Variation in the structure, composition, and dynamics of a foundation tree species at multiple scales and gradients

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ABSTRACT

Scientists and land managers often focus on the Southeastern Plains and Coastal Plain of the southeastern United States when considering the ecology, restoration, and management of longleaf pine (*Pinus palustris* P. Mill.) communities and ecosystems. However, the range of this foundation tree species and its associated communities and ecosystems also extend into the Piedmont and Montane Uplands: the Piedmont of Alabama, Georgia, North and South Carolina and Virginia; the Ridge and Valley of Alabama and Georgia; and the Southwestern Appalachians of Alabama. The composition, structure, and dynamics of Piedmont and Montane Uplands longleaf pine communities have been understudied compared to their Southeastern Plains and Coastal Plain counterparts, and knowledge is based on historical accounts and a handful of studies at site-specific scales. The biogeography and ecology of Piedmont and Montane Uplands longleaf pine communities differ significantly from those in the Southeastern Plains and Coastal Plain. My research combines geospatial and ecological approaches to provide insights on current composition, structure, and dynamics of longleaf pine communities in the Southeastern Plains, Piedmont, and Ridge and Valley at multiple scales and highlights differences and similarities with communities in the Coastal Plain. The Piedmont and Montane Uplands longleaf pine communities showed high variation in canopy tree diversity compared to those in the Coastal Plain. Longleaf pine was sometimes the only canopy tree, while in other communities longleaf pine was one constituent in a mixed oak-pine canopy. My study showed that longleaf pine communities were not just restricted to south-facing slopes as previously thought, but were found on northwestern-facing slopes as well. Analysis of tree rings across my study sites showed that as longleaf pine approaches its northern range margin in the Piedmont and Montane Uplands, its radial growth is restricted by minimum temperature especially at longleaf pine's elevational, latitudinal, and longitudinal extremes; at all sties radial growth was influenced by drought and precipitation. At the local scale, I found that an Alabama Piedmont longleaf pine community showed a diameter-class distribution typical of an old-growth site but contrary to current knowledge, diameter was not a good indicator of age.

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Table of Contents

List of Tables

Chapter 1: Introduction

1. Research Context and Justification

The southeastern United States' landscape will be altered over the next century due to changes in climate and land use patterns (IPCC 2007; Napton et al. 2010). A variety of different climate scenarios suggest that the southeastern United States will experience warmer temperatures while periods between precipitation events will be longer. These scenarios imply increased drought stress which would affect human populations, agriculture, and forests (Seager et al. 2009). From 1973–2000, land use has fluctuated between the two dominant land covers, agriculture and forests (both natural and commercial; Napton et al. 2010). As human populations have grown faster than the national average, both agricultural lands and forests are also being converted to urbanized lands (Napton et al. 2010). Two forest regions, the southern-mixed and mesophytic, are found across three ecoregions, the Piedmont, Ridge and Valley, and the Southeastern Plains, and make up much of the southeastern landscape (Dyer 2006). These forest regions are a mosaic of small remnant patches of old-growth forests and larger patches of second-growth or commercial forests, especially in the southern-mixed forest region. The composition, structure, and dynamics of communities and ecosystems in these forest regions could be significantly altered as a result of climate and land use change as individual tree species ranges contract or expand depending on their ability to adapt to these changes (Iverson and Prasad 1998).

Pinus palustris P. Mill. (longleaf pine) was historically a dominant tree species in the southeastern-mixed forests regions in Alabama, Georgia, South and North Carolina, and Virginia. This species also occurred in mixed forests along the southern portions of the mesophytic forest regions in Alabama, Georgia, and North Carolina, its northern range limit.

