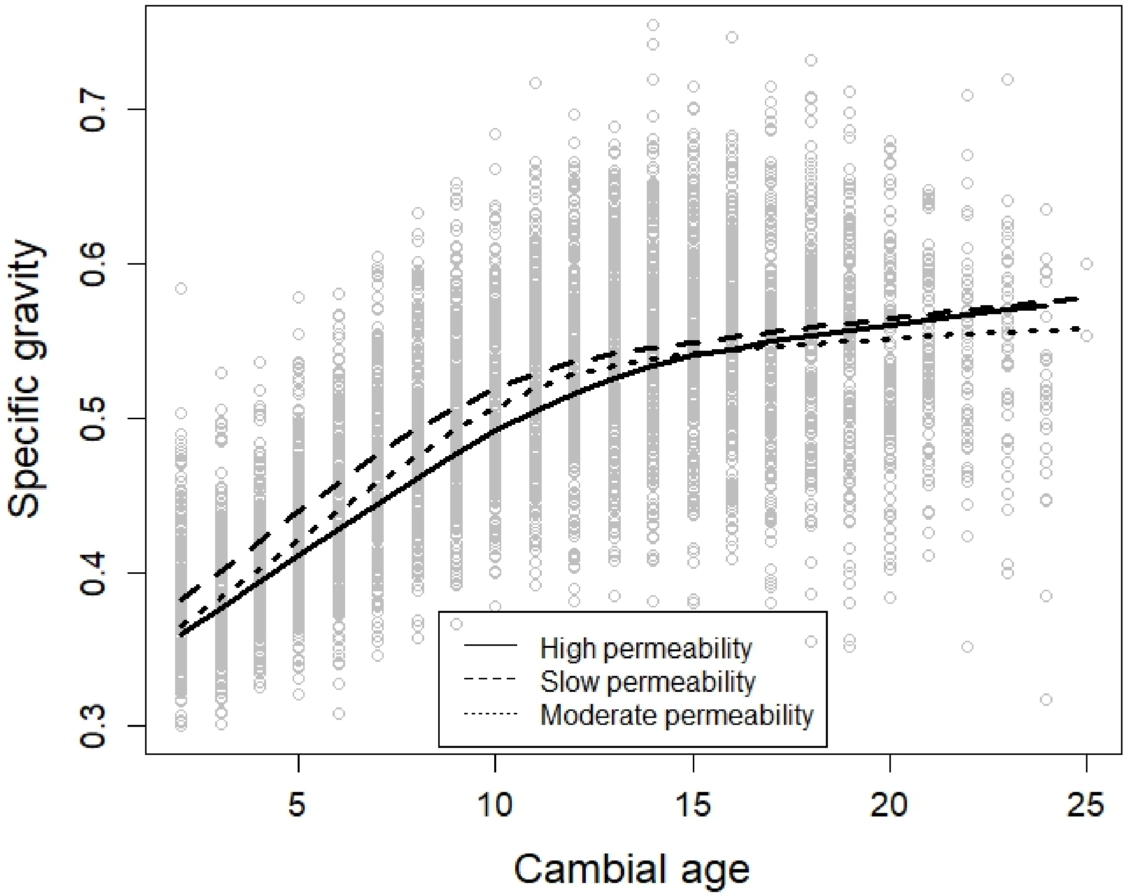

Figure 6: Predicted population mean trends of SG for different permeability classes. The lines represent loess line curves fitted to each permeability class.

The parameter estimates, standard errors and uncertainty coefficients for the final model for ring SG are shown in Table 10. Estimates of the standard deviation of the random effects represent the estimated between-tree variation around the population-level parameter estimates (Genet et al. 2012). All the parameters were significant at $p<0.005$. Figure 7 shows the residual plots of the final model. Plots of standardized residuals indicated no obvious residual trend in predicted SG and the residuals were normally distributed.

