COMPARING WOOD QUALITY BETWEEN NATURALLY REGENERATED LONGLEAF, PLANTED LONGLEAF, AND PLANTED LOBLOLLY PINE

by

MORGAN SANDERA

(Under the Direction of Joseph Dahlen)

ABSTRACT

Longleaf pine (*Pinus palustris*) is a southern pine species that can produce high quality wood. Efforts to increase longleaf pine via planting have raised questions about wood properties of planted versus naturally regenerated material. This study compared wood and fiber quality of four species-regeneration combinations as follows: naturally regenerated longleaf pine, planted longleaf pine on forest cutover sites, planted longleaf pine on old agricultural field sites, and planted loblolly pine on forest cutover sites. We measured ring specific gravity (SG) and ultrasonic velocity (USV), and SG and moisture content of both the wood and bark from disks that we scaled to whole-tree values. We found significant differences between species and regeneration types for some measured properties; the main differences we found were on ring SG and USV in the corewood (juvenile wood). Generally, naturally regenerated longleaf pine produced the highest quality corewood followed by longleaf pine grown on cutover sites.

INDEX WORDS: moisture content, *Pinus palustris*, *Pinus taeda*, southern pine, specific gravity, ultrasonic velocity, wood and fiber quality

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CHAPTER 1

COMPARING WOOD QUALITY BETWEEN NATURALLY REGENERATED LONGLEAF, PLANTED LONGLEAF, AND PLANTED LOBLOLLY PINE

1.1 INTRODUCTION

Longleaf pine and land use changes

The southeastern United States (U.S.) is one of the leading forest products producing regions in the world (Donagh et al. 2019). An important species group within the region is southern pine, with the 'major' southern pines consisting of loblolly (*Pinus taeda*), slash (*Pinus elliottii)*, shortleaf (*Pinus echinata*), and longleaf pine (*Pinus palustris)* (Wear and Greis 2002). Longleaf pine was once the most dominant and important southern pine species (Schultz 1999; McKeand et al. 2003; So et al. 2018), but over time factors including exploitation, reduction of fire on the landscape, forestlands being converted to agricultural fields, and urban expansion have all led to the decline of longleaf pine ecosystem (Peet and Allard 1993; Walker 1999; Van Lear et al. 2005; Oswalt et al. 2012). Prior to the 1800's, there were an estimated 30 million hectares of longleaf pine from southern Virginia to eastern Texas (Frost 1993; Landers et al. 1995; Brockway et al. 2006; Oswalt et al. 2012). This vast swath of forestland gave rise to a unique ecosystem rich in botanic diversity (Barnett 1999), but now represents less than 4% of its original extent.

All of the southern pines are shade intolerant pioneer species (Demers et al. 2021; Grebner et al. 2022). Compared to other southern pines, longleaf pine has a unique characteristic known as the "grass stage" that happens after germination and lasts anywhere between 2 to 20 years (Brockway et al. 2005; Dickens et al. 2018). During this phase, the tree consists of a terminal bud with a tuft of needles that is rooted into the ground until the rootstock is sufficiently developed, initiating a spurt of rapid growth in the tree (Boyer 1990; Brockway et al. 2005). This adaptation enables longleaf pine seedlings to survive on a fire-prone landscape since the tree has no stem during this phase, there is no damage to the cambium during a fire (Barnett 1999; Brockway et al. 2005). Fire has historically been an important feature of the landscape, whether it be from a natural lightning strike or intentional burning practiced by Native Americans, European colonists, and now modern land managers (Schwartz 1994; Landers and Boyer 1999; Van Lear et al. 2005; Oswalt et al. 2012). Without fire, and the bare mineral soil it creates, longleaf pine seeds cannot germinate, and the tree can have difficulties with establishment. When competition becomes severe more rapidly growing species such as sweetgum (*Liquidambar styraciflua)* and other southern pines can outcompete naturally regenerated longleaf pine (Schwartz 1994; Landers et al. 1995; Wear and Greis 2002; Oswalt et al. 2012).

In the late 18th century, the expansions in the railroad system allowed timber to be transported and thus harvested from previously inaccessible locations. At the same time demand from naval stores for longleaf pine to extract pitch and rosin accelerated. These factors initiated the accelerated removal of longleaf pine, leading to exploitation (Oswalt et al. 2012; Van Lear et al. 2005). By the late 19th century, a large proportion of longleaf pine forests, as well as forestland in general in the southeastern U.S. had been replaced with agricultural crops (Barnett 1999; Oswalt et al. 2012). Land use changes as a result of urban expansion, and conversion to loblolly pine plantations in the 20th century further reduced the extent of longleaf pine forests (Landers et al 1995; Van Lear et al. 2005; Oswalt et al 2012). These changes caused considerable habitat fragmentation for the longleaf pine ecosystem, to which only 2 million hectares of longleaf pine remains (Van Lear et al. 2005; America’s Longleaf 2009). By the mid-20th century, the southeast was dealing with agricultural land abandonment because of low soil fertility. This occurrence gave rise to the government assisted Conservation Reserve Program which set out to convert marginal cropland into forestland (Clabo et al. 2020).

While the “grass stage” has been evolutionarily beneficial to longleaf pine (Jin et al. 2019), it is one of the main deterrents when considering the planting of longleaf pine (Demers et al. 2021). The duration of the “grass stage” is determined by genetics and environmental factors, such as the level of competition (Nelson et al. 2003). Intensive site preparation and herbicide control of volunteer hardwoods, herbaceous weeds, and grasses have been shown to reduce the amount of time that longleaf pine spends in the “grass stage” (Demers et al. 2021). Nevertheless, there is the possibility of years passing before the tree starts to put on any vertical, aboveground growth, resulting in a longer rotation age than other species such as loblolly pine (Dickens et al. 2018). This resulted in loblolly and slash pine becoming the dominant southern pines in the region through planting efforts (Fox et al. 2007).

Longleaf pine can produce high-quality timber (Connor et al. 2014); however, landowners in the past have not considered it as profitable as loblolly pine or slash pine due to the increased price of bare-root seedlings, its extended grass stage, and longer rotation periods (Brockway et al. 2005; Haywood et al. 2015). Since the 1950’s, tree improvement programs in the southeastern U.S. have been selecting loblolly pine and slash pine trees with desirable traits and crossbreeding them with the goal of creating trees with superior phenotypic and genotypic characteristics as compared to currently available or naturally occurring stocks (Nelson et al. 2015; Isik and McKeand 2019). Loblolly pine and slash pine are currently on their fourth selection cycles, while longleaf pine is only on its first (Fikret and McKeand 2019). Although the rotation age is longer than other southern pine species, the long needles of longleaf pine also make it highly valued for pine straw production that is used for landscaping, which provides an additional source of revenue to landowners (Susaeta and Gong 2019).

As the uncertainties of climate change increase and natural disasters continue to gain intensity throughout the southeastern U.S. there may be a need to reevaluate current forestry practices (Measham et al. 2011). Planting longleaf pine may help to reduce the risk associated with drought, hurricanes, wildfires, and insects and diseases (Clark et al. 2018; Martinson 2007). Compared to other southern pines, longleaf pine has a greater resistance to attack and lower rates of mortality from the southern pine beetle (*Dendroctonus frontalis)*; the exact reasons for this are contentious and not fully understood (Martinson et al. 2007; Duerr and Mistretta 2013). Pye et al. (2011) reported that landowners growing southern pine had lost approximately $1.2 billion between 1973 and 2003 due to the southern pine beetle, which represents approximately 8% of the annual roundwood harvest of southern pines. Increased climate variability has led to more frequent and intense hurricane events in the southeastern U.S. (Goldenberg et al. 2001; Johnsen et al. 2009; Rutledge et al. 2021). Johnsen et al. (2009) and Diop et al. (2009) found that longleaf pine had lower mortality than loblolly pine following hurricane Katrina with longleaf pine (36%), slash pine (48%), and loblolly pine (84%) stems having sustained some form of damage. Additionally, research conducted on the damages from hurricane Michael in 2018 concluded that longleaf pine had lower rates of damage (11%) than loblolly (17%) and slash (27%) pine for trees within the 10 cm – 30 cm diameter at breast height (DBH) range (Rutledge et al. 2021). A tree's resistance to strong winds is due to several mechanical and physical factors, with tree height, crown size, and shape as some of the most important (Ancelin 2004).

Due to the ecological importance of the longleaf pine ecosystem, efforts have been underway since the early 1990's by the Longleaf Alliance, the Natural Resource Conservation Service, and United States Forest Service to provide financial assistance and information regarding the restoration, regeneration, and management of longleaf pine to landowners (Brockway et al. 2005; Connor et al. 2014). A fifteen-year goal is currently underway to increase longleaf pine to 3.2 million hectares by 2025; this goal is being accomplished through the support of federal and state agencies that provide financial incentives and cost-share programs to help encourage private landowners to plant longleaf pine (America's Longleaf 2009). Since 2010, approximately one million hectares have been enrolled through America's Longleaf Restoration Initiative for practices to maintain, improve, and restore longleaf pine on non-industrial private lands in the south (Burger 2019). Because of these efforts, longleaf pine now grows on three major regeneration types, naturally regenerated sites, planted cutover sites where the land prior to the current rotation was forested, and lastly, planted sites where the land previous to the current rotation was used for agricultural crops (Dickens et al. 2018).

Longleaf pine wood and fiber quality

Historically longleaf pine has been regarded as having similar wood quality to slash pine, and higher quality relative to the other southern pines (Zobel et al. 1972; Snyder et al. 1977). Specific gravity (SG), which is the wood density divided by the density of water, an indicator of wood quality, is one of the most important properties of wood (Larson et al. 2001). According to the Wood Handbook (Kretschmann 2021), longleaf pine has the same average SG (0.59), modulus of elasticity (13.7 GPa), and modulus of rupture (100 MPa) as slash pine; loblolly pine has lower average SG (0.51), lower modulus of elasticity (12.3 GPa), and lower modulus of rupture (88 MPa). One reason why longleaf pine and slash pine have higher wood quality is because historically, they grew below the fall-line, which is a geologic boundary that divides the piedmont and coastal plain regions in the U.S. southeast (Peet and Allard 1993) where there are lower levels of water stress during the summer months and a longer growing season (Jordan et al. 2018). As an example of regional variation in wood properties for loblolly pine, SG is highest near the southern coasts and decreases with increasing latitude (Jordan et al. 2008). Jordan et al. (2007) and Antony et al. (2011) found similar trends for microfibril angle measured at the ring level, and modulus of elasticity and modulus of rupture measured on clearwood static bending samples. These trends show that a longer growing season leads to 'better' wood properties.

When grown on the same site, Eberhardt et al. (2017) found that slash pine had slightly higher whole-disk SG compared to loblolly pine at 21-24 years old, but the differences (0.52 vs 0.49) were less than what was reported in the Wood Handbook which represents mature trees (Kretschmann 2021). Eberhardt and Samuelson (2022) compared SG values of mature (50 years old) longleaf, loblolly, and slash pine that were grown on the same site in Mississippi and found that after very wet years, longleaf pine had the highest ring SG values (0.65), followed by slash pine (0.63) and loblolly pine (0.60). As an example of an impact on SG from silvicultural practices, So et al. (2018) reported a lower mean whole tree SG value of 0.526, compared to 0.541 at DBH, for pruned 70-year-old mature longleaf pine growing in Louisiana.

