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I present a study that attempts to quantify the relationship between morphological characteristics and tree age in the montane variant of common southeastern U.S. species of pine trees in the Uwharrie Mountains of North Carolina, USA. I collected one 5.15 mm diameter increment core from each of 60 shortleaf pine trees and 45 longleaf pine trees. I crossdated and estimated the pith of each sample using established dendrochronological laboratory methods. In addition, I visually assessed and measured each tree for the following morphological characteristics: diameter at breast height (DBH), the height of the lowest living branch, bark thickness, and stem sinuosity. Natural breaks in tree age were determined using the k-means algorithm that separated tree age into three groups within each species. I ran several iterations of multiple regression to test if each morphological characteristic can accurately predict tree age in each species and tested for the strength and direction of relationships between tree age and each morphological characteristic between species, within species, and within age classes using nonparametric Spearman's rank-order correlation analysis. While age-morphology relationships are poorly defined for each species when analyzed both together and separately, stronger relationships emerge when tested by age class. Height of the lowest living branch and DBH are positively correlated with shortleaf tree age ($p < 0.05$). Sinuosity is positively correlated with both species tree age ($p < 0.05$). Within age classes, longleaf tree age is positively correlated with DBH in the first age class and bark

thickness in the third age class. These findings suggest that it may be difficult to assess

shortleaf and longleaf pine tree age accurately via external morphological indicators.

AGE-RELATED MORPHOLOGY OF MONTANE POPULATIONS OF SHORTLEAF

PINE (*Pinus echinata*) AND LONGLEAF PINE (*Pinus palustris*) IN THE UWHARRIE

MOUNTAINS, NORTH CAROLINA, USA

by

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Approved by

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APPROVAL PAGE

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CHAPTER I

INTRODUCTION

Mature trees play a critical role in ecosystem processes as they regulate
hydrologic regimes, impact sub-surface nutrient exchange, and control the spatial and age
distribution of individuals of the same species (Lindenmayer et al. 2014; Lindenmayer
and Laurance 2017). Mature trees also contain invaluable environmental histories within
their ring structure, morphology, and injuries (Douglas 1920; Fritts and Swetnam 1989).
Little work has been done to quantify the characteristics that potentially indicate agedness
in trees and no work has examined the common pine species in the Piedmont or Coastal
Plain region of North Carolina. A gap in research of this type exists in the Piedmont and
Coastal Plain of North Carolina where longleaf pine and shortleaf pine dominate the
landscape in these regions.

This study investigates the common morphological characteristics of two
southeastern species of pine that may provide quantifiable estimations of tree age.
Morphological characteristics have the potential to be indicative of tree maturity which is
important to identify old trees accurately to strengthen dendrochoronological studies. In
this research, I have examined the following characteristics: (1) diameter at breast height
(DBH); (2) sinuosity (longitudinal twist); (3) bark characteristics (4) height of the lowest
living branch in common montane variants of southeastern U.S. pine species
shortleafpine (*Pinus echinate* Mill.) and longleaf pine (*Pinus* palustris Mill.). The more of

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these characteristics present in an individual, the more likely it is the individual can be

termed "old" (Van Pelt 2008; Pederson 2010; Brown 2019). However, what is unknown

is which morphological traits best represent age in these common pine species.

CHAPTER II

AGE-RELATED MORPHOLOGY OF MONTANE POPULATIONS OF SHORTLEAF

PINE (*PINUS ECHINATA*) AND LONGLEAF PINE (*PINUS PALUSTRIS*) IN THE

UWHARRIE MOUNTAINS, NORTH CAROLINA, USA

2.1 Abstract

I present a study that attempts to quantify external morphological characteristics

in the montane variant of common southeastern U.S. species of pine trees in the Uwharrie

Mountains of North Carolina, USA. I collected one 5.15 mm diameter increment core

from each of 60 shortleaf pine trees and 45 longleaf pine trees. I crossdated and estimated

the pith of each sample using established dendrochronological laboratory methods. In

addition, I visually assessed and measured each tree for the following morphological

characteristics: diameter at breast height (DBH), the height of the lowest living branch,

bark thickness, and stem sinuosity. Natural breaks in tree age were determined using the

k-means algorithm that separated tree age into three groups within each species. I ran

several iterations of multiple regression to test if each morphological characteristic can

accurately predict tree age in each species and tested for the strength and direction of

relationships between tree age and each morphological characteristic between species,

within species, and within age classes using nonparametric Spearman's rank-order

correlation analysis. While age-morphology relationships are poorly defined for each species when analyzed both together and separately, stronger relationships emerge when tested by age class. Height of the lowest living branch and DBH are positively correlated with shortleaf tree age ($p < 0.05$). Sinuosity is positively correlated with both species' tree age ($p < 0.05$). Within age classes, longleaf tree age is positively correlated with DBH in the first age class and bark thickness in the third age class. These findings suggest that it may be difficult to assess shortleaf and longleaf pine tree age accurately via external morphological indicators.

2.2 Introduction

Mature trees play a critical role in ecosystem processes as they regulate hydrologic regimes, impact sub-surface nutrient exchange, and control the spatial and age distribution of individuals of the same species (Lindenmayer et al. 2014; Lindenmayer and Laurance 2017). Mature trees contain invaluable environmental histories within their ring structure, morphology, and injuries (Douglas 1920; Fritts and Swetnam 1989) providing proxy information of environmental variation (e.g., climate, fire, land-use history). Including mature trees in dendrochronological research is essential in extending environmental and climatological histories into the past (Douglas 1920; Fritts and Swetnam 1989), therefore it is important for researchers to identify mature trees in the field with accuracy. Often, the age of a tree is unknown until a core has been collected, processed, and crossdated as tree age is difficult to determine visually via external morphological characteristics (Pederson 2010; Brown 2019). This study investigates the

common morphological characteristics of two southeastern U.S. species of pine that may provide quantifiable estimations of tree age. Morphological characteristics have the potential to be indicative of tree maturity. I examined the following morphological characteristics: (1) diameter at breast height (DBH); (2) trunk sinuosity (longitudinal twist); (3) height of the lowest living branch; and (4) bark thickness. Specifically, this study investigates these four morphological characteristics for two, long-lived southeastern conifers (Earle 2014), shortleaf pine (*Pinus echinata* Mill.) and longleaf pine (*Pinus palustris* Mill.).

Shortleaf pine is a long-lived (>300 years, Earle 2014) species native to the southeastern United States. Shortleaf pine habitat ranges from Maryland to Mississippi, with outlier populations in Pennsylvania and a disjunct population in the southern Great Plains from Missouri to Texas (Earle 2014). Shortleaf pine trees have rounded crowns, dark red-brown, scaly plated bark with deep resin pockets, and are a valuable resource for the long environmental histories captured in its rings (Stambaugh and Guyette 2004). The species provides diversity to the central hardwoods in the Ozarks and played a major role in the economic growth of the Ozark Highlands of Missouri and Arkansas (Stambaugh and Guyette 2004). Shortleaf pine abundance has decreased following European settlement including the loss of shortleaf pine savanna communities via logging and fire suppression (Stambaugh 2001; Stambaugh and Guyette 2004). Shortleaf pine is a valuable species for climatological records (Stambaugh 2001; Stambaugh and Guyette 2004). Shortleaf pine trees have characteristics of value in the scientific community including the ability to capture multi-century environmental histories, and in the

commercial domain because of economic viability as a lumber species (Stambaugh 2001; Stambaugh and Guyette 2004).