Human land-use patterns resulted in the removal of old-growth forests, some containing *P. palustris*, in the southern-mixed and mesophytic forest regions and their conversion into agriculture, urban, and second-growth or commercial forest lands. *Pinus taeda* and *Pinus echinata* became the dominant pine tree species in the second-growth communities and forests of both of these forest regions. The removal of *P. palustris* not only in these two forest regions, but also in the subtropical evergreen forest region to the south, resulted in the elimination of around 97% of the *P. palustris* communities over the course of the last four hundred years (Frost 2006). Remnant *Pinus palustris* communities do exist in patches of old-growth or second growth forests, but not at the extent they once were on the landscape (Varner 2003). The *P. palustris* communities in the Piedmont, Southwestern Appalachians, and Ridge and Valley are referred to as the *P. palustris* Piedmont and Montane Uplands (Peet 2006).

Most information on Piedmont and Montane Uplands *P. palustris* communities is gathered from historical accounts and current studies at the local scale. My dissertation examines the variation in canopy tree diversity, the relationship between *P. palustris* radial growth and climate, and the effects of exogenous and endogenous disturbance events on *P. palustris* structure and composition at multiple scales combining geospatial and ecological approaches. This research on *P. palustris* communities in the Piedmont and Montane Uplands is timely as interest has grown in properly managing them for their ecological importance on the landscape and because this species may better suited to handle the environmental stresses involved with climate and land use change (Eckhardt et al. 2010). Research across multiple scales in the Piedmont and Montane Uplands will contribute to a better understanding of *P. palustris* forest communities by putting them into a context of differences and similarities in form and function across local and broader scales.

2. Dissertation Components

This dissertation consists of three chapters that have been prepared as manuscripts for submission to peer-reviewed academic journals. This dissertation examines the ecology and biogeography of Piedmont and Montane Upland *P. palustris* communities in the southeastern United States at the regional scale (Chapters 2 and 3) and at the local scale (Chapter 4). *Pinus palustris* communities exist in the Piedmont and Ridge and Valley southern-mixed forests of Alabama, Georgia, and South Carolina and in the North Carolina Piedmont mesophytic forests (Omernik 1997). I also investigated a site in the more heavily-dissected interior section of the Southeastern Plains of Alabama, which differs significantly from the flatter and less dissected Coastal Plain. Chapter 2 examines the variation in tree species diversity of *P. palustris* communities relative to environmental variables in the interior portions of its range at broader scales, based on ten sites with a total of 56 plots from Alabama to North Carolina. Chapter 3 studies the influence of climate on radial growth of *P. palustris* from chronologies developed from some of my study sites along with other *P. palustris* chronologies that have been contributed from other scientist at other sites throughout the range of longleaf pine from Alabama to Virginia, excluding Florida. I explore how climate affects this species along two gradients, one along a north to south gradient occurring within Alabama and Georgia and the other gradient which is along its northern range margin, from Alabama to Virginia. Chapter 4 is a localized study, focusing on disturbance dynamics of one site in the Piedmont of Alabama. Piedmont *P. palustris* community structure and dynamics is not well known relative to communities in the Coastal Plain and Ridge and Valley and my goal is to understand structure and disturbance dynamics at this site. Together these individual studies contribute to the ecology

of longleaf pine communities at different spatial and temporal scales in the Piedmont and

Montane Uplands and the results have implications for its management for future generations.

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Chapter 2: Variation of southern pine communities approaching their northern range margin in transitional, fragmented, and managed oak-pine and hardwood forests

Note: This chapter was prepared for submission to the journal Ecography

Abstract

Transitional forests around the globe serve as important areas to study the impacts of changing climate and land use. The southern-mixed pine-hardwood forest region is a transitional area, located between the subtropical evergreen and mesophytic forest regions of eastern North America, warranting further study. Climate and land-use scenarios suggest a warmer, more stressed, environment for these fragmented and managed forests, causing the southern-mixed forests to expand in size, the subtropical evergreen forest to shrink, and the mesophytic to shift northward. *Pinus taeda* and *Pinus echinata* are expected to be the dominant pine species in these transitional forests although they might not be as highly adaptable to stress in these future forests. This study considers another pine species, *Pinus palustris*, which occurs at its northern range margin in the southern mixed and mesophytic forests. We examined the variation in the composition of *P. palustris* communities in these forests to establish a baseline inventory from which to understand how climate and land use change could impact these communities in the future. The importance values for all tree species in *P. palustris* communities were used to determine the dissimilarity of tree diversity from 56, 20 m x 50 m plots across ten actively-managed sites using an indirect multivariate gradient ordination and analysis. *Pinus palustris* communities were associated with Ultisols located on ridges, hills, and terraces, depending on ecoregion, and exhibit different compositional patterns with diversity increasing towards the

northeast from Alabama to North Carolina. The wide ecological amplitude of this species

throughout the southeast suggests that it could be of more importance in these forests, especially

if active management to promote this species continues in the future along with climate and land

use change.