Acceleration of individual tree growth in plantations has reduced the time required to grow trees to merchantable size (Clark et al. 2006; Fox et al. 2007). For example, intensive management has decreased the rotation age to grow loblolly pine sawtimber (DBH $\geq$ 30.5 cm) to approximately 25 years old (Yin and Sedjo 2001). Lower planting densities, fertilizer applications, woody and/or herbaceous vegetation control, optimizing the timing of thinning for continued growth, and the use of enhanced genetics all contribute to a reduction in rotation age as well (Allen 2005). The rapid growth that occurs in plantations results in the trees having a high amount of lower quality corewood (juvenile wood) relative to outerwood (mature wood) (Larson et al. 2001). Corewood has lower SG, modulus of elasticity, modulus of rupture, and tracheid length, while having higher microfibril angle and higher longitudinal shrinkage than outerwood (Ying et al. 1994; Larson et al. 2001; Jordan et al. 2007; Dahlen et al. 2018; 2020). Slower growth results in trees reaching merchantable size at later ages, which allows for higher quality and more uniform wood properties (Larson 1969).

Project rationale

As the reintroduction of longleaf pine gains momentum, it is imperative to understand how site selection and regeneration method will influence the wood quality, since this is one of the touted advantages of planting longleaf pine (Snyder et al. 1977; Wear and Greis 2002). Referencing historical comparisons of wood quality for naturally regenerated longleaf pine may not be representative for trees grown in plantations, because cambial age (ring number from pith) is a major driving factor with regards to changes in wood and fiber quality (Eberhardt et al. 2019). Here our objective was to determine wood property differences in longleaf pine by comparing different regeneration methods (naturally regenerated, planted on forest cutover sites, and planted on old agricultural field sites); we also included planted loblolly pine grown on forest cutover sites in our comparison. We focused our comparison on stands that contained trees that are large enough (DBH > 20.3 cm) to be used to produce structural lumber. The objective of this study is to provide useful information about how regeneration methods and land-use history affect wood properties in longleaf pine, which will inform landowners interested in planting longleaf pine as an alternative to the other southern pine species.

1.2 MATERIALS AND METHODS

Stand selection

In the southeast U.S., merchantable trees are generally categorized as pulpwood (minimum diameter at breast height (DBH) of 15.2 cm), chip-n-saw (minimum DBH of 20.3 cm), and sawtimber (minimum DBH of 30.5 cm) (TimberMart-South 2022). Stand selection for the present study focused on sites that were chip-n-saw or larger trees since stands with these sized trees are most often clearcut and the products used for structural lumber. We selected three stands from each of the following four species-site combinations (naturally regenerated longleaf pine, planted longleaf pine on forest cutover sites, planted longleaf pine on old agricultural fields, and planted loblolly pine on forest cutover sites) were selected for sampling; note that for logistical purposes, we did not select slash pine. The forest cutover sites refer to sites where the prior crop was trees, and the old agricultural fields refer to sites where the prior crop was not trees (e.g. cotton, corn).

The longleaf pine ‘natural stands’ were located at the Jones Center at Ichauway (N = 3) in southwest Georgia. This region served as the target area for the stand selection since we attempted to reduce the effect of environmental variation on the wood and fiber properties (Jordan et al. 2008). The longleaf pine ‘old ag sites’ were also selected from sites on the Jones Center at Ichauway property (N = 3). Longleaf pine ‘cutover sites’ were located on a mixture of private land (N = 2) and federal land (St. Marks National Wildlife Refuge) (N=1). Loblolly pine ‘cutover sites’ were all located on private land (N = 3). Altogether, 11 stands in southwest Georgia and 1 stand in the panhandle of Florida (St. Marks refuge) were selected; all stands were located within 209 kilometers of each other (Figure 1).

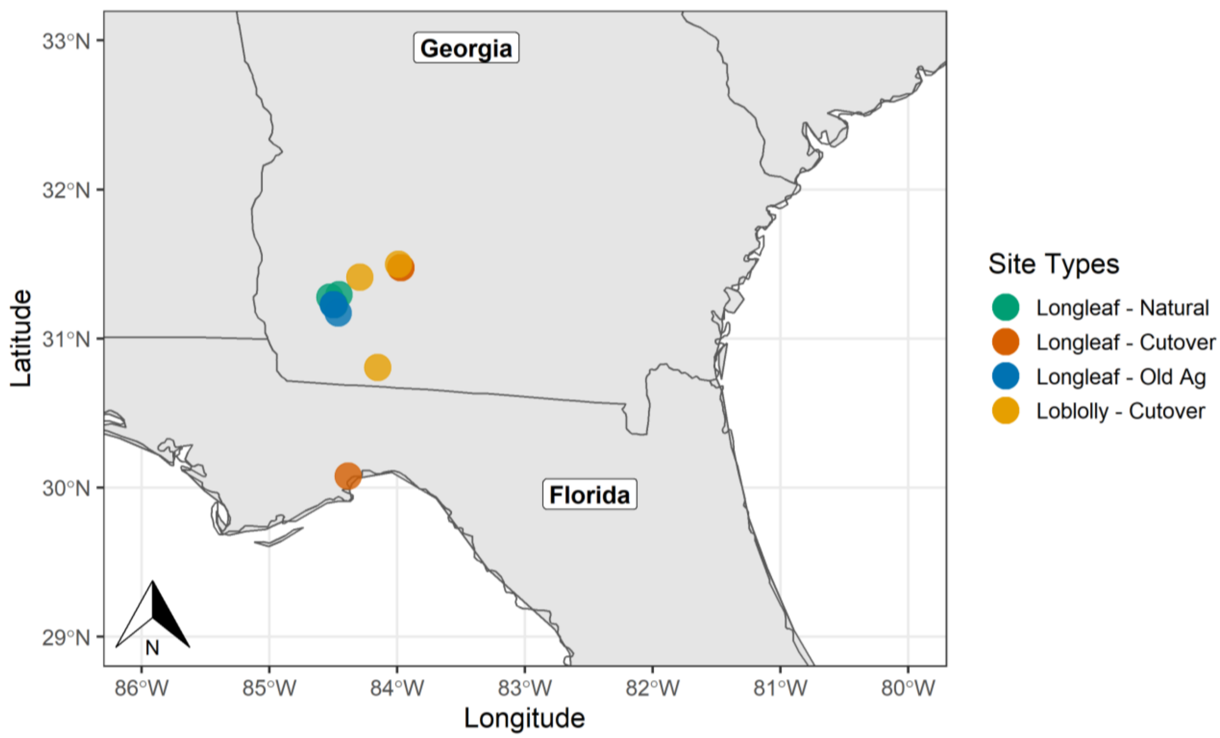

Figure 1. Map of stand locations by regeneration type.

Given the differences in management between longleaf pine and loblolly pine, in addition to the differences in regeneration methods, no specific silvicultural treatments were considered for the stand selection. We focused instead on finding sites that contained trees as described above. However, each planted stand had been thinned at least once and most of the longleaf pine stands were on a three-year burn regimen except the stand at St. Marks which is burned less frequently, with the last time being in 2014. All the planted trees were bare root seedlings except one longleaf pine cutover stand which was from containerized seedlings.

Tree and field sampling methods and sample processing

We conducted an inventory cruise within a 22.8 m by 33.5 m rectangular subsection of each stand to determine average height and diameter distributions. Planted stands were between the ages of 30-40 years old except for the longleaf pine at St. Marks which was 53 years old. The natural stands had trees that ranged from 32-71 years old (determined later via ring counting on the X-ray densitometer).

Results from the stand inventories grouped by regeneration type (Table 1) show that the loblolly pine – cutover stands had the highest mean DBH of 31.6 cm, which was expected because loblolly pine grows quickly. The longleaf pine – natural stands have the lowest average DBH of 23.5 cm but the highest average height of 23.9 m. The reason for these observed trends is due to one of the stands having a high stocking density, forcing the trees to grow more in height and less in diameter (Harrison and Shiver 2002). The differences in regeneration type averages between longleaf pine – old ag stands (DBH 26.5 cm, height 22.1 m) versus longleaf pine - cutover stands (DBH 24.8 cm, height 20.9 m) may be due to residual fertilizers in the soil from agricultural management (Dickens et al. 2018). Basal area (BA) ranged from 26.2 m^2/ha for loblolly pine - cutover to 17.5 m^2/ha for longleaf pine - old ag.

Table 1. Stand location and general inventory characteristics for each species and regeneration type (BA = Basal area, DBH = Diameter at breast height, SD = Standard deviation).

						DBH (cm)		Height (m)	
Stand	Latitude	Longitude	Species	Regeneration type	BA (m^2/ha)	Mean	SD	Mean	SD
1	31.294	-84.455	Longleaf	Natural	17.7	23.5	3.7	21.2	9.2
2	31.227	-84.494	Longleaf	Natural	15.6	20.1	3.7	20.3	10
3	31.277	-84.527	Longleaf	Natural	34.0	25.7	1.7	28.0	4.5
4	30.077	-84.385	Longleaf	Cutover	19.7	21.8	1.6	20.8	6.7
5	31.477	-83.970	Longleaf	Cutover	25.6	25.9	0.9	21.3	3.8
6	31.476	-84.397	Longleaf	Cutover	24.0	27.3	1.6	20.6	6.2
7	31.227	-84.500	Longleaf	Old Ag Field	13.1	29.1	1.2	23.1	5.0
8	31.227	-84.502	Longleaf	Old Ag Field	21.7	24.2	1.7	20.5	5.3
9	31.170	-84.464	Longleaf	Old Ag Field	17.8	28.5	1.6	23.8	6.2
10	30.807	-84.152	Loblolly	Cutover	34.0	30.8	2.0	24.3	0.4
11	31.412	-84.295	Loblolly	Cutover	16.2	33.5	0.9	24.9	6.9
12	31.498	-83.991	Loblolly	Cutover	28.4	30.7	1.2	22.9	3.8
Overall			Longleaf	Natural	22.4	23.5	3.0	23.9	14.3
			Longleaf	Cutover	23.1	24.8	1.6	20.9	5.0
			Longleaf	Old Ag Field	17.5	26.5	1.8	22.1	7.3
			Loblolly	Cutover	26.2	31.6	1.7	23.4	5.2

Tree selection and felling

We selected ten trees from each stand for sampling across the diameter distribution of trees that were chip-n-saw or sawtimber size. The general characteristics of the trees that we felled from each stand can be found in Table 2. We only sampled trees which were straight and had minimal defects (no cankers, forks, ramicorn branching, excessive sweep). Sampling occurred during the summer of 2021 except for one stand which was sampled during January of 2021 (stand 1: longleaf pine - natural) which was harvested prior to the summer to allow us to work out the methodology for the project. We felled trees using a chainsaw and measured total height and height to live crown using a logger's tape. We collected disks at 0.15 m (stump height), 0.61 m, 1.37 m (breast height), 2.6 m, 5.3 m, 9.9 m, 14.8 m, and at the 10.1 cm diameter top and 7.6 cm diameter top; if the 10.1 cm top occurred after 19.8 m, we cut an additional disk at 19.6 m (Figure 2). If one of the fixed height disks landed on a major defect or branch whorl, the height was adjusted and recorded. This effort focused on sampling more disks within the first 5 m of the tree (e.g. log 1) where wood properties change rapidly (Dahlen et al. 2020; 2022). One 45 mm and one 25 mm (longitudinal) thick disks were collected from each height level sampled. One disk was used for ring-by-ring property work. The second disk was used to measure whole-disk properties, and these were placed in individual plastic bags as soon as possible to retain moisture. One tree from stand 12 (longleaf pine - cutover) was accidently left in the woods. Thus, a total of 119 trees were sampled with a total of 1,119 cross sectional disks. All the disks were transported to the Wood and Fiber Quality Lab at the University of Georgia where they were frozen at -20°C until they were processed.