Longleaf pine is a long-lived tree (>400 years, Earle 2014) native to the southeastern United States. Longleaf pine ranges from southeastern Virginia to central Florida, and east into Louisiana with a disjunct population in Texas. In North Carolina, longleaf pine ranges from the lower Piedmont into the Coastal Plain (Earle 2014). The species extent has diminished from 37 million hectares to 1.74 million hectares (Frost 1993; Oswalt et al. 2012). Along with the Piedmont physiographic region of Appalachia, montane longleaf pine populations exist on mountainous terrain ranging from Alabama to North Carolina (Patterson and Knapp 2016). Before European settlement, longleaf pine forests dominated the largest geographic range in temperate North America (Wahlenberg 1946; Frost 1993). Longleaf pine populations declined largely due to the commercialization of ship construction post-European settlement as well as 20th-century fire-suppression policies (Stokes et al. 2010). A variant component of this forest type are the montane longleaf populations in the higher elevations (i.e., 450–700 m) of the Blue Ridge and Ridge and Valley regions in Georgia and Alabama, the Cumberland Plateau in Alabama (Stokes et al. 2010), and Uwharries Mountains (200–300 m) of North Carolina (Patterson and Knapp 2016). Longleaf pine forests suffered a decline by the same mechanisms that occurred in the Piedmont and Coast Plains (Stokes et al. 2010, Patterson and Knapp 2016). Further, although the montane variant of longleaf pine is not genetically different than other populations (Schmidtling and Hipkins 1998), their growth on steep and often bouldery slopes confer greater climatic sensitivity compared to non-

montane populations (Mitchell et al. 2019). The rich history and the long historical record are valuable characteristics of this species.

Tree diameter at breast height (DBH) is defined as the diameter of the trunk at breast height of the person measuring the tree (approximately 1.1 m above the surface) (Speer 2010). This measurement is commonly used in forest inventories and dendrochronological studies. DBH is useful because it is related to the amount of growing space taken up by the tree (Gerling and May 1995). Dendrochronologists measure DBH and the height of the trees they are coring in their study (Speer 2010) to determine overall tree size (Gerling and May 1995; Sumida et al. 2012). Researchers have found that DBH can be a means of determining the age of groups of trees, rather than individual trees (Shoda and Shibata 2020). Likewise, DBH can be used to estimate root system biomass for various species (Drexhage and Colin 2001). Various species of oak and hickory as well as loblolly and shortleaf pine, DBH was found to be a significant predictor of crown diameter ($R^2 = 0.64 - 0.93$) (Gerling and May 1995) but that relationship, and interactions between tree height and DBH were found to vary based on stand conditions [open floor v. high density] (Sumida et al. 2012). Though DBH is a useful measurement in estimating tree size and volume (Corral-Rivas et al. 2007), DBH is not a reliable measure of tree age (Patterson and Knapp 2016; Brown et al. 2019). Dendrochronologists follow the maxim of "longevity under adversity" where the oldest trees are found in stressed site conditions such as xeric, steep, rocky slopes (Schulman 1956). Adverse growing conditions lead to a relatively low productivity grove where trees produce narrow annual rings due to rocky slope or shallow soils are small in

diameter in comparison to trees living in a grove with abundantly available nutrients will produce wide annual rings (Schulman 1956; Black et al. 2008; Pederson 2010). For example, in a sample of nine species in the Rocky Mountains, USA, Brown et al. (2019) found DBH was not a significant predictor of tree age in transitional or old morphology trees but was useful to divide tree into young and old age classes. However, we intend to test this relationship with shortleaf and longleaf pines in the Uwharrie Mountains.

Studies on stem sinuosity in relation to tree age are limited. Stem sinuosity is defined as "any stem crookedness occurring in the segment within two whorls" (Campbell 1965, p. 1) and "it is a measure of displacement from its original direction over the total length of the displacement" (Dwivedi et al. 2019, p. 1). Most studies regarding stem sinuosity focused on conifers—primarily Douglas-fir (*Pseudotsuga menziesii* Mirb.)—so a comparison to shortleaf pine and longleaf pine in this study will be meaningful (Campbell 1965; Timel 1986; Spicer et al. 2000; Baker et al. 2005; Gartner and Johnson 2006). Sinuous growth has many potential causes, both intrinsic and extrinsic, including elongation relative to radial growth rates and leader damage, nutrient deficiency, or genetics (Spicer et al. 2000). Studies find that trees that were sinuous in one year are more often sinuous in other years (Spicer et al. 2000), suggesting sinuosity is a predictor of tree age (Pederson 2010). Krause and Plourde (2008) found sinuous young black spruce (*Picea mariana* Mill.) and jack pine (*Pinus banksiana* Lamb.) could out-grow the deformity as they got older. Trees in the *Quercus* subgenus are often sinuous at ages greater than 300 years – a relationship between great age and sinuosity is similarly true in trees with lower shade tolerance (Stahle and Chaney 1994; Stahle 1996; Pederson

2010). In this study, I will attempt to determine if sinuosity in shortleaf and longleaf is a positive indicator of tree age.

There is little work done regarding the height of the lowest living branch in relation to tree age. The height of the lower branches varies between a young tree and an old tree (Van Pelt 2008). As trees age, they shed their lower branches to conserve energy so photosynthesis can be achieved more efficiently in the upper branches Brown et al. 2019; Van Pelt 2008), a function of site conditions in some cases (Sumida et al. 2007). Older trees typically have large, thick, gnarled branches high in the stem, which indicate a long history of withstanding disturbance regimes, and fewer branches lower in the stem (Swetnam and Brown 1992; Stahle and Chaney 1994; Van Pelt 2008; Pederson 2010). In this study, I attempt to determine if the height of the lowest living branch in shortleaf pine and longleaf pine is associated with tree age.

Bark morphology (bark thickness and crevice depth) changes with age (Wahlenberg 1946; Pederson 2010). Pederson (2010) notes that some species have great bark variability. For example, white oak (*Quercus alba* Willd.) ranges from peeling, flaky bark in young trees to patchy balding bark in older trees (Pederson 2010). Likewise, young ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and Douglas-fir (*Pseudotsuga menziesii*) have thin, scaly patches of bark, which thicken to form fissures and deep crevices as the tree ages insulating the cambium from heat (Huckaby 2003; Van Pelt 2008). Older trees of many species have thick bark plates and deep crevices, and this is a well-documented morphological feature of agedness in trees (Van Pelt 2008; Pederson 2010). That said, research attempting to describe shortleaf pine and longleaf pine bark in

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the southeastern U.S. is sparse. This study intends to describe bark thickness as it appears

in trees sampled with either deep bark crevices and thick plates, or shallow crevices and

thin, scaly bark plates.