1. Introduction

Shifts in the geographical ranges of individual tree species along transitional gradients are altering the composition of forests throughout the world and are associated with climate change and human alteration of the landscape (Hansen et al. 2001, IPCCC 2007). Such shifts have been observed along elevational gradients of mountains, especially at tree line, and in high northern-latitude forests, such as boreal forests (Soja et al. 2007, Elliott and Kipfmueller 2011). The southern-mixed forests of eastern North America are transitional forests between the mixed-*Pinus*-dominated subtropical evergreen forests to the south and the *Quercus*-other hardwood dominated mesophytic forests to the north (Braun 1950, Dyer 2006). Compositional changes in these forests have occurred in the geologic past and will occur in the future due to climate and land use change as individual tree species' ranges expand, contract, or shift along elevational and poleward gradients resulting in new forest types or migration of forest regions northward (Delcourt and Delcourt 1987, Delcourt and Delcourt 1988, Shao and Halpin 1995, Iverson and Prasad 1998, Hansen et al. 2001, Iverson and Prasad 2001, Iverson et al. 2004). These forests could be further fragmented by urban, suburban, and exurban land use; more susceptible to fires, hurricanes, thunderstorms, insect outbreaks, and non-native species; and affected by land management practices (Flannigan et al. 2000, Dale et al. 2001, Iverson and Prasad 2002, McKenney et al. 2007, Drummond and Loveland 2010, McEwan et al. 2011).

Five climate scenarios suggest that the southern-mixed forests could expand in area up to 290% throughout the southeast, with mesophytic forests expanding north and east by 34%, and a reduction in *Pinus*-dominated subtropical evergreen forests (Iverson and Prasad 2001, Hansen et al 2001). These models, which utilized tree species inventory data from over 100,000 plots contained within the United States Forest Service's forest inventory and analysis database,

suggest that *Pinus taeda* L. (loblolly pine) and *Pinus echinata* P. Mill. (shortleaf pine) will

expand their ranges and increase their importance in the southern-mixed forests (Iverson and

Prasad 2001).

One important tree species not often included in analyses of these forests is *Pinus palustris* P.

Mill. (longleaf pine). *Pinus palustris* is associated with diverse, fire-adapted forest communities

that once covered over 37 million ha of the southeastern landscape, from the subtropical

evergreen forests to the southern fringes of the mesophytic forests up to 600 m in elevation

(Landers et al. 1995, Varner et al. 2003b, Frost 2006). Land use patterns after European

settlement since the 1600s has led to a 97% historical decline in these communities and included

changes in fire regimes and land management, over-utilization by both the timber and navel

stores industries, and conversion to second-growth *P. taeda* forests, *P. taeda* plantations, or

agricultural or urbanized lands (Dyer 2006, Frost 2006). Accounts and studies, both historical

and current, place *P. palustris* in pure and mixed stands with other *Pinus sp.*, *Quercus* sp., and

other hardwoods in the southern-mixed and mesophytic forests of Georgia, Alabama, and North

Carolina (Campbell and Ruffner 1883, Mohr 1901, Harper 1905, 1910, 1911, 1923, 1928, Reed

1905, Golden 1979, Frost 2006, Peet 2006, VegBank 2011, personal communication, Milo Pyne,

southeastern senior regional ecologist, NatureServe). The mixed *P. palustris* forests, which were

also composed of *P. taeda*, *P. echinata*, *Quercus stellata* Wagnenh. (post oak)*, Quercus alba* L.