Table 2. General characteristics of the trees felled by species and regeneration type (BA = Basal area, DBH = Diameter at breast height, SD = Standard deviation).

				DBH (cm)				Height (m)			
Stand	Species	Regeneration type	Age (years)[1]	Mean	SD	Min	Max	Mean	SD	Min	Max
1	Longleaf	Natural	32-51	29.4	1.3	24.1	34.5	10.6	9.8	21.2	25.4
2	Longleaf	Natural	37-66	28.5	1.3	24.4	34.8	12.2	5.5	20.0	26.6
3	Longleaf	Natural	66-71	29.0	1.5	23.6	35.3	21.7	6.2	27.1	30.2
4	Longleaf	Cutover	53	26.6	1.3	23.4	32.0	14.9	5.4	19.8	24.4
5	Longleaf	Cutover	32	28.3	1.1	23.9	32.5	13.6	3.2	20.1	23.7
6	Longleaf	Cutover	34	28.9	1.5	23.4	34.3	11.3	4.4	17.7	23.2
7	Longleaf	Old Ag Field	36	28.4	1.6	22.9	35.3	16.0	7.0	21.6	26.8
8	Longleaf	Old Ag Field	36	28.8	1.5	23.4	34.0	12.6	6.4	19.6	22.6
9	Longleaf	Old Ag Field	30	28.7	1.6	22.9	36.1	14.8	6.0	21.9	25.6
10	Loblolly	Cutover	32	28.4	1.4	23.4	34.5	15.3	8.0	21.5	28.4
11	Loblolly	Cutover	33	32.9	0.6	31.0	35.8	15.5	7.0	23.8	28.8
12	Loblolly	Cutover	35	29.1	1.5	23.9	34.8	15.3	5.0	20.8	25.7
Overall	Longleaf	Natural	54	28.9	1.4	24.0	34.9	14.8	7.2	22.7	27.4
	Longleaf	Cutover	40	27.9	1.3	23.5	32.9	13.3	4.3	19.2	23.8
	Longleaf	Old Ag Field	34	28.6	1.6	23.0	35.1	14.5	6.5	21.1	25.0
	Loblolly	Cutover	33	30.1	1.1	26.1	35.1	15.4	6.7	22.1	27.7

[1]Ages reported exclude the time that longleaf pine was in the “grass stage”

Figure 2. Example of cross-sectional disks that were collected incrementally up the tree.

Pith to bark sample preparation

We cut the first set of disks on a bandsaw into approximately 32 mm wide (tangential) bark-to-bark strips taking care to avoid any defects (e.g. branches) and then gently dried at ~35°C for 24 to 48 hours until they reached a moisture content (MC) less than 18% (oven-dry basis). The strips were then cut in half at the pith. One of the halves was cut on a bandsaw into a 35 mm longitudinal and 12 mm wide tangential sample with the intent to keep the grain as close to vertical as possible; this was done to increase the accuracy of the measurements obtained from the various instruments. Then the sample was glued between two pieces of yellow-poplar wood core holders. After the glue dried, the samples were then cut using a 4-blade saw to create one X-ray densitometry sample (2 mm longitudinal), one ultrasonic velocity sample (8.5 mm longitudinal), and one 'other' sample (15 mm longitudinal) (Figure 3). The radial dimensions varied by the length of each sample.

Figure 3. Radial strips used for measuring X-ray densitometry (bottom) and ultrasonic velocity (top) values.

X-ray densitometry

The X-ray densitometry samples were submerged in acetone for approximately 24 hours to remove extractives and then left in a fume hood to allow the acetone to evaporate. The air-dried samples were then conditioned at 22°C and 52% relative humidity (approximate MC of 10%). Samples were scanned by using a QTRS-01X Tree Ring Scanner (Quintek Measurement Systems, Knoxville TN, USA) with the X-ray beam passing through the sample on the transverse face. The instrument was calibrated to basic specific gravity (oven dried weight, green volume). The radial step resolution was 0.04 mm. Earlywood and latewood were differentiated by using a SG threshold value of 0.48 (Antony et al. 2011; Eberhardt and Samuelson 2015) and this threshold value was also used as a preliminary distinction between rings; all rings were manually checked for accuracy. Through X-ray densitometry, ring SG, earlywood and latewood SG, latewood percent, and growth (ring width, ring basal area) information were obtained.

Ultrasonic testing

Microfibril angle is an important contributor to wood stiffness (high microfibril angle is associated with low stiffness wood) (Tabet 2013) and it has been shown to have a strong inverse correlation with dynamic modulus of elasticity in a variety of softwood species (Cave 1968; Ando et al. 2018). Microfibril angle is typically measured via a microscope or using X-ray diffraction instrumentation (such as the SilviScan) (Schimleck et al. 2019). An alternative is to measure ultrasonic velocity (USV) because the dynamic modulus of elasticity of a material is a function of the density times the square of the ultrasonic velocity (Ross 2015). Dahlen et al. (2022) measured ultrasonic velocity using ultrasonic frequencies (>20 kHz) and found strong relationships between microfibril angle measured using SilviScan (R^2 = 0.91, RMSE = 2.6°) in loblolly pine.

To measure USV from pith to bark, the same protocol was followed as explained in Dahlen et al. (2022). Briefly, the 8.5 mm longitudinal samples were sanded on both sides using 320-grit sandpaper to achieve a smooth uniform surface. Sample thickness after sanding was approximately 8.2 mm. Samples were then conditioned to approximately 10% MC before measuring the USV on an OPUS ultrasonic testing machine (SoniSys, Atlanta GA, USA). The instrument needs to be calibrated for thickness measurements before each session by using two reference shims. USV is determined by measuring the time it takes for an ultrasonic signal to pass through a sample compared against the sample thickness. USV is measured in 10 mm radial increments on the transverse face. Both transducers have a layer of neoprene attached to them which works as a couplant by facilitating the transmission of the ultrasonic frequency from the transducer into the wood. The bottom transducer is fixed in place and the top transducer moves vertically (Figure 4). The sample is mounted onto a stage which moves 10 mm at a time where the total number of measurements is determined by the length of the particular sample. If there is a portion of the sample left after the measured increments have been completed, the instrument will move the remaining distance and take a final reading near the bark.

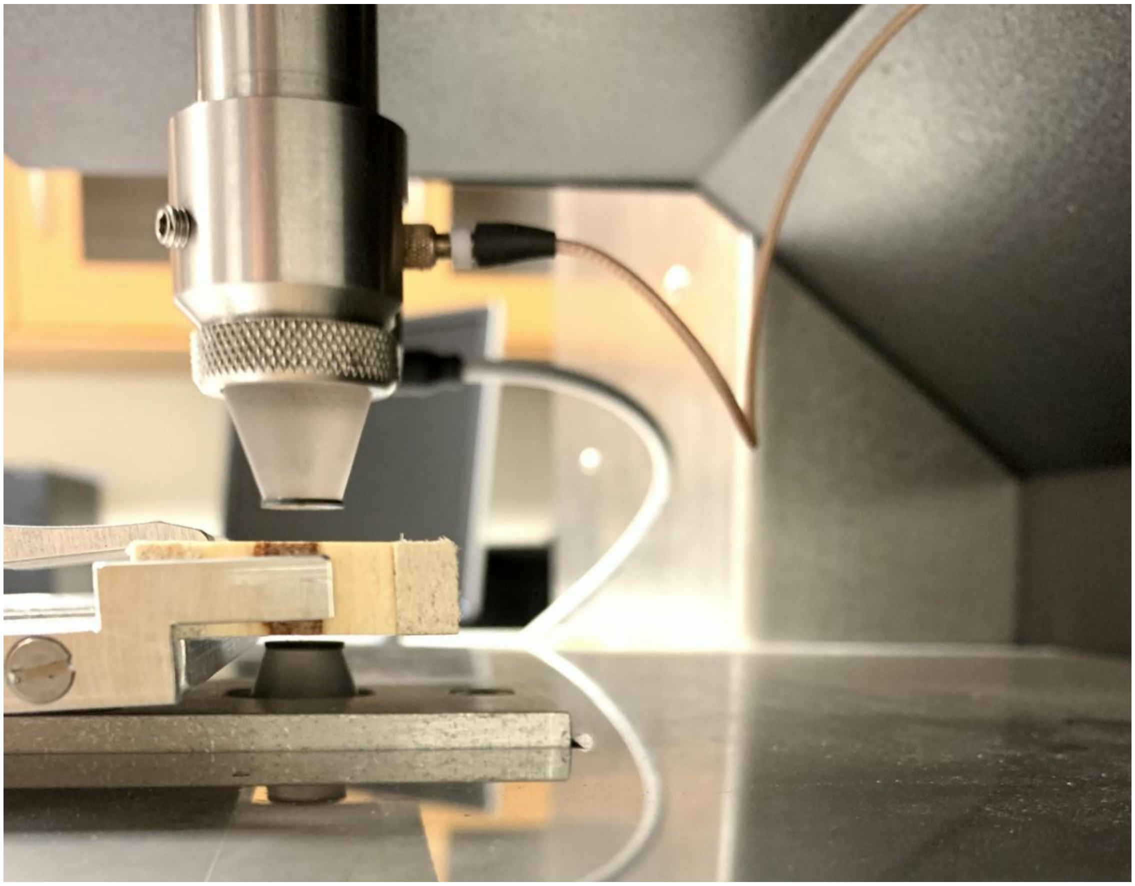

Figure 4. Ultrasonic testing machine transducers with a radial strip sample in place.

Data analysis

All statistical analysis was conducted using the R statistical software (R Core Team 2022) environment along with the RStudio interface (RStudio 2022). The following packages were utilized during data analysis, gridExtra (Auguie and Antonov 2017), lmerTest (Kuznetsova et al. 2020), multcomp (Hothorn et al. 2022), needs (Katz 2016), nlme (Pinheiro et al. 2022), and tidyverse (Wickham 2021).

All data except whole tree wood and bark values were fit in nonlinear mixed effects models (Pinheiro et al. 2022) with stand and tree as random effects. Serial correlation (autocorrelation) due to the repeated measurements (multiple measurements of rings within each disk, and/or multiple disks measured per tree) was addressed by adding a first-order continuous autoregressive AR(1) autocorrelation structure (Pinherio and Bates 2000). We assessed differences between regeneration types by testing whether they had significantly different parameter values, with p-values ≤ 0.05 indicating statistical significance (Table A.1.1). Models were evaluated using the AIC (Akaike information criterion) values, the fit indices (R^2) of the fixed effects, and the model error values (RMSE). Analysis of variance (ANOVA) using a linear mixed effects model with stand and tree within stand as random effects was done to test for regeneration type differences; significant differences of the mean values were then determined using a Tukey Test.