Little research has been done to quantify the characteristics that potentially

indicate agedness in trees and no work has examined the common pine species in the

Piedmont region of North Carolina. A gap in research of this type exists in the Piedmont

and Coastal Plain of North Carolina where long-leaf pine and shortleaf pine dominate the

landscape in these regions. These species are valuable resources of environmental history

for biogeographers and dendrochronologists. Shortleaf and longleaf pines are commonly

used in southeastern climate reconstructions (Bragg 2002; Patterson and Knapp 2016;

Mitchell et al. 2019, Knapp et al. 2021). This study attempts to define common

morphological characteristics in shortleaf pine and longleaf pine that may indicate

agedness.

2.3 Materials and Methods

2.3.1 Study Site

The Uwharrie Mountains is a 4,500-hectare tract within the Uwharrie National

Forest located in central North Carolina, USA [35.366306, -79.964034] (Figure 1). The

Uwharrie Mountains range from 150 to 335 m elevation and have 150 m in prominence.

The geology of the Uwharries is a part of the Carolina Slate Belt, a portion of the

Appalachian Piedmont consisting of primarily volcanic-sedimentary rocks found

(Stuckey 1965; Wells 1974). The Uwharries support an array of Piedmont and disjunct

coastal plant species, primarily a mixed mesophytic community with scattered xeric

communities on rocky outcrops on south- and southwest-facing slopes (Wells 1974). Pine communities on gently rolling hills are common (Wells 1974; Bates 2001), but montane shortleaf and longleaf pine populations flourish on the xeric slopes (Patterson and Knapp 2016) where they are more competitive. Common species in the Uwharrie Mountains range from hardwoods including white oak (*Quercus alba* L.) and red oak (*Quercus rubra* L.) to pine tree including Virginia pine (*Pinus virginiana* Mill.), shortleaf (*Pinus echinata*) and longleaf pine (*Pinus palustris*) (Wells 1974; Bates 2001; Patterson and Knapp 2016).

During summer and fall 2020, I collected one 5.15 mm diameter increment core per tree from 60 shortleaf pine and 45 longleaf pine. I targeted adult trees (> 10 cm diameter at coring height) on upland, south-facing slopes in known shortleaf pine and longleaf pine groves (Patterson and Knapp 2016). Uwharrie National Forest offers an environment in North Carolina to study shortleaf and longleaf in sites that are stressed and highly sensitive to climate data. These two species represent remnant populations following extensive 20th Century logging and grow at sites where either lumber quality, land-ownership practices, or inaccessibility curtailed logging (Patterson and Knapp 2016). Thus, remnant adult to old-growth trees in this forest allow a rare opportunity for age-related studies such as this. Sites within the Uwharries were selected based on the abundance of shortleaf and longleaf within each grove, as well as south-facing to mitigate for the difficulty of assessing morphological characteristics across diverse site conditions.
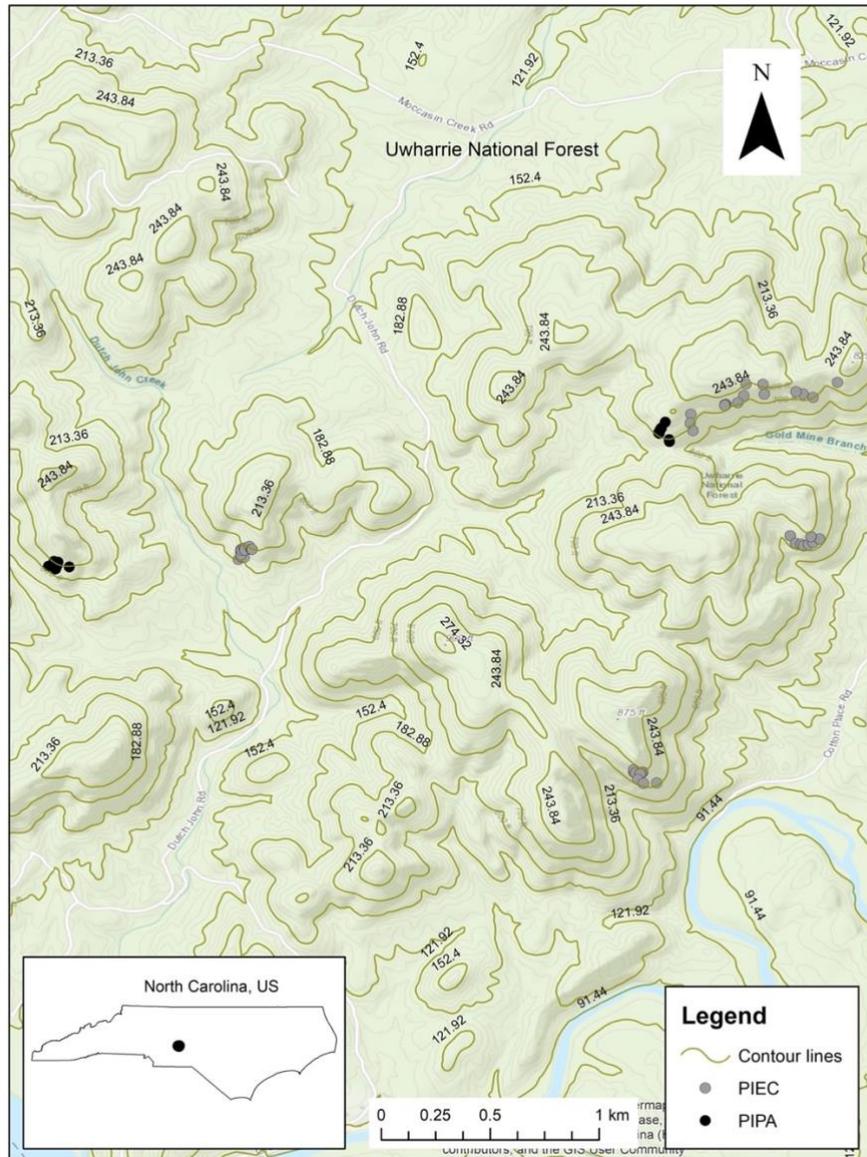
Figure 1. A map of the study area Uwharrie Mountain located in Uwharrie National Forest in North Carolina. Gray dots represent shortleaf pine trees and black dots represent longleaf pine trees which samples were collected from five known groves within the forest.

2.3.2 Morphological Characteristics Data

Diameter at Breast Height (DBH)

I used the traditional dendrochronological method of measuring the diameter of each tree at breast height (Speer 2010) using a diameter-calibrated measuring tape and targeted trees that were greater than 10 cm diameter.