(white oak), other *Quercus sp.*, and *Carya* sp., experienced low-intensity fires every four to

twelve years that varied by topography and were ignited by lightning or Native Americans (Mohr

1901, Harper 1905, 1923: 1928, Frost 2006).

Current *P. palustris* communities exist in fragmented and often degraded conditions in

the southern-mixed and mesophytic forests of the Piedmont, Ridge and Valley, and the northern

Southeastern Plains with the variability in the composition and structure of these communities at local scales only beginning to be understood (Landers et al. 1995, Maceina et al. 2000, Varner et al. 2003a, Varner et al 2003b, Frost 2006, Stokes et al. 2010, Womack and Carter 2011). Current estimates place the extent of *P. palustris* communities at around 40,000 ha for the southern-mixed and mesophytic forests in the Piedmont, Southwestern Appalachians, and Ridge and Valley of Alabama and Georgia. Estimates for the communities in the southern mixed and mesophytic forests of the North and South Carolina Piedmont are lacking while longleaf pine communities in Virginia are almost extirpated (Varner et al. 2003b, Frost 2006; Bhuta et al. 2008).

Pinus palustris and its associated communities deserve further investigation at broader scales in southern-mixed forests in light of escalating changes in climate and land use. The natural history of *P. palustris* suggests that it is well adapted to frequent low-intensity fires and, unlike *P. taeda*, *P. echinata*, and other southern pine species, it is not as susceptible to insect and other diseases and is less prone to wind damage from hurricanes (Komarek 1964, Platt et al. 1988, Boyer 1990, Gresham et al. 1991, Moser et al. 2003, Frost 2006, Johnsen et al. 2009). It is possibly the most tolerant of the southern yellow pine species in mitigating the conditions of a warming climate compounded with other environmental stressors that may affect these future forests. *Pinus palustris* communities could also serve as biogeographical islands and corridors from which this species could expand into other southern mixed forest stands under such conditions (Opdam and Wascher 2004, Damschen et al. 2006). Some land managers are selectively managing for *P. palustris* in the southern mixed and mesophytic forests, but are eliminating the mixed-natural communities and replacing them with pure *P. palustris* (Frost 2006). Most decisions about management of *P. palustris* communities along its range margins

are based on ecological knowledge and management practices of this species in southern portions of the southern-mixed and the subtropical evergreen forests of the Coastal Plains (Varner et al. 2003a). Spatial variation in fire intervals, soil, topography, climate, and competition amongst other hardwoods and pines for resources suggest a different ecology for longleaf pine compared to its southern populations, which are usually dominated by pure stands (Platt et al. 1988, Noel et al. 1998, Frost 2006, Peet 2006). Our primary objective for this study is to document and examine the variation in β diversity for fragmented and managed *P. palustris* communities in the mesophytic and southern-mixed forests of eastern North America (Anderson et al. 2011). We specifically investigate (1) this variation across sites for *P. palustris* along its northern range margin from Alabama to North Carolina and (2) the relationship between this variation and management practices. Our main question guiding this research is: what are the differences in tree diversity for *P. palustris* communities as we approach its northern range margin? We further elaborate on how our findings and past research could guide future management and what it could mean for *P. palustris* communities in the future. This research establishes baseline data that can be used to examine the influence of future trends in climate, land use, and management in these communities and forests (Beauchamp and Shafroth 2011). This type of research also contributes to a basic understanding of the ecology and natural history of *P. palustris* as this species is only beginning to be understood in the Piedmont and Ridge and Valley ecoregions (Maceina et al. 2000, Varner et al. 2003a, 2003b, Stokes et al. 2010, Womack and Carter 2011).

2. Methods

2.1. Study area description

Our study was conducted in the southern-mixed and mesophytic forests of the southeastern

United States (**Figure 2.1**). The southern-mixed forest region is mostly dominated by *P. taeda*

plantations and second-growth mixed stands of *P. taeda* with other pine, *Quercus* spp., and other

hardwoods (Dyer 2006). Historically, these forests were dominated by *P. palustris* (Dyer 2006,

Napton et al. 2010). The mesophytic forest region is the most diverse in eastern North America

with 162 tree species consisting of *Quercus* spp. and other hardwoods in mixed canopies (Dyer

2006). Currently, both of these forest regions, especially the mesophytic, are experiencing shifts

in composition with *Acer* spp. replacing *Quercus* spp. and other hardwoods due to changes in

trophic patterns, fire regime, land use, and climate (Abrams 1998, McEwan et al. 2011).