Ring specific gravity model development

A four-parameter logistic function was used for modeling variation of SG in relation to cambial age (Dahlen et al. 2022):

$$SG_{ijkl} = \beta_0 + \frac{\beta_1 - \beta_0 + \beta_4 * log\ (DH_{ijk} + 1)}{1 + exp^{\frac{(\beta_2 - CA_{ijkl})}{\beta_3}}} \qquad (1)$$

where *SG* is the average ring SG and *CA* is the cambial age (ring number), with each representing the *l*th annual ring of the *k*th disk from the *j*th tree at the *i*th site, *DH is* the disk height (m) of the *k*th disk from the *j*th tree at the *i*th site, and exp is the mathematical constant e. The fixed effects parameters in the model are $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4$; where β_0 is the intercept or the starting value at cambial age 0, β_1 is the asymptote as cambial age approached infinity, β_2 is the inflection point, β_3 is the scale parameter, and β_4 is the fixed effect that accounts for the variation in disk height. Previous studies indicate that southern pine SG varies by height within the tree, the common trend shows that at a specified cambial age, SG decreases as height increases (Megraw 1985; Wiemann and Williamson 2014; Dahlen et al. 2018).

Ring-by-ring ultrasonic velocity model development

We found that longleaf pine and loblolly pine had different patterns of USV variation and thus chose to model each species using a different model. Longleaf pine USV was modeled using a three-parameter logistic function:

$$USV_{ijkl} = \frac{\beta_1}{1 + exp^{\left(\frac{\beta_2 - CA_{ijkl}}{\beta_3}\right)}} + \beta_4 * log(DH_{ijk}) \quad (2)$$

where USV_{ijkl} is the velocity value of the lth ring of the kth disk from the jth tree in the ith stand. The fixed effects parameters in the model are $\beta_1, \beta_2, \beta_3, \beta_4$; where β_1 is the asymptote as cambial age approached infinity, β_2 is the inflection point, β_3 is the scale parameter, and β_4 is the fixed effect that accounts for the variation in disk height. For loblolly pine we used a four-parameter logistic function (Dahlen et al. 2022):

$$USV_{ijkl} = \beta_0 + \frac{\beta_1 - \beta_0}{1 + exp^{\frac{(\beta_2 + \beta_4 * log\ (DH_{ijk})) - CA_{ijkl}}{\beta_3 + \beta_5 * log(DH_{ijk})}}} \quad (3)$$

where β_4 alters β_2 and β_5 alters β_3 based on height within the tree; the remaining variables are the same as in equations 1 and 2.

Whole-disk measurements of specific gravity, moisture content, and percent wood to bark

For each of the whole-disks, the diameter outside bark (DOB) was recorded using a diameter tape and the green weight of the disk with the bark intact was recorded using a digital scale. The bark was removed from each disk using a combination of a hand chisel and a custom-made debarker (Figure 5). One large piece of intact inner and outer bark from each disk was saved, labeled, and weighed to determine bark properties. The diameter inside of the bark (DIB) was measured and the disk was weighed. The difference between the green weight of the whole disk (wood and bark) and the green weight of the wood represented the total weight of the bark. Each sample (wood and piece of bark) was submerged in water and left to soak for 3-4 days until fully saturated and then volumes were measured using water displacement (ASTM International 2022). The samples were oven dried at 103 ± 2°C until a constant mass was obtained, at which point the oven dried weights were recorded. The wood and bark SG were each calculated:

$$SG = \frac{Weight_{OD}}{Volume} * \frac{1}{K} \quad (4)$$

where *SG* is the basic specific gravity of the wood or bark, $Weight_{OD}$ is the oven dried weight (g), *Volume* is the green volume (cm^3), and *K* is the density of water (1 g/cm^3). The MC (dry-basis) was calculated:

$$MC = \frac{(Weight_G - Weight_{OD})}{Weight_{OD}} * 100 \quad (5)$$

where *MC* is the percent moisture content, $Weight_G$ is the green weight (g) and $Weight_{OD}$ (g) is the oven dried weight of the particular sample.

Figure 5. Debarked cross sectional disks and bark “pieces”.

Relationship between disk diameter outside bark and diameter inside bark and disk moisture content as a function of specific gravity

We determined if there were differences in the amount of bark between species and regeneration type. To do so, we used the data to create a linear model without an intercept term:

$$DOB = \beta_1 * DIB \tag{6}$$

where DOB is the diameter outside bark (cm), β_1 the slope term, DIB is diameter inside bark (cm).

On an intraspecies level, it has been observed in the literature that SG and MC usually have an inverse relationship (Antony et al. 2015; Eberhardt et al. 2017; Dahlen et al. 2020; Raut et al. 2022). To determine the relationship between MC and SG for the dataset, an adapted nonlinear model found in Raut et al. 2022 was used:

$$MC_{Woodijk} = \beta_0 * \left(1 + SG_{Woodijk}\right)^{\beta_1} \quad (7)$$

where, $MC_{Woodijk}$ is the MC for the wood of the *k*th disk from the *j*th tree at the *i*th site derived from the SG of the wood of the *k*th disk from the *j*th tree at the *i*th site. The fixed effect regression parameters are β_0 and β_1. Equation 7 was used to model each species and regeneration type to predict the relationship between percent moisture content of wood and wood specific gravity by calculating MC as a function of SG.

Whole tree wood and bark calculations

Whole disk inner bark measurements that were recorded in the lab were used to calculate wood area, volume, SG, MC, and percent dry wood per bolt and tree. The area of each disk and the length between disks was calculated and then Smalian's formula was used to calculate bolt volumes. The top section of the tree that spanned from the 76 mm top disk to the tip of the crown was treated as a cone. The area of each section was also used to calculate weighted properties at the bolt level. The bark properties of each bolt were calculated in a similar manner as the wood, with the exception that the bark piece measurements were first scaled to a disk level by multiplying the inside bark disk area by the percent bark. Whole tree properties were derived by summing the wood and bark bolt volumes, and then weighting the SG and MC values of each bolt by the total volume. Whole tree wood and bark values were calculated as percent dry tonnes per green tonne of wood.

1.3 RESULTS

Comparison of specific gravity model parameters by regeneration type

We measured a total of 11,298 rings for longleaf pine – natural, 7,159 rings for longleaf pine – cutover, 6,597 rings for longleaf pine – old ag, and 6,410 rings for loblolly pine – cutover**.** Modeling ring-by-ring specific gravity values for each species-regeneration combinations showed that all regeneration types follow the same general trend of SG increasing from pith to bark, and SG decreasing for a given cambial age as height increases (Figure 6). All four regeneration types share a common intercept ($\beta_0 = 0.356$) and asymptote value ($\beta_1 = 0.618$) (Table 3). There were significant differences between regeneration types with the inflection point (β_2), rate parameter (β_3), and the β_4 parameter which is the effect that disk height has on the model's asymptote (β_1) parameter. Longleaf pine - natural reaches its inflection point (β_2) (4.44 years) at a younger age than the other regeneration types, followed by longleaf pine – cutover (5.03 years), loblolly pine – cutover (6.15 years), and longleaf pine - old ag reaching its inflection point last (7.24 years). The same trend was found for the rate parameter, with longleaf pine - natural having a greater increase in SG ($\beta_3 = 1.82$) and longleaf pine – old ag having the lowest increase ($\beta_3 = 3.88$). There were minor differences with regards to height within tree, with longleaf – old ag having the least impact ($\beta_3 = -0.03$). The fixed effects (cambial age, disk height within tree) of the model (equation 1) resulted in a RMSE of 0.070 and $R^2 = 0.47$ (Table 4). The random effects of the model (stand, tree within stand) were associated with 13% of the variation.

Table 3. Parameter estimates for the specific gravity and ultrasonic velocity models (DH = disk height).

<table>
<tr><th></th><th></th><th></th><th colspan="4">Parameter estimates</th></tr>
<tr><th></th><th></th><th></th><th colspan="3">Longleaf</th><th>Loblolly</th></tr>
<tr><th>Property</th><th>Parameter</th><th>Description</th><th>Natural</th><th>Cutover</th><th>Old Ag</th><th>Cutover</th></tr>
<tr><td>Specific gravity (Eq. #1)</td><td>β_0</td><td>Intercept</td><td colspan="4">0.356</td></tr>
<tr><td></td><td>β_1</td><td>Asymptote</td><td colspan="4">0.618</td></tr>
<tr><td></td><td>β_2</td><td>Inflection</td><td>4.44</td><td>5.03</td><td>7.24</td><td>6.15</td></tr>
<tr><td></td><td>β_3</td><td>Rate</td><td>1.82</td><td>2.49</td><td>3.88</td><td>2.99</td></tr>
<tr><td></td><td>β_4</td><td>DH effect on β_1</td><td>-0.05</td><td colspan="2">-0.03</td><td>-0.04</td></tr>
<tr><td>Ultrasonic velocity (3-parameter) (m s^{-1}) (Eq. #2)</td><td>β_1</td><td>Asymptote</td><td colspan="3">4,866</td><td>-</td></tr>
<tr><td></td><td>β_2</td><td>Inflection</td><td>-1.91</td><td colspan="2">-0.27</td><td>-</td></tr>
<tr><td></td><td>β_3</td><td>Rate</td><td>5.25</td><td colspan="2">4.83</td><td>-</td></tr>
<tr><td></td><td>β_4</td><td>DH effect on β_1</td><td>20.80</td><td>106.20</td><td>122.06</td><td>-</td></tr>
<tr><td>Ultrasonic velocity (4-parameter) (m s^{-1}) (Eq. #3)</td><td>β_0</td><td>Intercept</td><td>-</td><td>-</td><td>-</td><td>3,273</td></tr>
<tr><td></td><td>β_1</td><td>Asymptote</td><td>-</td><td>-</td><td>-</td><td>4,927</td></tr>
<tr><td></td><td>β_2</td><td>Inflection</td><td>-</td><td>-</td><td>-</td><td>5.67</td></tr>
<tr><td></td><td>β_3</td><td>Rate</td><td>-</td><td>-</td><td>-</td><td>2.25</td></tr>
<tr><td></td><td>β_4</td><td>DH effect on β_2</td><td>-</td><td>-</td><td>-</td><td>-1.81</td></tr>
<tr><td></td><td>β_5</td><td>DH effect on β_3</td><td>-</td><td>-</td><td>-</td><td>-0.10</td></tr>
</table>

Table 4. Fit indices and model errors for the specific gravity and ultrasonic velocity models (AIC = Akaike information criterion, RMSE = Root mean square error).