Stem Sinuosity

Stem sinuosity was determined if a tree had either a longitudinal twist or any degree of crookedness present within one inter-whorl (circular growth of branches) of the top four whorls of the stem (Campbell 1965). The dense foliage of each grove made it difficult to assess sinuosity so high in the tree stem, so the tree was assessed from multiple angles to determine the best estimate. Trees expressing sinuosity were recorded in the dataset as sinuous, and trees not expressing sinuosity were recorded as not sinuous (Figures 2A and B).
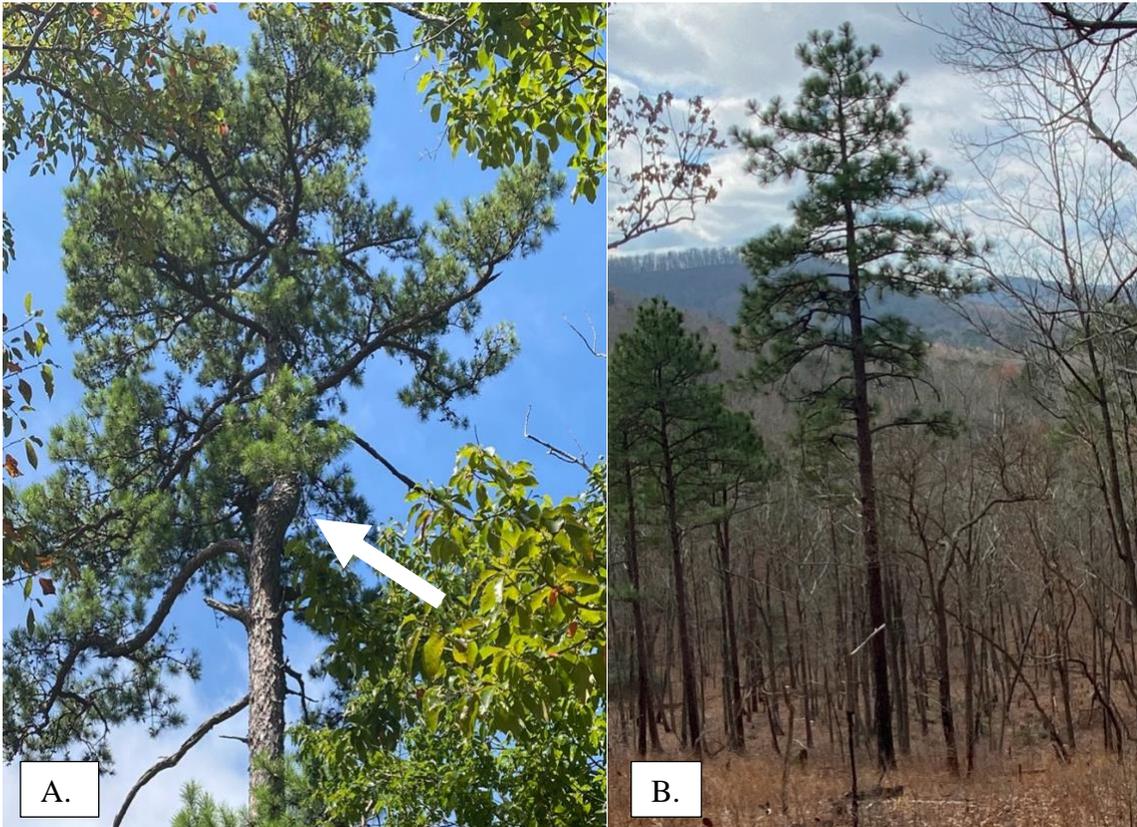
Figure 2. (A). The shortleaf pine (right) shows twist in the upper three whorls indicated by the arrow – this tree is presenting sinuosity. (B). The longleaf pine (left) does not have crookedness present in any part of the stem, this is an example of not sinuous.

Height of the Lowest Living Branch

For this study, the use of a range finder was impractical due to dense foliage impeding the beam and the steep, rocky slopes prohibited the use of an inclinometer. Therefore, an estimation of the height of the lowest live branch of each tree was made using a rudimentary measurement technique. The height of the lowest branch of each tree was estimated in comparison to the height of a 1.8-meter-tall person standing at the base of the tree. The use of this technique does increase the potential for error, however, there is variability in height of lowest living branch between each tree similar to prior field

experience (Knapp, pers. Comm. 2021) has shown this to be an effective technique when more precise measures are not viable. This measurement was recorded in meters.

Bark Thickness

Bark thickness was categorized by assessing the thickness of plates and deepness of crevices. Thick bark plates create deep crevices giving the tree the appearance of a smooth surface with bark firmly adhered to the tree (Van Pelt 2008; Pederson 2010). Thin bark plates have a rough appearance with thin, scaly patches that are easily shed because they do not adhere to the tree (Van Pelt 2008; Pederson 2010). If the tree had thin, scaly bark that was easily shed, the tree was reported as not smooth. If the tree had deep bark crevices and thick bark plates firmly attached to the tree, it was reported as smooth (Figure 3A and B).
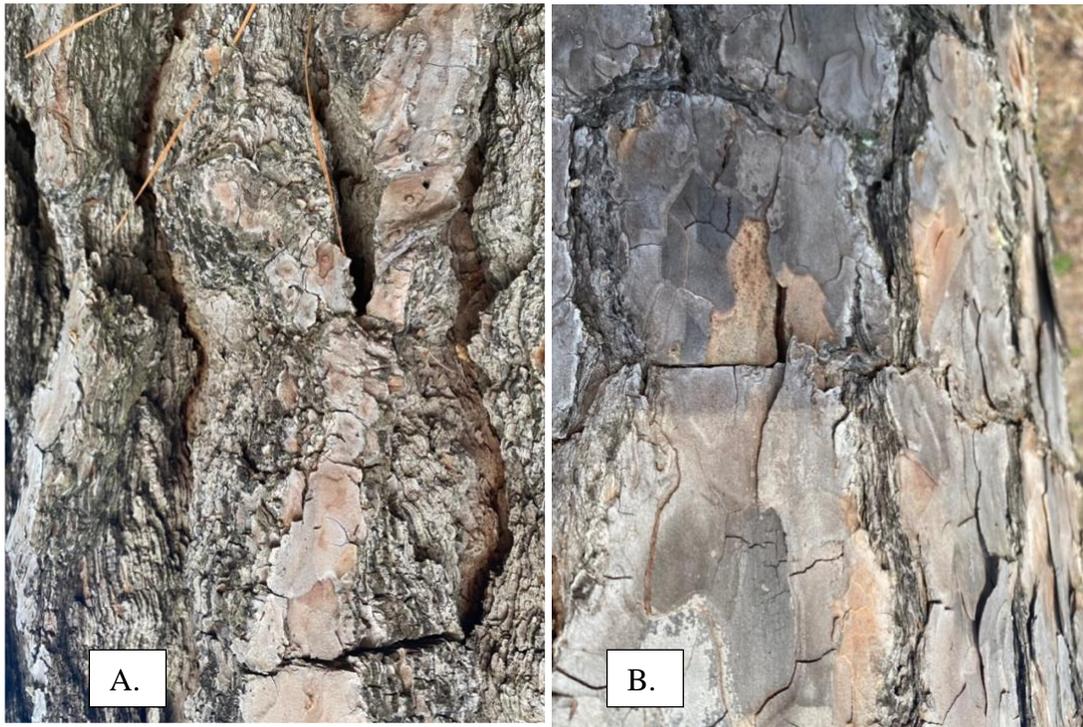
Figure 3. (A). A longleaf pine with thick bark plates and deep crevices. (B). A longleaf pine with thin, scaly bark plates and shallow crevices.