These two forest regions, the southern mixed and mesophytic, are distributed among three

ecoregions in the study area, the Southeastern Plains, the Piedmont, and the Ridge and Valley.

The Southeastern Plains is the largest (336,000 km^2) ecoregion in eastern North America. It is an

irregularly-dissected, Cretaceous-Tertiary aged plain cradling the southern areas of the Interior

Plateau, the Southwestern Appalachians, the Ridge and Valley, and the Piedmont. About half of

the lands (52%) are forested, primarily southern-mixed, followed by agricultural (21.5 %) and

human-developed lands and wetlands (both 10.3%) (USGS 2011a). Wherever *P. palustris*

historically occurred in this ecoregion, it usually was the forest dominant, especially on upland

sites in both the subtropical evergreen and southern-mixed forests (Frost 2006). The climate for

the Southeastern Plains consists of temperature ranging from -1.7 (January) to 32.7 C° (July),

precipitation ranging from 1346 to 1422 mm, and frost free days ranging from 210 to 240 days.

The Piedmont is a transitional southwesterly to northeasterly region occurring from east-

central Alabama to northern Virginia and is situated between the Coastal Plains to the southeast

and the Ridge and Valley to the Northwest. Precambrian to Paleozoic-aged metamorphic and

igneous rocks underlie the region. Much of the southern-mixed and mesophytic forests of the Piedmont were cleared for their timber and converted to agriculture, however with westward settlement of the United States, many of these lands were abandoned and replaced by second-growth and old-field forests (Mohr 1901, Brender 1974, Golden 1979, Cowell 1995). Southern-mixed and mesophytic forests make up 55.1 % of the Piedmont, followed by agricultural lands (23.1 %) and urban/suburban lands (16.4 %) (USGS 2011a). The climate for the Piedmont consists of temperature ranging from -2.7 (January) to 32.2 C° (July), precipitation ranging from 1118 to 1524 mm, and frost free days ranging from 185 to 230 days.

The Ridge and Valley ecoregion occurs from northeastern Alabama to southeastern New York, trending similarly as the Piedmont. In Alabama and Georgia the Ridge and Valley borders the Piedmont, but the Blue Ridge wedges between both the Ridge and Valley and the Piedmont from north-central Georgia all the way to New York. Geologic folding and faulting has led to the development of Paleozoic-aged mountainous terrain consisting of low valleys and parallel ridges running the length of this ecoregion. Around 56 % of the Ridge and Valley is composed of forested lands and like the other regions agricultural (30.5 %) and human developed lands (9.3 %) are the other major land covers (USGS 2011b). Mesophytic forests are dominant for the majority of the Ridge and Valley with the southern-mixed forests transitioning in when approaching the Piedmont border. The climate for the Ridge and Valley consists of monthly mean temperatures ranging from -2.7 (January) to 32.2 C° (July), precipitation ranging from 1321 to 1524 mm, and frost free days ranging from 180 to 225 days. A humid subtropical climate regime with thermic and udic soils is typical of the entire study area.

We selected ten sites in the study area based on personal communication with landowners who knew of sites were *P. palustris* was naturally occurring component of the canopy (**Table**

2.1). Our sites were located throughout four states: Alabama (Reed Brake Natural Area (RBN),

Oak Mountain State Park (OMS), and Big Smith Mountain (BSM)); Georgia (Berry College

(BOC)); South Carolina (Forty Acre Rock (FAR), Harbison State Forest (HSF), Long Cane

Ranger District (LCR)); and North Carolina (Clarkes Grove/West Montgomery (CGM), Eastern

Railroad, (ERD), Nichols (NICH)). Seven sites were managed by either state or federal agencies

while BC is managed by a private, four-year liberal arts college, NICH is managed by a private

non-industrial land owner, and BSM is managed by a private industrial landowner. RBNA is in

the Southeastern Plains southern-mixed forests and BC and OMSP are in the Ridge and Valley

southern-mixed forests. RBN, LCR, HSF, and FAR occur in Piedmont southern-mixed and

CGM, ERD, and NIC occur in Piedmont mesophytic forests. While each site has its own unique

management plan, all sites include or will include strategies ensuring conservation and

restoration of *P. palustris*.