			Fit Indices (R^2)			Model Errors
Property	Equation	AIC	Fixed	Site	Tree	RMSE
Specific gravity	1	90743	0.47	0.51	0.60	0.070
Ultrasonic velocity (m s^{-1})	2	320156	0.71	0.73	0.76	358
Ultrasonic velocity (m s^{-1})	3	81849	0.74	0.74	0.77	312

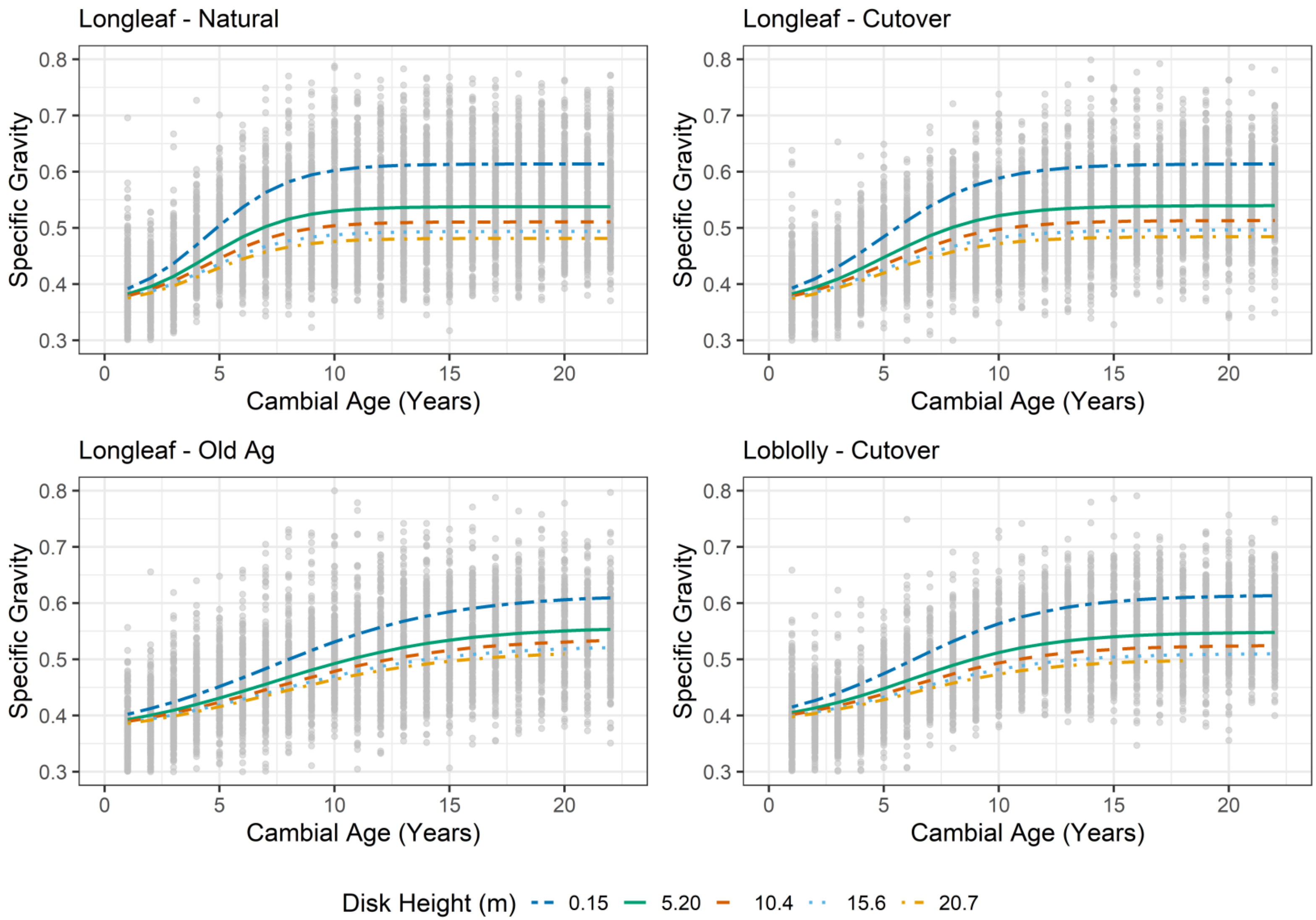

Figure 6. Ring-by-ring specific gravity in relation to cambial age and height within tree for each regeneration type.

Comparison of ultrasonic velocity model paraments by regeneration type

We found minor differences in USV for longleaf pine (Figure 7). Using a three-parameter logistic function, each regeneration type had the same asymptote value (β_1 = 4,866 m s^{-1}) (Table 3). The inflection point for naturally regenerated longleaf pine was slightly lower (β_2 = -1.91) than planted longleaf pine (β_2 = -0.27) but the rate of change was slightly higher for naturally regenerated longleaf pine (β_3 = 5.25) than planted longleaf pine (β_3 = 4.83). The three-parameter logistic function (equation 2) resulted in R^2 = 0.71 with an additional 5% of the variation being attributed to the random effects (Table 4). The RMSE value for the model was 358 m s^{-1}. The loblolly pine - cutover USV model with the four-parameter logistic function had an intercept value of 3,273 m s^{-1} and reached its asymptote at 4,927 m s^{-1} (equation 3). The model resulted in an RMSE value of 312 m s^{-1}, with R^2 = 0.74. Random effects of the model explained an additional 3% of the variation. Figure 8 highlights the differences in wood properties by regeneration type at the stump (0.15 m) and breast height (1.37 m) for SG and USV. The variation in trends between regeneration types for both properties is greatest at the stump. The trends in USV between species is quite variable at the stump but starts to follow a similar trajectory at breast height. It is important to note that some of the variation that we observed can be attributed to the use of separate models between the species.

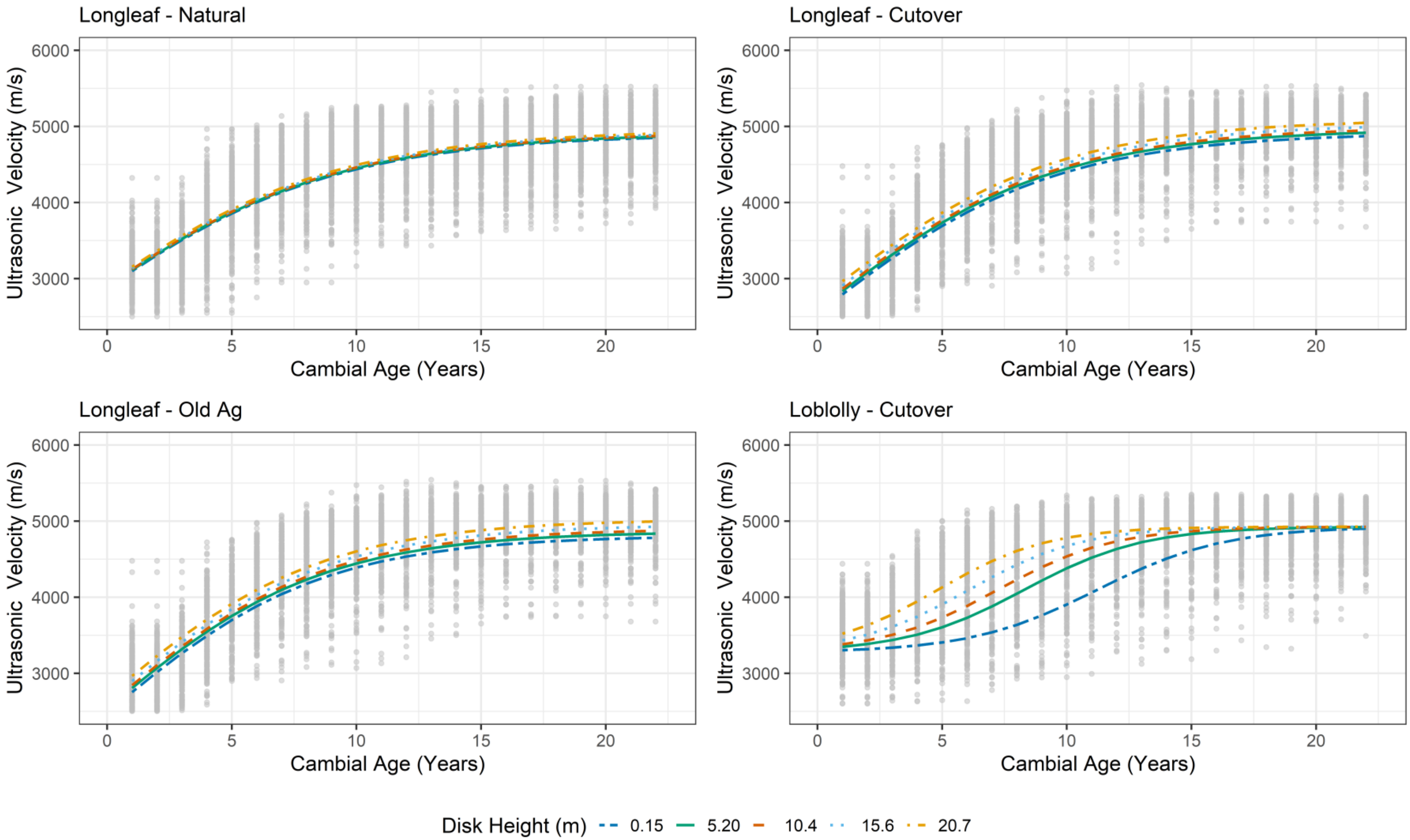

Figure 7. Ring-by-ring ultrasonic velocity in relation to cambial age and height within tree for each regeneration type.

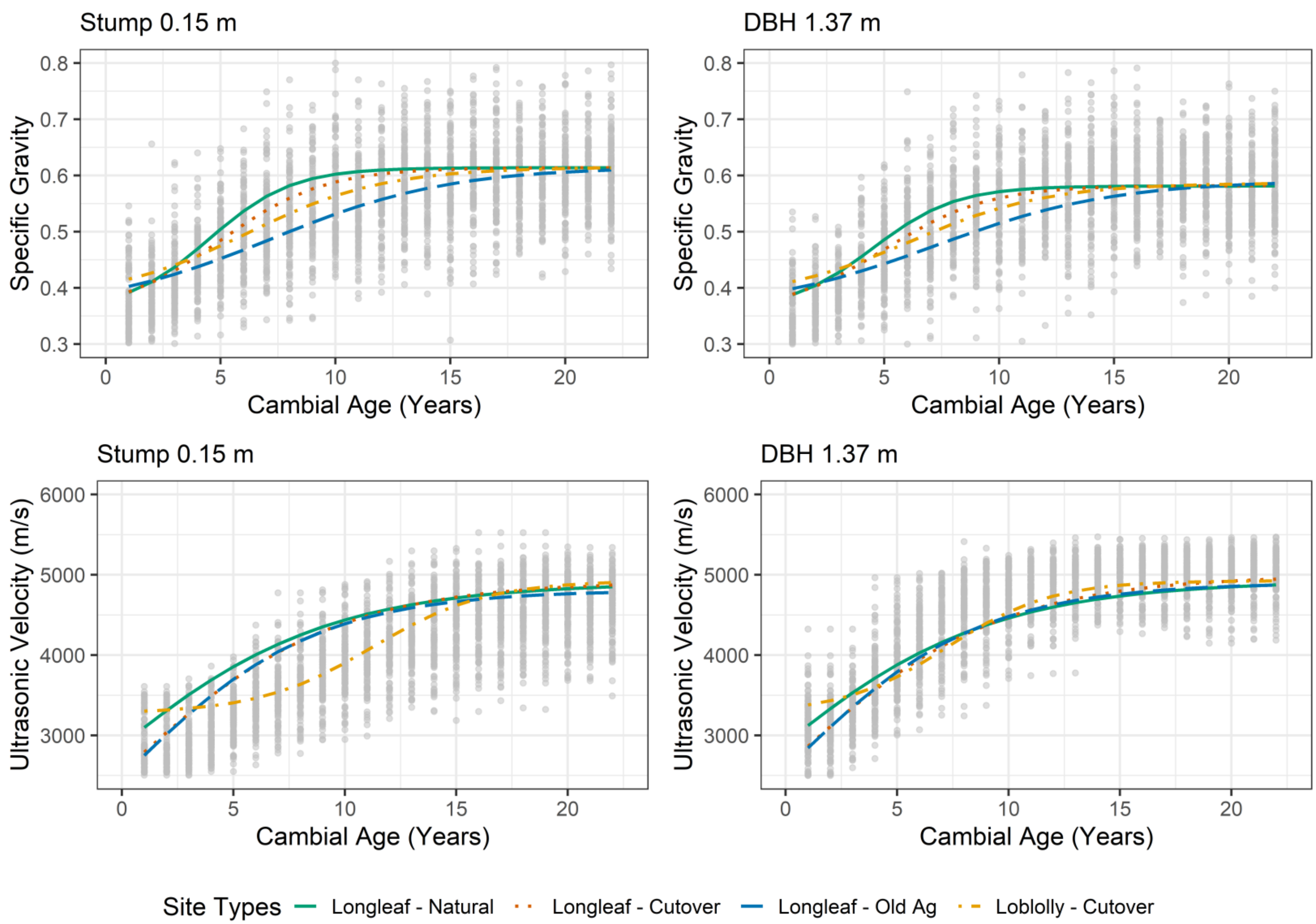

Figure 8. Comparison of specific gravity and ultrasonic velocity trends by regeneration type at stump (0.15 m) and breast height (1.37 m).