Table 10: Nonlinear parameter estimates, standard errors and uncertainty coefficients for the final model for ring SG

	Lower asymptote	Difference between upper and lower asymptote			Inflection					Shape
Parameter	β_0	β_{10}	β_{11}	β_{12}	β_{20}	β_{21}	β_{22}	β_{23}	β_{24}	β_3
Estimate	0.3492	0.195	- 0.0045	0.0043	6.986	0.0012	0.176	- 1.122	-2.073	0.3492
Std. error	0.0043	0.009	0.0013	0.0007	0.298	0.0004	0.032	0.274	0.264	0.0043
	Residual σ	ϴ (Correlation parameter)	α (Variance parameter)	Standard deviation explained by the random effects						
				SD (b1)		SD(b2)		Cov (b1, b2)		
Estimate	0.025	0.169	0.2286	0.041		0.98		-0.25		

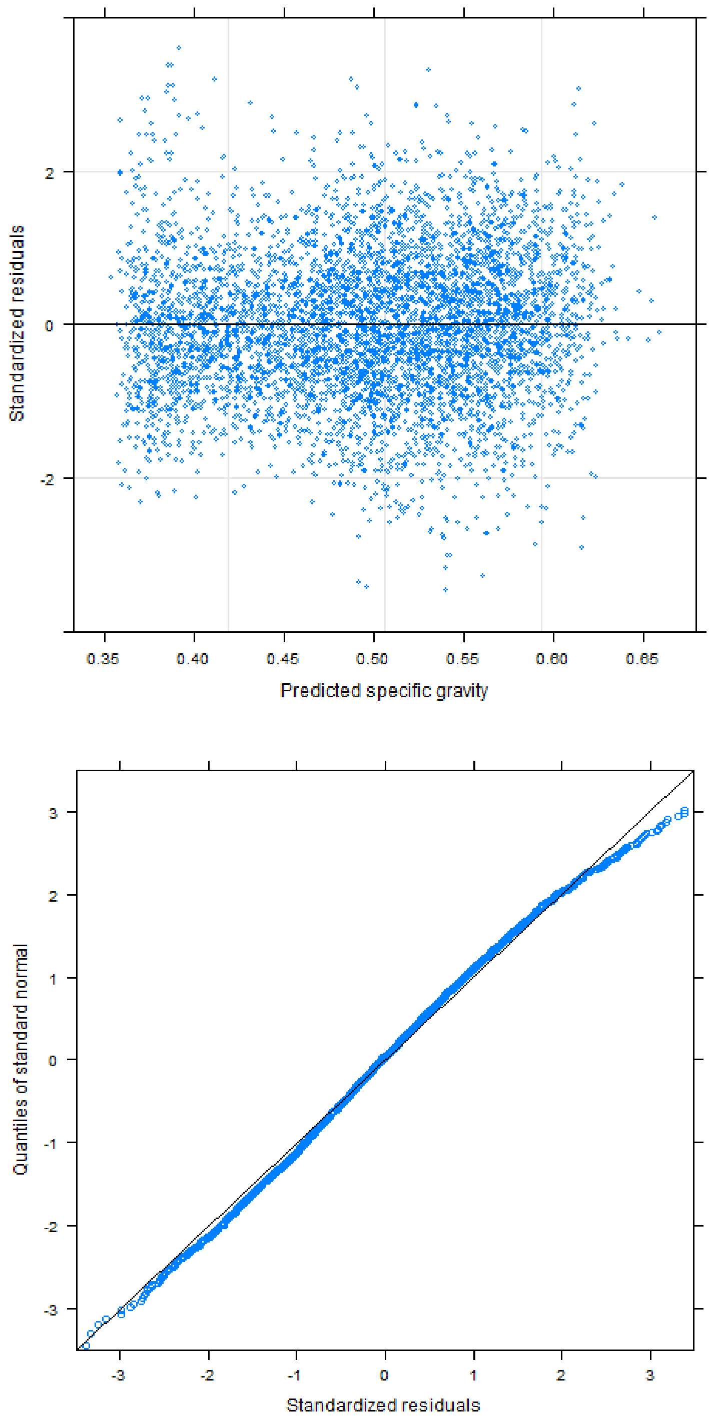

Figure 7: Scatter plot of standardized residuals vs fitted values for the final model

Table 11 shows the results of the two models, the base model without environmental covariates and the final model considering environmental variables using equation 28. The best model had RMSE at 0.055, AIC = -16535 and BIC = -16431. In comparison, the base model without environmental covariates had RMSE = 0.057, AIC = -16199 and BIC = -16147. This was reduction of RMSE by 3.5%, RSE by 40%, AIC and BIC by 2% and an increase in R^2 by 5%.