2.3.3 Age Determination

The 60 shortleaf pine (PIEC) and 45 longleaf pine (PIPA) samples were air-dried then glued in mounts. Each sample was sanded each sample with progressively finer sandpaper grit (177 µm–210 µm; 53 µm–74 µm; 32.5 µm–36.0 µm) so that cells could be seen clearly under a microscope (Speer 2010; Orvis and Grissino-Mayer 2002). I scanned an image of each sample to 1200 dpi and measured each sample using computer software Coorecorder (Larsson 2014), which measures each ring to the nearest 0.01 mm. Measuring a tree core sample in Coorecorder creates a measurement file that can then be loaded into crossdating software CDendro (Larsson 2014). Measuring and crossdating tree core samples ensured accuracy in determining the age of each shortleaf and longleaf

tree. Once the inner ring of each sample was acquired, I estimated the pith using a pith estimator for the samples without a pith (Applequist 1958). The estimators are transparent sheets containing concentric circles used to imitate tree rings and are overlain on the core and adjusted until the ring patterns match. Thus, the reported age for samples without a pith was the verified crossdate of the innermost ring plus the number of pith estimator years to determine the earliest ring-width year that was then subtracted from the outmost year (Villalba & Veblen 1997). All tree ages were based at coring height.

Several samples were excluded from the analysis for various reasons. For example, PIEC 023 and PIEC 024 could not be mounted because of their deteriorated condition after sample collection. PIEC 047, PIPA 011, PIPA 013 could not be accurately crossdated therefore, do not have an inner-ring date to obtain an accurate tree age. PIPA 016, PIPA 024, PIPA 034 and PIPA 041 are without curvature therefore I could not obtain an accurate tree age with the pith estimator. The final numbers of observations are 57 shortleaf pine and 38 longleaf pine.

2.3.4 Data Analysis

Distribution

Shapiro-Wilk's normality test was used to determine if each variable was normally distributed (Shapiro and Wilk 1965). The test was performed on combined PIEC and PIPA tree age with the four morphological characteristics. The normality test was also performed on PIEC and PIPA data separately with the four morphological characteristics. A total of 15 iterations were performed. Shapiro-Wilk tests the hypothesis

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that a variable is normally distributed and calculates a p-value. If the resulting p-value is less than 0.05, the variable is not normally distributed. Normality was also assessed visually.

Natural Breaks

Tree age and morphological data were analyzed separately by species using the statistical software R (R Core Team 2017). Natural breaks in age were determined to parse out potential age classes using k-means clustering (Pham et al. 2005). K-means partitions n observations into k clusters in which each observation belongs to the cluster with the nearest mean center based on within sum of squares. Each observation is allocated to the closest cluster and the distance between an observation and the cluster is calculated from the Euclidean distance between each observation and the cluster mean (Pham et al. 2005). The number of clusters is pre-specified based on within sum of squares (Pham et al. 2005).

Regression and Correlation

Multiple regression was used to determine if any combination of DBH, sinuosity, bark thickness, and height of the lowest living branch could accurately predict tree age. A multiple regression model was run using a dataset that included all data from both species. Likewise, six other iterations were performed using the k-means determined shortleaf pine and longleaf pine age classes and the morphological characteristics. Using three shortleaf pine tree data age classes ($k = 3$), independent variables DBH, sinuosity,

bark thickness, and height of the lowest living branch were regressed on the independent

variable tree age. Using three longleaf pine age classes ($k = 3$), independent variables

DBH, sinuosity, bark thickness, and height of the lowest living branch were regressed on

the independent variable tree age.

Based on the results from Shapiro-Wilk's normality tests, the non-parametric

Spearman Rank Order Correlation (r_s) test was used to examine the strength and direction

of relationships between age and the four morphological components by individual

species and species combined for the entire data set as well as the three age classes used

for the multiple regression analysis.

2.4 Results

Normality Test

Shapiro-Wilk's normality tests indicated that four of the 15 variables were

normally distributed (Table 1). Age in the combined dataset, as well as age in the PIPA

dataset, were both normally distributed. DBH in the separate PIEC and PIPA datasets

was normally distributed (Table 1).

Table 1: Shapiro-Wilk's normality test to determine if a variable is significantly
different from the normal distribution (p-values < .05 are not normally distributed).
*significant

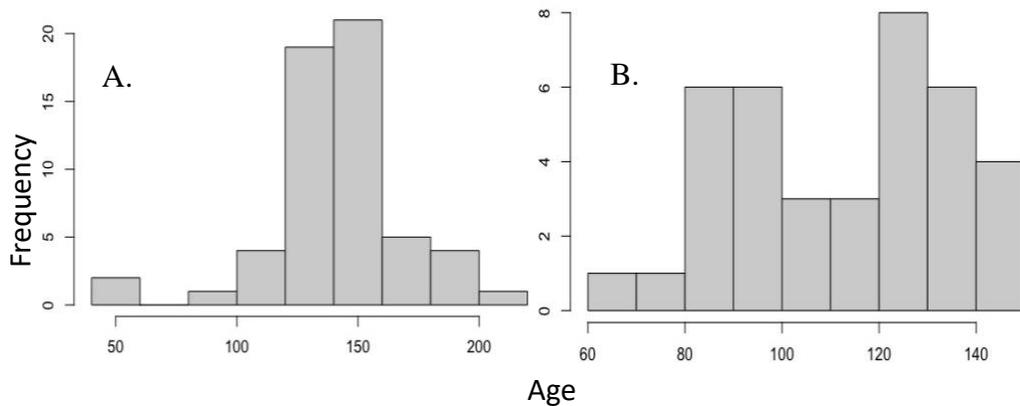| **Species**	**Age**	**DBH**	**Bark**	**Sinuosity**	**Ht. Lowest branch**
PIEC	**0.004392***	0.3551	**5.80E-12***	**1.04E-10***	**1.67E-09***
PIPA	0.1853	0.308	**1.80E-08***	**1.30E-09***	**5.79E-08***
Combined	0.226	**0.04209***	**1.70E-14***	**1.70E-14***	**1.34E-11***

Figure 4. A. Shortleaf pine age distribution. B. Longleaf pine age distribution.