Diameter outside bark as a function of diameter inside bark

The linear model (equation 6) for the ratio of diameter outside bark to inside bark was not significantly different between regeneration types, indicating that the ratio between outer bark and inner bark was the same across regeneration types. The β_1 parameter was 0.915 and the model resulted in an R^2 value of 0.99 and an RMSE value of 5.88 cm. Figure 9 shows the linear relationship between diameter outside bark and inside bark.

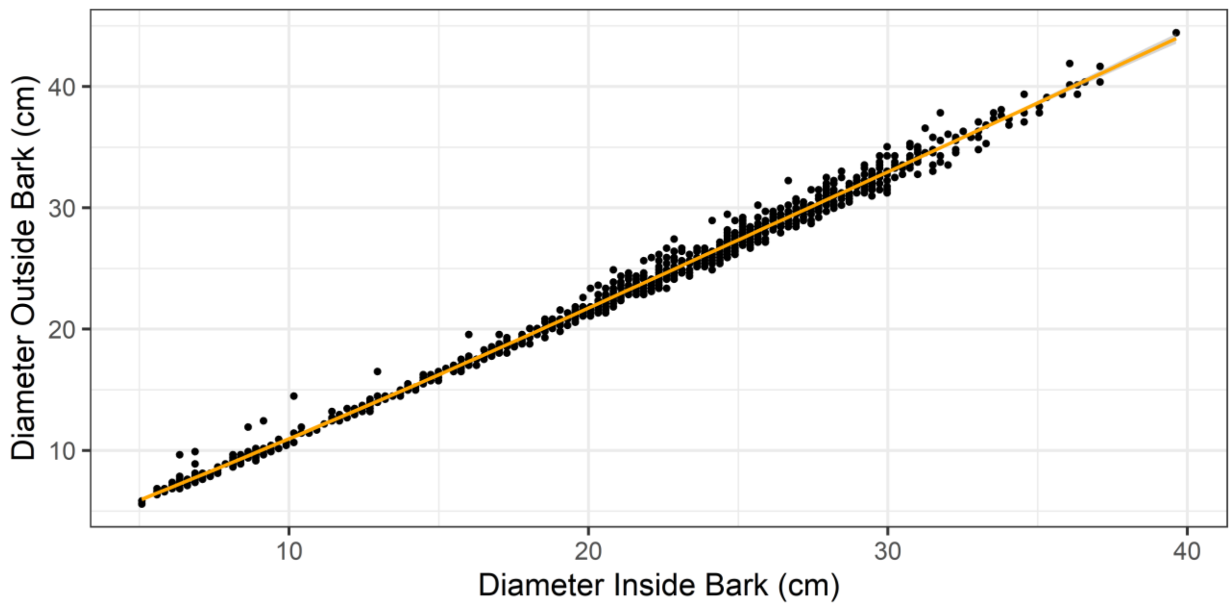

Figure 9. Linear relationship between diameter outside bark and diameter inside bark for all species and regeneration types (longleaf – natural, longleaf – cutover, longleaf – old ag, loblolly – cutover).

Wood moisture content as a function of disk specific gravity

For wood MC as a function of SG, all of the longleaf pine regeneration types shared a common β_0 (1087) and β_1 (-5.8) value, indicating that they are not statistically different than one another (Table 5). The parameters for loblolly pine were found to be significantly different from longleaf pine. The model for MC as a function of SG had an R^2 of 0.85 and an RMSE of 9.20%, the random effects explained an additional 8% of the variation (Table 6). The relationship between wood MC and SG is shown in Figure 10.

Table 5. Parameter estimates and fit statistics relating to wood moisture content (%) as a function of wood specific gravity for each species and regeneration type.

			Parameter Estimates			
			Longleaf			Loblolly
Property	Equation	Parameter	Natural	Cutover	Old Ag	Cutover
Moisture content as a function of specific gravity	7	β_0		1087		628
		β_1		-5.8		-4.61

Table 6. Fit indices and model error values for the moisture content as a function of specific gravity model (AIC = Akaike information criterion, RMSE = Root mean square error).

			Fit Indices (R^2)			Model Error
Property	Equation	AIC	Fixed	Site	Tree	RMSE
Moisture content as a function of specific gravity	7	7580	0.85	0.87	0.93	9.20

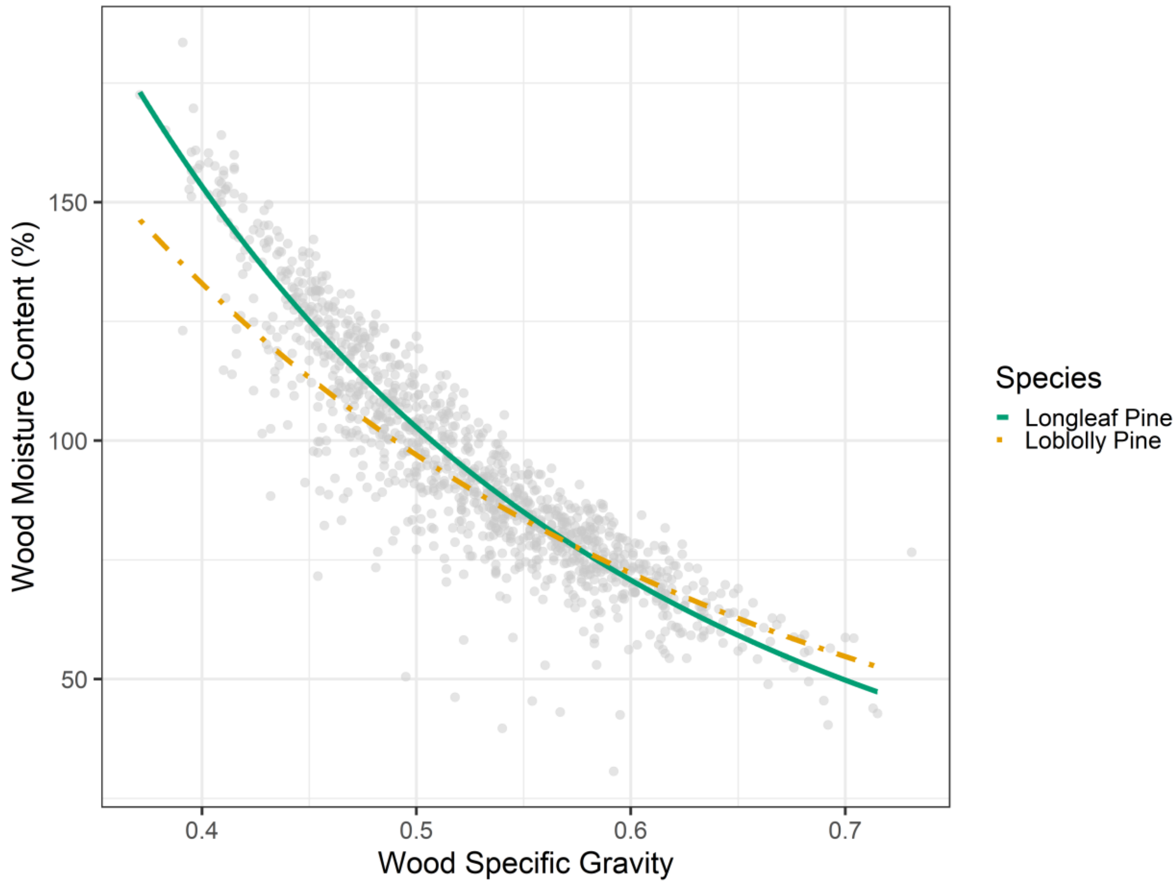

Figure 10. Graph comparing the relationship of wood moisture content (%) as a function of wood specific gravity between species.

Whole tree wood and bark specific gravity, moisture content, and percent dry biomass

Whole tree wood and bark properties were analyzed, and a Tukey's multiple comparisons test was conducted to determine significant differences by species and regeneration types. Longleaf pine - natural has the highest whole tree wood SG (0.549) and the lowest wood MC (86%) (Table 7). Loblolly pine - cutover had the lowest wood SG (0.512) with both planted longleaf pine regeneration types having similar wood SG values (longleaf pine - cutover = 0.523 and longleaf pine - old ag = 0.522). The wood MC generally tracked with the wood SG except for longleaf pine -cutover sites which had the highest wood MC (98%). Whole tree bark SG values were similar for longleaf pine – natural (0.395) and longleaf pine - cutover sites (0.401) and slightly higher than longleaf pine – old ag sites (0.392). Loblolly pine – cutover sites had the lowest bark SG (0.333).

Table 7. Average whole tree specific gravity (SG) and moisture content (MC) for wood and bark by species and regeneration type (SD = Standard deviation). Letters indicate significant differences determined via a Tukey test.

			Wood SG		Wood MC (%)		Bark SG		Bark MC (%)	
Stand	Species	Regeneration Type	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	Longleaf	Natural	0.533	0.042	92	15	0.380	0.032	59	15
2	Longleaf	Natural	0.534	0.019	90	9	0.396	0.048	50	14
3	Longleaf	Natural	0.580	0.040	76	12	0.410	0.043	44	20
4	Longleaf	Cutover	0.540	0.030	88	7	0.425	0.028	48	15
5	Longleaf	Cutover	0.512	0.035	104	11	0.394	0.022	64	16
6	Longleaf	Cutover	0.517	0.029	103	8	0.383	0.033	76	21
7	Longleaf	Old Ag	0.538	0.025	82	9	0.401	0.017	54	14
8	Longleaf	Old Ag	0.516	0.031	96	11	0.397	0.024	59	10
9	Longleaf	Old Ag	0.512	0.017	97	9	0.379	0.028	73	22
10	Loblolly	Cutover	0.526	0.011	96	6	0.356	0.031	49	12
11	Loblolly	Cutover	0.513	0.015	86	8	0.296	0.027	54	16
12	Loblolly	Cutover	0.496	0.018	103	9	0.345	0.045	58	12
Overall	Longleaf	Natural	0.549	0.041	86	14	0.395A	0.042	51	17
	Longleaf	Cutover	0.523	0.033	98	12	0.401A	0.032	62	20
	Longleaf	Old Ag	0.522	0.027	92	12	0.392A	0.024	62	18
	Loblolly	Cutover	0.512	0.019	95	11	0.333B	0.043	53	13

Converting from green tonnes to dry tonnes reveals that woody biomass makes up 49% for longleaf pine – natural, 46% for longleaf pine - cutover and loblolly pine – cutover, and 47% for longleaf pine – old ag sites consisted of 47% dry woody biomass (Table 8). Whole tree dry bark percent is the same (7%) for all the longleaf pine sites, regardless of regeneration method. Loblolly pine is not much different, with 6% of its total dry biomass being attributed to bark. Longleaf pine – natural has the highest whole tree percentage of dry biomass (56% dry biomass, 44% water). All the forest cutover sites, regardless of species, have a combined wood + bark dry biomass percentage of 53%; however, loblolly pine has one percent more dry wood and one percent less dry bark than longleaf pine. Longleaf pine – old ag was in the middle with whole tree values consisting of 54% wood + bark and 46% water.