Table 11: Model comparison between base model and final model

Fit statistics summary	SG prediction model		Gain in precision (%)
	Without environmental variables	With environmental variables	
RMSE	0.057	0.055	3.5
RSE	0.042	0.025	40
AIC	-16199	-16535	2
BIC	-16147	-16431	2
R^2	0.51	0.53	5

The inclusion of water deficit, temperature index, permeability and depth to water table in the prediction model significantly improved fit statistics. We examined model fit for each stand by plotting observed ring SG, fixed model predictions (base model), mixed model predictions without environmental variables, and the predictions obtained when the model was fitted with environmental covariates. The plot for 2 randomly selected stands is shown in Figure 8. The first one represents the loblolly stand of South Atlantic coastal plain and the second one represents the loblolly stand of Gulf coastal plain.

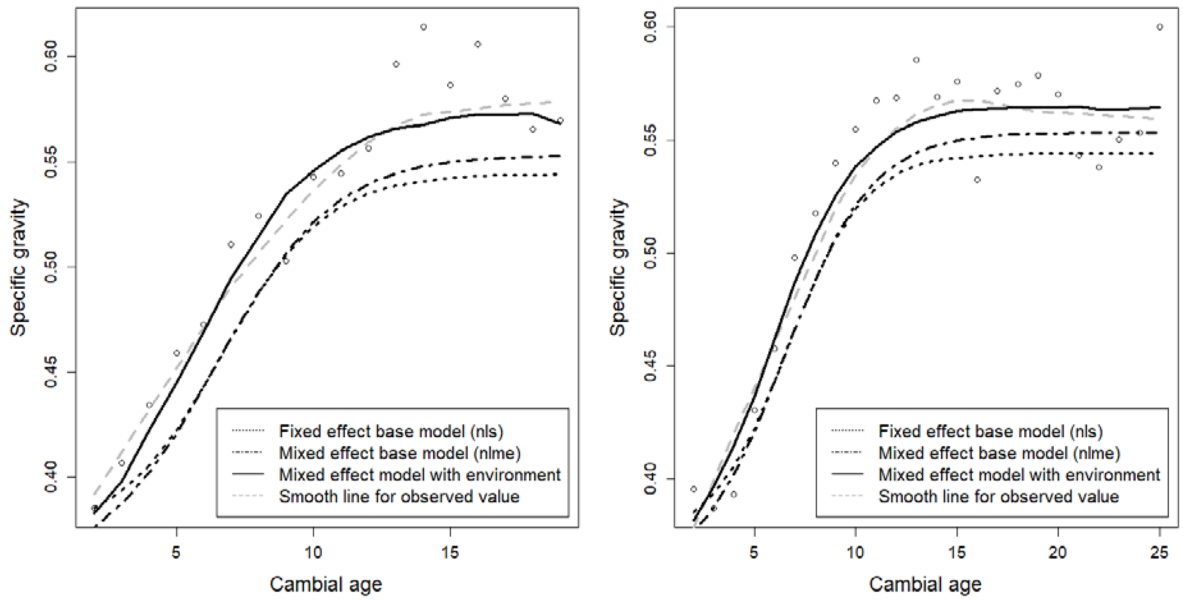

Figure 8: Observed mean ring SG of 2 randomly selected stands with predicted mean values from different models with and without environmental covariates