Shortleaf Pine

The final sample consisted of 57 shortleaf pine and 38 longleaf pine. The shortleaf pine mean age is 142.6 ranging from 54–206 ($\sigma = 27.3$). K-means determined the optimal number of clusters for shortleaf pine is three. Age classes for shortleaf pine surrounded three means. The first age class (54–102) surrounded a mean of 77.5 ($n = 4$), the second age class (108–148) surrounded a mean of 132.5 ($n = 28$), and the third age class (150–206) surrounded a mean of 164.4 ($n = 25$).

None of the morphological characteristics were significant when regressed on shortleaf pine tree age in any of the three age classes. However, there is a weak relationship between shortleaf pine tree age and the height of the lowest branch ($r_s = 0.27$, $p < 0.046$) when only shortleaf pine data was tested (Table 2). Also, there is a weak positive relationship between tree age and DBH ($r_s = 0.26$, $p < 0.047$) when only shortleaf pine data was tested (Table 2).

Table 2. Spearman rank-order correlation coefficients for shortleaf (PIEC) and longleaf (PIPA) separately and combined. ***significant**

	n	*df*	Sinuosity		Ht. Lowest Branch		Bark		DBH	
			r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
Species										
PIEC	57	55	0.056	0.68	**0.27**	0.046	0.15	0.28	**0.26**	0.047
PIPA	38	36	0.29	0.091	0.21	0.20	0.17	0.31	0.21	0.20
Combined	95	93	**0.21**	0.04	-0.11	0.31	-0.04	0.72	0.12	0.25

Longleaf Pine

The final longleaf pine sample consisted of 38 cores (1 core per tree). Longleaf pine mean age is 111.9 ranging from 62–149 ($\sigma = 22.4$). K-means determined the optimal number of clusters for shortleaf pine is three. Age classes for the longleaf pine surrounded three means: the first age class (62–103) surrounded a mean of 88.0 ($n = 10$), the second age class (103–126) surrounded a mean of 119.4 (n = 13), and the third age class (131–149) surrounded a mean of 138.2 ($n = 15$).

None of the morphological characteristics were significant when regressed on longleaf pine tree age in any of the three age classes. However, there is a moderately positive relationship between longleaf age and DBH in the first age class ($r_s = 0.57$, $p = 0.027$, Table 3). Likewise, there is a strong positive relationship between longleaf age and bark in the third age class ($r_s = 0.87$, $p < 0.05$, Table 5).

Table 3. Spearman rank-order correlation coefficients for the first age class PIEC (54 – 102) and PIPA (62 – 103). **significant*

	n	*df*	Sinuosity		Ht. Lowest Branch		Bark		DBH	
Species			r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
PIEC	4	2	0.77	0.23	-0.26	0.74	0.77	0.23	0.8	0.2
PIPA	10	8	0.47	0.07	-0.28	0.31	0.24	0.39	**0.57**	0.027

Table 4. Spearman rank order correlation coefficients for the second age class PIEC (108 – 148) and PIPA (103 – 126). **significant*

	n	*df*	Sinuosity		Ht. Lowest Branch		Bark		DBH	
Species			r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
PIEC	28	26	0.04	0.84	0.17	0.38	-0.26	0.18	0.09	0.64
PIPA	13	11	0.19	0.53	0.23	0.45	-0.36	0.23	0.06	0.84

Table 5. Spearman rank order correlation coefficients for the third age class PIEC (150 – 206) and PIPA (131 – 149). **significant*

	n	*df*	Sinuosity		Ht. Lowest Branch		Bark		DBH	
Species			r_s	*p*	r_s	*p*	r_s	*p*	r_s	*p*
PIEC	25	23	.078	.71	0.33	0.11	.19	.38	0.07	0.75
PIPA	15	12	.34	.33	-0.09	0.81	**.87***	.00097	0.40	0.24

Combined dataset

None of the multiple regression models were significant when all the data from both species were included, however, there is a weak positive relationship between tree age and sinuosity based on Spearman correlations ($r_s = 0.21$, $p < 0.04$, Table 2).

2.5 Discussion

Based on the samples collected in Uwharrie National Forest, relationships between age and morphological characteristics are either weak (shortleaf pine) or non-significant (longleaf pine) when the full age-range datasets are analyzed (Table 2), but a few stronger relationships for both species emerge when analyzed by age class (Tables 3–5). Shortleaf pine age and morphological indicators of lowest branch height and DBH show weak but statistically significant correlations (Table 2). These results agree with other studies that suggest that the lowest branch height is known to be a common indicator of adult trees because coniferous trees shed lower branches as they age (Brown et al. 2019; Van Pelt 2008). However, this indicator was not significantly correlated with either species or both species combined for any age class. Conversely, DBH is considered an unreliable predictor of tree age (Patterson and Knapp 2016; Brown et al. 2019) because it is impacted by site conditions (Sumida et al. 2012). Thus, these results indicate that larger diameter trees are only weakly correlated with increasing age for shortleaf pine.

In the dataset that includes both shortleaf and longleaf tree age and the four morphological indicators, sinuosity is weakly correlated but statistically significant (Table 2). This study finds that sinuosity is positively correlated with both shortleaf and longleaf pine age which concurs with Campbell (1965) who found that variation in stem sinuosity is responsible for 2.5% of the variation in age of Douglas fir (a weak but significant result). Within the age classes, two combinations are highly correlated and statistically significant. Longleaf pine tree age and DBH in the first age class ($r_s = 0.57$)

and bark thickness in the third age class ($r_s = 0.87$), are statistically significant ($p < 0.05$). While DBH is not a reliable predictor of tree age, Brown et al. (2019) found that DBH was useful in dividing young trees into age classes based on morphology— improving their model by 15% ($R^2 = 0.53$). Likewise, Brown et al. (2019) found that DBH was not a significant predictor of age for either transitional or old trees. The finding in this study is that bark thickness decreases in the oldest age class, which agrees with Sonmez et al. (2007) who found that bark thickness increases with age in oriental spruce (*Picea orientalis*) – including age improved their model by 2% ($r^2 = 0.052$). Other studies have defined these characteristics in eastern deciduous hardwoods (Pederson 2010) and Rocky Mountain conifers (Van Pelt 2008). That said, I recognize that low sample sizes for each age class and the overall dataset raise the possibility that the significant values between age with DBH and age with bark thickness may be spurious. The weak signal can be attributed to the low sample size of trees greater than 150 years—a common threshold for old-growth trees (Pederson 2010)—and in this sample, only two shortleaf pine and no longleaf pine exceeded this threshold.