Table 8. Percentage of dry biomass for wood, bark, and wood + bark by species and regeneration type.

			Dry Biomass (%)		
Stand	Species	Regeneration Type	Wood	Bark	Wood + Bark
1	Longleaf	Natural	48	6	54
2	Longleaf	Natural	47	8	55
3	Longleaf	Natural	52	7	59
4	Longleaf	Cutover	48	7	55
5	Longleaf	Cutover	45	7	52
6	Longleaf	Cutover	45	6	51
7	Longleaf	Old Ag	50	7	57
8	Longleaf	Old Ag	46	7	53
9	Longleaf	Old Ag	47	6	53
10	Loblolly	Cutover	47	7	54
11	Loblolly	Cutover	49	6	55
12	Loblolly	Cutover	45	6	51
Overall	Longleaf	Natural	49	7	56
	Longleaf	Cutover	46	7	53
	Longleaf	Old Ag	47	7	54
	Loblolly	Cutover	47	6	53

1.4 DISCUSSION

Wood specific gravity

This study compared naturally regenerated longleaf pine, longleaf pine planted on forest cutover sites, longleaf pine planted on old agricultural fields, and loblolly pine planted on forest cutover sites. Because regional variation throughout the southeast influences wood properties, we sampled sites that were within 209 km from each other to limit the amount of variation (Jordan et al. 2008; Antony et al. 2015). Ring SG for both longleaf pine and loblolly pine follow a similar radial and longitudinal trends as found in previous studies (Mora et al. 2007; Antony et al. 2011; Jordan et al. 2008; Dahlen et al. 2018; 2022). The radial trends are indicative of changes in SG due to cambial age which occur from corewood (juvenile wood) to outerwood (mature wood). Mora et al. 2007 used a four-parameter logistic function to model SG from samples collected at breast height; this equation was later modified by Dahlen et al. 2022 to account for changes in height within the tree. We utilized the modified version to model ring SG to capture the effects of disk height. Mora et al. (2007) reported comparatively lower intercept ($\beta_0 = 0.265$) and asymptote values ($\beta_1 = 0.573$), while Dahlen et al. (2022) reported similar values ($\beta_0 = 0.338$, $\beta_1 = 0.613$) to what we found here for loblolly and longleaf pine ($\beta_0 = 0.356$, $\beta_1 = 0.618$). The other model coefficients (β_2 - inflection point, β_3 - rate parameter, β_4 - disk height parameter) were different than those in Dahlen et al. (2022); this could be due to differences in species, these stands being older (33-40 years old vs. 24-33 years old), as well as silvicultural treatments. Longleaf pine - natural reaches the asymptote SG value at the youngest cambial age, followed by longleaf pine - cutover, loblolly pine - cutover, and then longleaf pine – old ag. Longleaf pine grown on old ag sites probably have lower SG than cutover sites because of the effect of residual fertilizer in the soil (Clabo et al. 2020; Raut et al. 2022). In loblolly pine, Love

– Meyers et al. (2010) noted decreased wood SG values on sites that had received a fertilizer application. Residual fertilizer in the soil increases the rate at which the tree grows, resulting in large lower density trees at final harvest (Pienaar and Shiver 1993; Love – Meyers et al. 2010).

While there were significant differences in ring SG by species and regeneration method, the differences are subtle when compared to the magnitude of differences in the growth rate between planted and naturally regenerated trees. Here the naturally regenerated longleaf pine ring BA reaches its peak at 40 years old while planted reaches its peak at 20 years old (Figure 11), meaning that on average, the planted material grew two times faster than the naturally regenerated material. These results suggest that variation in ring SG is a consequence of biological age (Lachenbruch et al. 2011). With that said, we cannot help but wonder how much of an impact the reduced growth during the "grass stage" is having on the ring SG in naturally regenerated longleaf pine?

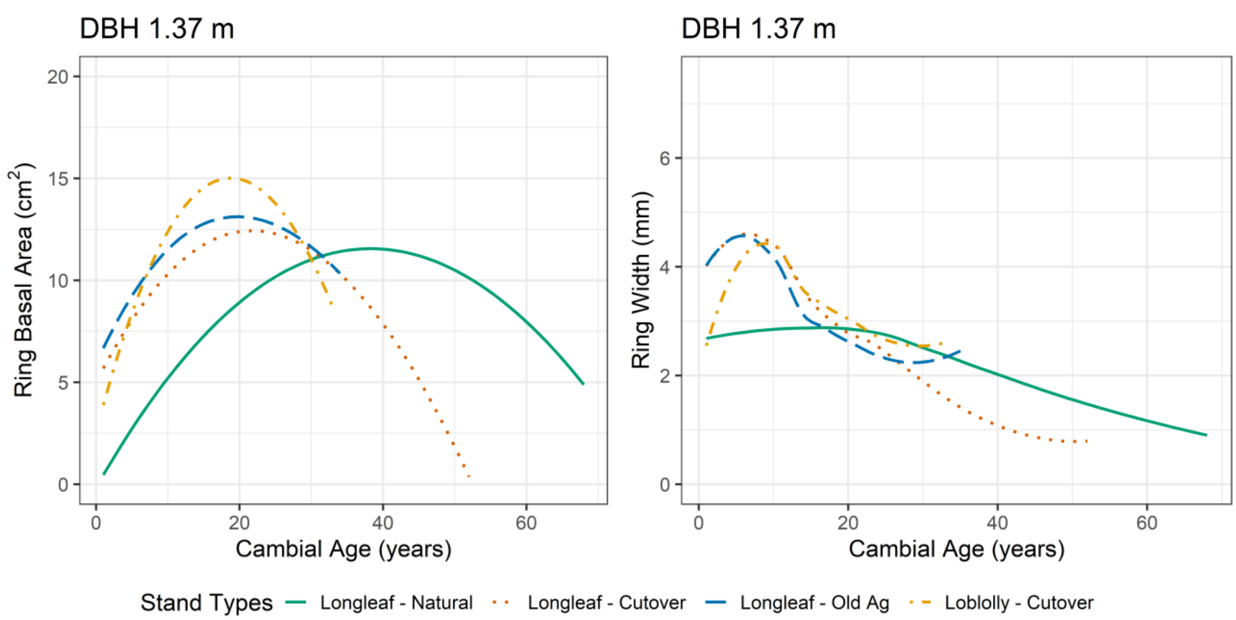

Figure 11. Ring basal area (cm^2) and ring width (mm) in relation to cambial age (years) for all species and regeneration types at breast height (DBH = Diameter at breast height).

A compilation table of whole tree wood and bark SG and MC is shown in Table 9. With regards to whole-tree SG, the *Wood Handbook* (Kretschmann 2021) reports longleaf pine having an average SG value of 0.59, which is higher than what we found (0.549) for naturally regenerated longleaf pine. With regards to loblolly pine whole tree SG, we found whole tree SG averages to be higher than what was reported in Eberhardt et al. (2017) who found an average SG value of 0.498 from loblolly pine sampled in the upper coastal region that were 21-24 years old.

For planted longleaf pine we did not find significant differences between regeneration types (longleaf pine – cutover = 0.523, longleaf pine - old ag = 0.522). This differs from recent work by Raut et al. (2022) who found significantly lower values for old ag sites (0.455) compared to forest cutover sites (0.504). Our results are interesting for two reasons, first the longleaf pine – cutover sites were on average older than the longleaf pine – old ag sites (40 years versus 34 years), which would indicate that we would have a greater amount of higher SG outerwood. Secondly, our ring-by-ring SG model shows that longleaf pine – cutover sites transitioned from corewood to outerwood earlier than longleaf pine – old ag. Ring level trends in relation to disk SG and cambial age show all the regeneration types converging between 30 to 40 years old (Figure 12). The difference in trends before and after the data convergence are likely due to competition and environmental factors. Within the sampling limits of the current study, the small sample size (3 stands per regeneration type) and the variation between stands could influence whether the results are statistically significant. With that being said, the findings from this study provide baseline for future research investigating longleaf pine – cutover and longleaf pine – old ag in greater detail.

Table 9. Compilation of whole tree wood and bark specific gravity and moisture content values between comparable studies (SG = Specific gravity, MC = Moisture content).

Species	Regeneration Type	Age	Whole Tree				Study
			Wood SG	Wood MC (%)	Bark SG	Bark MC (%)	
Longleaf pine	Natural	54	0.541	86	0.396	11	This study
Longleaf pine	Cutover	14-25	0.504	105	0.374	82	Raut et al. (2022)
Longleaf pine	Natural	50	0.526	73	-	-	So et al. (1998)
Longleaf pine	Natural	55	0.541	72	-	-	Eberhardt and Samuelson (2022)
Longleaf pine	Cutover	32-53	0.523	65	0.401	62	This study
Longleaf pine	Old Field	14-25	0.456	123	0.347	105	Raut et al. (2022)
Longleaf pine	Old Field	30-36	0.522	92	0.392	62	This study
Loblolly pine	Cutover	21-24	0.498	106	0.311	78	Eberhardt et al. (2017)
Loblolly pine	Cutover	32-35	0.521	95	0.333	53	This study