CHAPTER 5

DISCUSSION

The radial pattern of SG variation in the stem in this study was in accordance with previous studies on loblolly pine (Megraw 1985, Daniels et al. 2002, Tasissa and Burkhart 2007), and other species including Douglas-fir (Kantavichai et al. 2010) and radiata pine (Cown et al. 2002). The lower asymptote (β_0), which corresponds to the minimum ring SG at cambial age zero, was a fixed effect with a value of 0.33. Tasissa and Burkhart (2007) had found a lower asymptote value of 0.38 in their study on demarcation between juvenile-mature wood in loblolly pine in the Southeastern region. The value is also almost similar to what Kantavichai et al. (2010) found in their model predicting ring SG for Douglas fir (0.34). Mora et al. (2007) found that the lower asymptote differed between sites and treatments applied like site preparation and fertilization.

Parameter β_1 is the difference between lower and upper asymptote and it is a mixed effect containing a random tree effect and fixed effects related to temperature index and depth to SHW. We found that temperature is positively associated with this parameter. Mean SG increased by 0.0039 for every **1^0C** increase of annual temperature. Wiemann and Williamson (2002) found an increase of SG by 0.0049 per increase in mean annual temperature by **1^0C**. Their study looked at several angiosperms while ours focused only in loblolly pine. Higher density was associated with higher mean annual temperature in a study done on loblolly pine in the Southeast by Clark and Daniels (2002). Many studies have found different responses to seasonal temperature variation and many have found a positive relationship between the temperature of only a few months or for a growing season with SG, but we have used only a single annual temperature index representing fluctuations of temperature in different months. Samuelson et al. (2013) found that the SG and latewood percentage of Mississippi loblolly pine stands were positively correlated with November temperature. A positive effect of temperature on annual ring SG was also found by Filipescu et al. (2014) in their study of Douglas-fir. SG in Douglas-fir also follows the same sigmoidal pattern with cambial age like loblolly pine. Kantavichai et al. (2010) found that the upper asymptote of SG model in Douglas-fir increased by 0.0142^0C for every 1^0C increase in mean temperature of March to May. Filipescu et al. (2014) also found a slight increases in ring SG in Douglas-fir with increase in average temperature from March to May.

Our results show that depth to water table is negatively related to SG. Seasonal high water table is the highest average depth of free water during the wettest season. The less the depth to water table, the more the roots remain submerged in water. Plants respire 20 times more under water-logged condition (Pallardy 2010), resulting in less allocation of carbohydrate for growth. Reduction in growth rate within a year thus results in higher ring SG. Groundwater plays important role in vegetation transpiration too. A study on wetland plants in China by Xu et al. (2016) showed that under high water table conditions, the transpiration rate was higher compared to under low water table conditions. Conversely, when water table is high, faster growth may translate into low wood SG. Height and radial growth has been considered to be a function of water table depth in a study on loblolly pine (Balmer 1978). Czapowskyj et al. (1986) in their study of black spruce found that tree height and diameter growth significantly increased with depth to water table. Several studies have found that the intervention of manipulating water table produced good results from growth perspective. White and Prichett (1970) have shown that water table control produced greater growth response in five-year old loblolly pine than fertilization treatment. Previous studies have looked at the relationship between water table depth and growth rate but not to SG directly.

Parameter β_2, the inflection point where the shape of the curve changes is a mixed effect containing a random tree effect and fixed effects related to indices of water deficit and temperature, and soil permeability. Water deficit, which is an index to represent the annual atmospheric water availability (as affected by precipitation and potential evapotranspiration) appeared to positively affect SG by having its effect on the parameter representing the inflection point. The WD is a non-positive value, a larger value towards 0 meaning decrease in water deficiency. As the WD value decreases, meaning water deficit is high, SG tends to be lower by having an effect on the inflection point. Water deficit is an important limiting factor in plant growth in many studies. Alvarez et al. (2012), in their study in radiata pine also found that the sites with the highest productivities had the lowest annual water deficits. There are contrasting results regarding effect of water deficit on SG. According to Cregg et al. (1988), moisture stress is associated with initiation of latewood, which is a major determinant of SG, thus causing presence of false rings in many conifers including loblolly pine. However, prolonged water deficit has been associated with less latewood (Voegeli and Reinhart 1956) resulting in lower wood SG. Our results indicate that moderate to slow soil permeability is negatively related to SG with its effect on the inflection point. Permeability is the transmission of water and air through the soil surface and is related to saturated hydraulic conductivity, which is influenced by soil texture, porosity and bulk density. Usually, fine-textured soil like clay has slow permeability, silty soil has low to moderate permeability and high permeable soil is the sandy soil. When it is too slow, it can result in waterlogging and excess moisture pose physiological stresses as under drought (Schweingruber 2007), thus influencing plant growth. High permeability is associated with good aeration and good site condition, thus favoring faster growth and lower SG. However, extremely high permeability results in greater seepage and loses water easily and may create drought condition during summer.