2.2. Data collection and preparation

We randomly located 56, 20 m x 50 m (0.1 ha) permanent plots across our ten sites

throughout our study area, eight plots per site in Alabama and Georgia and four plots per site in

South and North Carolina (Table 1; Peet et al. 1998). Our sites in Alabama and Georgia were

larger in management areas, so more plots were used at these sites to obtain a better

representation of the larger areas. Using 1:24, 000 (7.5') USGS topographic quadrangle maps,

we visually interpreted the slopes at eight sites (RBN, BOC, LCR, HSF, FAR, CGM, ERD, and

NIC), assigned them each a number, and randomly assigned a plot to the selected slopes. For

plot placement, we determined minimum and maximum elevation from contour lines on the

topographic map, randomly selected an elevation along the slope, and then bisected the slope's

14

aspect using the center line as a transect to navigate to our randomly selected elevation, placing plot center on the transect. Plot selection and placement was slightly different for two sites: Oak Mountain State Park (OMS) and Big Smith Mountain (BSM). At OMS, we sampled a southeastern-facing slope that was ~10 km in length. We established a transect running along the ridgeline of the slope, selected eight random points along it and established transects perpendicular to the original transect from those points. While at BSM, eight transects were randomly selected from compass bearings originating from the summit of BSM. From these eight transects at each site, plot selection and placement was chosen similarly to the other eight sites using random elevations.

We calculated slope (%), aspect (%), and elevation (m) for all plots in a GIS (ArcGIS 9.3.1, Environmental Systems Research Institute, Inc. Redlands, CA, US) using our georeferenced data on permanent plot markers and trees and from 1/3 arc-second digital elevation models (United States Geological Survey 2011b). Georeferenced data were also used in ArcGIS 9.3.1 to reference our soil field data with the U.S Department of Agriculture's National Resources Conservation Service's Soil Survey Geographic Database to identify categorical soil data which was split into classes based on geomorphology, soil classification, and soil characteristics for all plots (**Table 2.3**). Slope and aspect data derived from the GIS were used to develop potential direct incident radiation and a heat load index for all plots using non-parametric regression in HyperNiche (McCune and Keon 2002, McCune and Mefford 2009, McCune 2007). We developed management classes for each plot based on personal communication with the landowners about management over the previous 30 years. Classes were designated as: 1) no management, 2) management with fire, 3) management with thinning, 4) management with

15

herbicides, 5) management with fire and thinning, 6) management with fire and herbicide, 7) management with fire, herbicide, and thinning, and 8) management with herbicide and thinning.

All plots were permanently marked with rebar and all trees ≥ 5.0 cm diameter at breast height (DBH) were tagged, identified, measured for DBH and height, and georeferenced with a global position system (GPS) unit or combination of a GPS unit, survey prism, and total station. We collected mineral soil samples with a soil auger at a depth of 15 cm and soil depth was measured using a steel tile probe inserted into the ground to bedrock the maximum length of the probe (150 cm in length). Soil depth and soil samples were collected at plot center and corners. Soil pH, concentrations of soil element concentrations (P, K, Ca, Mg, Zn, Mn, CU, Fe and B), cation exchange capacity, soluble salts, and organic matter were analyzed by the Virginia Tech's Soil Testing Laboratory (Maguire and Heckendorn 2011). All soil data processed by the soil testing lab and soil depth were averaged by plot and site (**Table 2.2**).