Old-growth forests are susceptible to environmental stressors such as pests, drought, fire, and human-induced landscape changes (Laurance et al 2000). Likewise, long-term predisposing stressors like neighboring-tree competition for limited resources in old-growth forests play a role in tree growth both on individual trees and neighborhoods (Aakala et al. 2013). Tree-tree competition during the developmental stages of a densely populated old-growth grove intensifies the aging process of individual trees, though stand structural and compositional changes in natural environments make

this relationship difficult to assess (Akala et al. 2013). The forests of the Uwharrie

Mountains have experienced considerable impacts from the selective logging practices

that occurred in the late 1800s and first half of the 1900s. Thus, many of the remnant

shortleaf pine and longleaf pine represent trees either too remote to log or not straight

enough for building purposes. Further, removing the larger trees from this landscape

opened up the canopy and forest floor increasing the amount of available light, water, and

soil nutrients. Trees that were left behind benefited from this reduction of competition,

potentially slowing the external morphological aging process. For example, two of the

primary causes of sinuosity in tree stems is increased competition for available light and

nutrient deficiency (Spicer et al. 2000). Likewise, trees shed their lower branches as they

age (Van Pelt 2008; Brown et al. 2019) to reserve energy and photosynthesize more

efficiently. Therefore, given an abrupt opening of the canopy, a tree would have less of a

reason to shed its lower branches as it ages.

The distribution of the tree-age data also may have contributed to the paucity of

strong relationships between age and morphology for both species. The age range for

shortleaf pine (54–206 years) and longleaf pine (62–149 years) at 1.1 m height coupled

with either the limited number of samples in the tails of the age distributions or lack of

200+ year-old trees may have limited the ability to identify relationships. It is also

possible that age-morphology relationships are not linear, but rather appear at age

thresholds. For example, the relationship between shortleaf pine age and DBH was best

expressed for the youngest age class (*c.f.* Brown et al. 2019), while the sole significant

relationship between longleaf pine age and bark existed only for the samples in the oldest age class.

2.6 Conclusion

The relationship between tree age and morphological characteristics has been sparsely researched. Here, I address this knowledge gap regarding southeastern pine trees and their external morphological characteristics as they relate to agedness. This study indicates that shortleaf pine and longleaf pine trees express weak morphological features of agedness. Of the four morphological characteristics: shortleaf tree age correlates positively with DBH and height of the lowest living branch. Sinuosity is correlated positively with both shortleaf and longleaf tree age, but not within any of the three age classes. Longleaf pine tree age correlates positively with DBH in the first age class as well as bark thickness in the third age class. Age-morphology relationship are poorly defined with the data analyzed in this study. However, the Uwharrie mountains have experience expansive logging, greatly reducing tree-tree competition. The remaining trees benefit from increased nutrient availability potentially reducing aging characteristics acquired over time. Nonetheless, the data suggest that the age of montane shortleaf and longleaf cannot be accurately determined visually via external morphological characteristics. This study helps to fill in a gap of knowledge that exists in dendroecological research related to common southeastern U.S. pine species.

CHAPTER III

CONCLUSION

Age-morphology relationships are seldomly researched and no work exists regarding common pine species in the southeast U.S. Several findings emerge from this study. Age-morphology relationships are poorly defined with the data I analyzed suggesting montane shortleaf and longleaf pine express weak morphological indicators of age. However, of the four morphological characteristics: shortleaf tree age correlates positively with DBH and height of the lowest living branch. DBH is not a reliable indicator of age in other studies (Brown et al. 2019) but can be used to divide trees into age classes (young, transitional, and old). Height of the lowest living branch also correlates positively with shortleaf age which is a common characteristic of hardwoods (Pederson 2010) and Rocky Mountain conifers (Brown et al. 2019) because shed their lower branches to conserve energy (Van Pelt 2008). Sinuosity is correlated positively with both shortleaf and longleaf tree age, but not within any of the three age classes, which is in agreement with Campbell (1965) who found that sinuosity is a weak signal of age in Douglas-fir. Longleaf pine tree age correlates positively with DBH in the first age class as well as bark thickness in the third age class. Again, DBH is not a reliable predictor of age. However, these results suggest that while overall, DBH-age is not

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statistically significant, relationships exist at age-diameter thresholds. Bark thickness was found to increase with age in Oriental spruce (Sonmez et al. 2007), it appears that this relationship only appears in longleaf pine in the oldest trees in this study. Forests in the Uwharrie Mountains have experienced expansive logging, greatly reducing tree-tree competition for remaining trees and thus, potentially reducing acquired aged characteristics. Nevertheless, the distribution of the data and small sample sizes, as well as few trees greater than 200-years old, potentially explain the paucity of strong relationships.

REFERENCES

Aakala, T., Fraver, S., D'Amato, A. W., & Palik, B. J. (2013). Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. *Forest Ecology and Management*, *308*, 128—135.

Applequist, M. B. (1958). A simple pith locator for use with off-center increment cores. *Journal of Forestry*, 56(2), 141.

Bates, M. (2001). Montgomery County Natural Heritage Inventory. *North Carolina Natural Heritage Program, Division of Parks and Recreation, Department of Environment and Natural Resources, Raleigh, NC.*

Black, B. A., Colbert, J. J., & Pederson, N. (2008). Relationships between radial growth rates and lifespan within North American tree species. *Ecoscience*, *15*(3), 349—357.

Bragg, D. C. (2002). Reference conditions for old-growth pine forests in the Upper West Gulf Coastal Plain. *Journal of the Torrey Botanical Society*, 261—288.

Brown, P. M., Gannon, B., Battaglia, M. A., Fornwalt, P. J., Huckaby, L. S., Cheng, A. S., & Baggett, L. S. (2019). Identifying old trees to inform ecological restoration in montane forests of the central Rocky Mountains, USA. *Tree-Ring Research*, *75*(1), 34—48.

Campbell, R. K. (1965). Phenotypic variation and repeatability of stem sinuosity in Douglas-fir. *Northwest Science*, 39(2), 47—59.

Corral-Rivas, J. J., Barrio-Anta, M., Aguirre-Calderón, O. A., & Diéguez-Aranda, U. (2007). Use of stump diameter to estimate diameter at breast height and tree volume for major pine species in El Salto, Durango (Mexico). *Forestry*, *80*(1), 29—40.

Douglass, A. E. (1920). Evidence of climatic effects in the annual rings of trees. *Ecology*, *1*(1), 24—32.

Drexhage, M., & Colin, F. (2001). Estimating root system biomass from breast-height diameters. *Forestry*, 74(5), 491—497.

Dwivedi, P., Sucre, E., Turnblom, E. C., & Harrison, R. B. (2019). Investigating Relationships between Nutrient Concentrations, Stem Sinuosity, and Tree Improvement in Douglas-Fir Stands in Western Washington. *Forests*, 10(7), 541.

Earle, C.J. 2014. Pinus palustris. The Gymnosperm Database. Acessed 13 January 2015 http://www.conifers.org/pi/Pinus_palustris.php

Fritts, H. C., & Swetnam, T. W. (1989). Dendroecology: a tool for evaluating variations in past and present forest environments. In *Advances in Ecological Research* (Vol. 19, pp. 111—188). Academic Press.