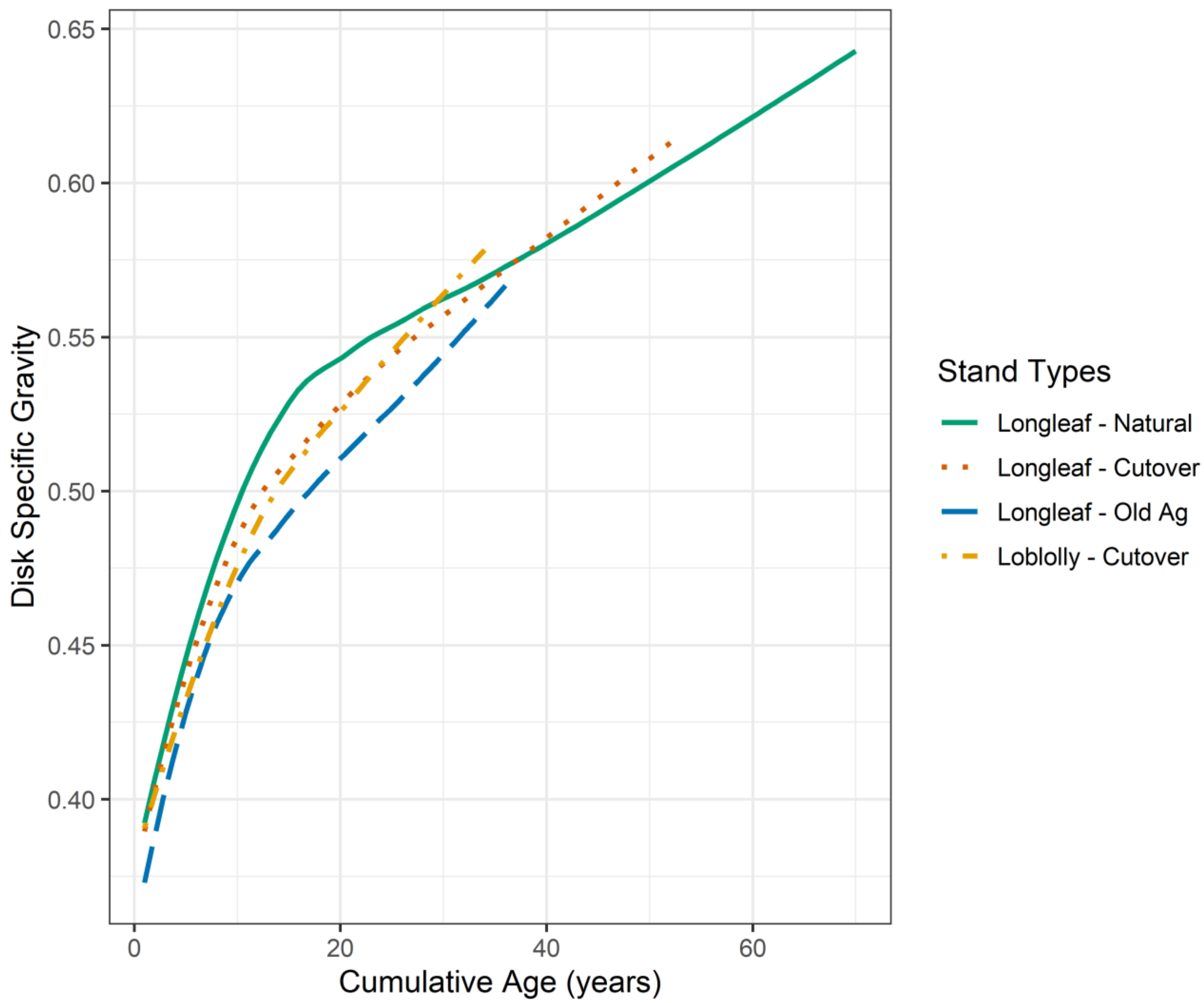

Figure 12. Ring level trends for disk specific gravity (SG) in relation to cumulative age (years) for each species and regeneration type.

Whole tree bark properties

We found that longleaf pine has significantly higher bark SG than loblolly pine (0.396 (average of the three longleaf pine regeneration types) versus 0.333). We observed higher whole tree bark SG values (longleaf pine - cutover = 0.401, longleaf pine - old ag = 0.392) than Raut et al. (2022) (longleaf pine - cutover = 0.374, longleaf pine - old ag = 0.347). Raut et al. (2022) found that 21% of the variation in the within-tree bark SG was attributed to different stands. It is not clear to us what is causing the variation in bark SG by stand for longleaf pine, but it could be due to a variety of site and silviculture treatment decisions. Because bark MC is inversely related to bark SG, we found lower values for bark MC (62%) than Raut et al. (2022) who reported values of 82% for cutover sites and 105% for old agricultural field sites. We did not find differences in bark MC for longleaf pine and loblolly pine. Unlike Raut et al. (2022) who found differences in the ratio of DIB to DOB for longleaf pine, we did not find any difference for longleaf pine or loblolly pine. We found loblolly pine to have an average whole tree bark SG value of 0.333 while Eberhardt et al. (2017) reported 0.311. Planted loblolly pine from this study had a calculated bark MC value of 53% while Eberhardt et al. (2017) reported a MC of 78%.

Wood ultrasonic velocity

Microfibril angle typically decreases from pith to bark which results in the outerwood being stiffer than corewood (Cave 1968; Jordan et al. 2017). Trees also have a core of very low stiffness wood near the butt of the tree which can be attributed to higher microfibril angles than what would be typically found higher in the tree (Jordan et al. 2007; Xu and Walker 2004). The changes in microfibril angle are hypothesized to be an adaptation to wind (Lachenbruch et al. 2011; Hale et al. 2012; Auty et al. 2013; Gardiner et al. 2016). We did not measure microfibril angle in this study, but we measured ultrasonic velocity which can be considered as a surrogate property to microfibril angle since both relate closely to wood stiffness (Mason et al. 2017; Dahlen et al. 2022). We modeled USV changes due to cambial age and height within tree and found that longleaf pine and loblolly pine had different patterns of variation. We modeled longleaf pine using a three-parameter logistic function, and for loblolly pine we used a four-parameter logistic function. Our results for loblolly pine are similar to recent work by Dahlen et al. (2022) who showed significant variation in USV trends within the first log (~5 m). These results are also similar to work by Jordan et al. (2007) in loblolly pine who measured microfibril angle. Xu and Walker (2004) report abnormally high microfibril angles at the base of radiata pine trees up to a height of 2.7 m. In contrast, longleaf pine has little variation in USV due to height within tree. Differences in USV for longleaf pine between regeneration types were subtle and not easily modeled.

We found fewer differences with regards to regeneration type for longleaf pine for USV than we did for ring SG. Donaldson (2008) concluded that the effects of site and silviculture on microfibril angle are relatively small within a species; however, a similar study has not been conducted on longleaf pine. Jordan et al. (2007) did find that significant regional variation with regards to microfibril angle, with the results being similar to SG (Jordan et al. 2008) whereby wood grown near the coasts has 'better' (i.e. lower) microfibril angle. Shupe et al. (1996) and Clark et al. (2006) indicate that in loblolly pine, variation in microfibril angle may be related to seed origin and not directly to site effects. Myszewski et al. (2004) reported moderate to high correlations between different genetics and microfibril angle for loblolly pine. Regarding other pine species, Baltunis et al. (2007) found microfibril angle to be a heritable trait in radiata pine growing in Australia. Auty et al. (2013), working with Scots pine, did not find significant effects from regeneration type, however they also hypothesize that their sample size may not have been large enough to detect significant differences.

1.5 SUMMARY AND CONCLUSIONS

In this study we investigated wood properties of longleaf pine grown on 3 different regeneration types (natural, forest cutover, old field) and loblolly pine grown on forest cutover sites. We analyzed ring specific gravity (SG), ultrasonic velocity (USV), and whole-disk and whole-tree SG and moisture content (MC) of the wood and bark. We conclude that ring-by-ring specific gravity is significantly different between regeneration types, however longleaf pine and loblolly pine shared a common intercept and asymptote value. We found that the differences between species and regeneration methods influences the amount of time it takes for wood to transition from corewood (juvenile wood) to outerwood (mature wood). Longleaf pine – natural transitions to outerwood at the youngest cambial age, followed by longleaf pine – cutover, loblolly pine – cutover, and then longleaf pine – old ag. The differences in corewood SG that we detected at the ring level did not carry over to whole tree SG differences by species and regeneration type, but the lack of significant differences found here could be due to the limited number of stands sampled by regeneration type (N = 3).

For ring-by-ring USV we found that the longleaf pine was best modeled using a three-parameter logistic function, whereas loblolly pine was best modeled using a four-parameter logistic function. For longleaf pine all regeneration types shared a common asymptote value and other differences as a function of height within tree were subtle compared to what we found for loblolly pine which has significant variation in USV within the first 5 m of the tree.

Generally, the corewood (juvenile wood) of natural longleaf pine was the highest quality, followed by planted longleaf pine on cutover sites. Planted loblolly pine on cutover sites and planted longleaf pine on old agricultural fields sites had corewood that was generally similar, with longleaf pine on old agricultural fields having lower SG but generally higher USV. By the time the trees reached merchantable size and were producing outerwood (mature wood), the differences in wood properties were less apparent between the different species and regeneration methods. These results may provide some positive reassurance to landowners that choosing to grow longleaf pine on cutover sites will produce high quality wood and that planting longleaf pine is a viable option for some aspects of longleaf pine restoration efforts.

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1.7 APPENDIX

Table A.1.1. P-values found for the different parameters and parameter differences by species – regeneration methods in this study.

			Species - Regeneration Type Comparison[1]					
Property	Parameter	Overall (Natural)	1	2	3	4	5	6
Ring Specific Gravity[2]	Intercept	<0.0001	-	-	-	-	-	-
	Asymptote	<0.0001	-	-	-	-	-	-
	Inflection	<0.0001	0.0004	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	Rate	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0033	<0.0001
	DH effect on β_1	<0.0001	0.4437	<0.0001	0.0003	<0.0001	0.0080	0.0185
Ring Ultrasonic Velocity - Longleaf Pine[3]	Asymptote	<0.0001	-	-	-	-	-	-
	Inflection	<0.0001	<0.0001	<0.0001	-	0.8941	-	-
	Rate	<0.0001	0.0035	<0.0001	-	0.0015	-	-
	DH effect on β_1	0.0023	<0.0001	<0.0001	-	0.3895	-	-
Ring Ultrasonic Velocity - Loblolly Pine[4]	Inflection	<0.0001	-	-	-	-	-	-
	Asymptote	<0.0001	-	-	-	-	-	-
	Inflection	<0.0001	-	-	-	-	-	-
	Rate	<0.0001	-	-	-	-	-	-
	DH effect on β_2	<0.0001	-	-	-	-	-	-
	DH effect on β_3	0.0065	-	-	-	-	-	-
Ratio of Diameter Outside Bark to Diameter Inside Bark[5]	β_1	<0.0001	0.8148	0.8566	0.7811	0.9562	0.9691	0.9242
Moisture Content as a Function of Specific Gravity[6]	β_0	<0.0001	0.2001	0.1486	<0.0001	0.3895	<0.0001	<0.0001
	β_1	<0.0001	0.4245	0.0491	<0.0001	0.9594	<0.0001	<0.0001
Whole tree[7]	SG	0.1570	-	-	-	-	-	-
	MC	0.4234	-	-	-	-	-	-
Bark[7]	SG	0.0139	0.9928	0.9960	0.0014	0.9594	<0.0001	0.0038
	MC	0.3486	-	-	-	-	-	-
Dry %[8]	Wood	0.4102	-	-	-	-	-	-
	Bark	0.7962	-	-	-	-	-	-
	Wood + Bark	0.4474	-	-	-	-	-	-

[1] Species - Regeneration Type Comparison
1: Longleaf - Natural & Longleaf - Cutover
2: Longleaf - Natural & Longleaf - Old Ag
3: Longleaf - Natural & Loblolly - Cutover
4: Longleaf - Cutover & Longleaf - Old Ag
5: Longleaf - Cutover & Loblolly - Cutover
6: Longleaf - Old Ag & Loblolly - Cutover
[2] Equation 1
[3] Equation 2
[4] Equation 3
[5] Equation 6
[6] Equation 7
[7] Table 7
[8] Table 8