Effects of climate can be explained based on plant ecophysiological prospective. Extreme temperatures and moisture stress can disrupt physiological processes, for example the reduction of light-use efficiency, increase in respiration and decrease in efficient water and nutrient use (Alvarez, et al. 2012). Variation in environmental conditions, especially in temperature and water availability affect cell formation and differentiation, which are ultimately responsible for tree rings' anatomical properties (Schweingruber 2007). Under high permeability and high water table, coupled with water deficit conditions, plants respond to conserve water by closing stomata at the expense of curtailing photosynthesis. If situation persists in summer, curtailed growth and tracheid formation during latewood formation results in lower SG. Plant water deficits can also increase susceptibility to diseases and insects. Variation in soil properties also causes the regional variation in SG (Megraw 1985) due to their influence in retention of moisture and nutrients available to plants. Moisture regulates the bio-physical and chemical activities of soil including transportation of nutrients and length of stomatal opening, thus influencing the photosynthesis (Walker and Perkins 1958).

The analysis augments the use of environmental variables to explain the regional variability in annual ring SG with greater accuracy of prediction. We accomplished this by expanding parameters representing the asymptotes and inflection point for the models. Kantavichai et al. (2010) showed improvement in their model by including climatic and soil variables only in the upper asymptote parameter in the modelling of ring SG of Douglas-fir in Western Washington. We found that a combination of climate indices and soil factors were significant in explaining variability in wood SG in our study. Our final model shows improvement in fit. Although environmental covariates improved model predictions, they did not account for all the variation across regions. This means there could be other important factors playing their role and that we did not consider in our model, which may include other environmental effects or the forest management regime or inherent tree characteristics as governed by genetics (Antony, et al. 2013).

CHAPTER 6

CONCLUSIONS

Several models used to describe variation in annual ring SG were tested, the best of which could describe 53% of the variation. Including environmental factors as covariables along with ring number improved the prediction capabilities of the SG models. Although climate and soil did not account for all the variability across regions, the importance of environment on SG prediction is evident. Unexplained variation in this study can be attributed to other external factors including individual inherent genetic characteristics of trees, different site factors (elevation, slope etc.), sampling design, stage of stand development and difference in the management regime. A controlled study likely could have produced better results. This study used indices of climate, which is a single value representative for whole year to avoid high correlation among each month’s climate, which gives more weight to the months that have more influence on wood formation and to avoid multicollinearity in modelling. This study does not account for variation of within-tree SG at different height levels along the bole due to lack of sample collection because the studied samples were only collected at breast height. However, measurements taken at breast height has been used by some studies to account for the vertical patterns in wood density variation within tree. However, the inclusion of samples from additional height levels could have given a more complete picture of the effect of climate on the specific gravity formation within tree, at the expense of additional cost related to sampling and analysis. All the trees harvested and the sample collected are from young trees up to age 25, thus limiting our model application. Considering the future predictions of climate change, climatic effects should not be ignored when modelling wood quality. It is expected that the best model will be useful for more accurate estimation of different mechanical wood properties like modulus of elasticity and modulus of rupture and of loblolly pine. This model can also be used in conjunction with an individual-tree growth and yield simulator. The model can be used by forest practitioners operating within the Southeastern region.

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