Frost, C. C. (1993, May). Four centuries of changing landscape patterns in the longleaf pine ecosystem. In *Proceedings of the Tall Timbers fire ecology conference* (Vol. 18, pp. 17—43).

Gartner, B. L., & Johnson, G. R. (2006). Is long primary growth associated with stem sinuosity in Douglas-fir? *Canadian journal of forest research*, *36*(9), 2351—2356.

Gering, L. R., & May, D. M. (1995). The relationship of diameter at breast height and crown diameter for four species groups in Hardin County, Tennessee. *Southern Journal of Applied Forestry*, *19*(4), 177—181

Guyette, R. P., & Stambaugh, M. C. (2004). Post-oak fire scars as a function of diameter, growth, and tree age. *Forest Ecology and Management*, *198*(1-3), 183—192.

Huckaby, L. S. (2003). Identification and ecology of old ponderosa pine trees in the Colorado Front Range. *US Department of Agriculture, Forest Service, Rocky Mountain Research Station*.

Krause, C., & Plourde, P. Y. (2008). Stem deformation in young plantations of black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) in the boreal forest of Quebec, Canada. *Forest ecology and management*, *255*(7), 2213—2224.

Knapp, P. A., Soulé, P. T., Maxwell, J. T., Ortegren, J. T., & Mitchell, T. J. (2021). Tropical cyclone precipitation regimes since 1750 and the Great Suppression of 1843—1876 along coastal North Carolina, USA. *International Journal of Climatology*, *41*(1), 200—210. DOI: https://rmets.onlinelibrary.wiley.com/doi/full/10.1002/joc.6615.

Larsson, L. (2014). CooRecorder and Cdendro programs of the CooRecorder. *Cdendro package version*, *7*.

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F., Likens, G. E., Banks, S. C., Blanchard, W., ... & Manning, A. D. (2014). New policies for old trees: averting a global crisis in a keystone ecological structure. *Conservation Letters*, *7*(1), 61—69.

Lindenmayer, D. B., & Laurance, W. F. (2017). The ecology, distribution, conservation and management of large old trees. *Biological Reviews*, *92*(3), 1434—1458

Mitchell, T. J., Patterson, T. W., & Knapp, P. A. (2019). Comparison of climate–growth responses of montane and piedmont longleaf pine (*Pinus palustris* Mill.) chronologies in North Carolina. *Trees*, *33*(2), 615—620.

Orvis, K. H., & Grissino-Mayer, H. D. (2002). Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree-ring Research*, Vol. *58(1/2)*, 2002, pp. 47—50

Oswalt, C. M., Cooper, J. A., Brockway, D. G., Brooks, H. W., Walker, J. L., Connor, K. F., ... & Conner, R. C. (2012). History and current condition of longleaf pine in the southern United States. *General Technical Report-Southern Research Station*, *USDA Forest Service*, (SRS—166).

Patterson, T. W., & Knapp, P. A. (2016). Observations on a rare old-growth montane longleaf pine forest in central North Carolina, USA. *Natural Areas Journal*, *36*(2), 153—161.

Pederson, N. (2010). Morphological indicators of old trees in the Eastern Deciduous Forest. *Natural Areas Journal*, *30*(4), 396—407.

Pham, D. T., Dimov, S. S., & Nguyen, C. D. (2005). Selection of K in K-means clustering. *Proceedings of the Institution of Mechanical Engineers, Part C: Journal of Mechanical Engineering Science*, *219*(1), 103—119.

Primicia, I., Camarero, J. J., Janda, P., Čada, V., Morrissey, R. C., Trotsiuk, V., ... & Svoboda, M. (2015). Age, competition, disturbance and elevation effects on tree and stand growth response of primary *Picea abies* forest to climate. *Forest Ecology and Management*, *354*, 77—86.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. DOI: https://www.R-project.org/.

Schmidtling, R. C., & Hipkins, V. (1998). Genetic diversity in longleaf pine (*Pinus palustris*): influence of historical and prehistorical events. *Canadian Journal of Forest Research*, *28*(8), 1135—1145.

Schulman, E. (1956). Dendroclimatic changes in semiarid America. *University of Arizona Press.*

Shapiro, S. S., and Wilk, M.B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52(3–4), 591–611. https://doi.org/10.1093/biomet/52.3-4.591.

Shoda, T., Imanishi, J., & Shibata, S. (2020). Growth characteristics and growth equations of the diameter at breast height using tree ring measurements of street trees in Kyoto City, Japan. *Urban Forestry & Urban Greening*, 49, 126627.

Sonmez, T., Keles, S., & Tilki, F. (2007). Effect of aspect, tree age and tree diameter on bark thickness of *Picea orientalis*. *Scandinavian Journal of Forest Research*, 22(3), 193—197.

Speer, J. H. (2010). Fundamentals of tree-ring research. *University of Arizona Press.*

Spicer, R., Gartner, B. L., & Darbyshire, R. L. (2000). Sinuous stem growth in a Douglas-fir (*Pseudotsuga menziesii*) plantation: growth patterns and wood-quality effects. *Canadian Journal of Forest Research*, 30(5), 761—768.

Stahle, D. W., & Chaney, P. L. (1994). A predictive model for the location of ancient forests. *Natural Areas Journal*, 14(3), 151—158.

Stahle, D. W. (1996). Tree rings and ancient forest history. *Eastern old-growth forests*, 321—343.

Stambaugh, M. (2001). Forest canopy gap disturbances in shortleaf pine forests of the Ozark highlands (*Doctoral dissertation, Master's Thesis, University of Missouri, Columbia, Missouri, USA*).

Stokes, T. A., Samuelson, L. J., Kush, J. S., Farris, M. G., & Gilbert, J. C. (2010). Structure and diversity of longleaf pine (*Pinus palustris* Mill.) forest communities in the Mountain Longleaf National Wildlife Refuge, northeastern Alabama. *Natural Areas Journal*, 30(2), 211—225.

Stuckey, Jasper L. (1965). North Carolina; Its Geology and Mineral Resources. *Department of Conservation and Development, Raleigh.*

Sumida, A., Miyaura, T., & Torii, H. (2013). Relationships of tree height and diameter at breast height revisited: analyses of stem growth using 20-year data of an even-aged Chamaecyparis obtusa stand. *Tree physiology*, *33*(1), 106—118.

Van Pelt, R. (2008). Identifying old trees and forests in eastern Washington. *Washington State Department of Natural Resources*.

Villalba, R., & Veblen, T. T. (1997). Improving estimates of total tree ages based on increment core samples. *Ecoscience*, 4(4), 534—542.

Wells, E. F. (1974). A vascular flora of the Uwharrie Wildlife Management Area Montgomery County, North Carolina. *Castanea*, 39-57.

Wahlenberg, W. G. (1946). Longleaf pine: its use, ecology, regeneration, protection, growth, and management. *Longleaf Pine: its use, ecology, regeneration, protection, growth, and management.*