We used principal components analysis using a correlation cross-products matrix, a distance-based biplot, and bootstrap simulations to statistically determine which soil nutrient components significantly contributed to a better understanding of the distribution of tree diversity across our study area (PC-ORD V.6, McCune and Mefford 2011). The eigenvalues from our significant axes were used in understanding how these soil nutrient components were associated with our community analysis. Field data were collected in the late spring, summer, and early fall (leaf on) of 2009 and 2010. Species nomenclature follows the Integrated Taxonomic Information System (2011). Tree species identification, counts, and DBH were used to calculate importance values for all tree species at the plot level by dividing by two the summation of relative dominance and relative density. At the site level, importance values were also calculated for all tree species but summed with relative frequency and dividing by three.

16

2.3. Data analysis

Multivariate statistics and analyses were carried out in PC-ORD V.6 using the Sørenson (Bray-Curtis) dissimilarity index for all matrices (Faith et al. 1987, McCune and Mefford 2011). The community matrix consisted of importance values at the plot level described above. This matrix was used in developing a species-area curve, determining species dominance, estimating α and β diversity across our plots, defining groups, and ordinating our plots using non-metric multidimensional scaling (NMDS). We generated a species area curve by randomly reiterating subsamples from our matrix across our sampled plots and calculating average total richness at each plot point. The average richness at each point was then plotted against the number of plots. The species area curve allowed us to spatially explore how often new species occurred along our study area and in determining if our sampling was adequate in capturing tree species within our study area. A dominance curve involved plotting log abundance by distribution by species to assess dominance in our study area. To better understand variation in composition across our study area α and β diversity were calculated for all plots, sites, and study areas (Anderson et al. 2011). Species richness, evenness, and Shannon's diversity index (H') were used in understanding this diversity.

Hierarchical agglomerative cluster analysis assisted in defining groups for the dataset using the flexible β method (β = -0.25) because it is well-suited for Sørenson (Bray-Curtis) distance measures (McCune and Grace 2002). We performed an indicator species analysis to determine the appropriate number of groups from the cluster analysis using the phi coefficient (Tichý and Chytrý 2006). This analysis converts all species to presence-absence scores and determines diagnostic species by grouping the sample unit one way correcting for unequal samples sizes

among groups. A Monte Carlo test with 1000 permutations determined the significance of the indicator values for each group. A two-way cluster analysis allowed us to examine how our tree species data matched up with our groups. The two-way cluster analysis incorporates a matrix showing presence and absence of tree species across our selected groups allowing for a better understanding of grouping related to tree species in our groups.

These grouping and the management class per site aided in understanding the variation along our axes from our NMDS ordination. NMDS is an unconstrained indirect gradient ordination analysis allowing for multivariate, nonparametric, and homogeneous ecological data of large datasets containing many zero values to be ordinated based on community dissimilarity. To determine the final NMDS ordination to use, we ran four sets of stress tests on our data starting at six dimensions, 250 iterations, an instability criterion of 10^{-5}, and orthogonal principal axes: 1) all plots and all species, 2) all plots but omitted species with an importance value less than 5 %, 3) all species but omitted outlier plots, and 4) plots and species sans the omitted species and plots. To determine which plots and species to omit from the NMDS analysis, an outlier analysis was performed on all plots with outliers greater than a standard deviation of two being omitted, while for tree species, they were omitted if their importance values were < 5 % when accounting for all zero values in the matrix. We removed three plots and eight species based on these criteria. We used Pearson correlation coefficients to better understand the association of our ordination to continuous environmental variables and multi-response permutation procedure (MRPP) for our categorical environmental variables (McCune and Grace 2002).

3. Results

18

We surveyed 4,147 trees representing 30 tree species across all 56 plots and 10 sites. Plot aspects ranged from eastern (78°) to northern facing slopes (350°) with the majority between 90° and 270° (**Figure 2.2**). Forty eight plots were located on mostly south-facing slopes, but there were seven plots with western to northern facing slopes that had *P. palustris* with the highest importance value. These seven plots are located on three sites, BSM, RBN, HSF, and FAR, all of which are in the Piedmont. The northernmost plot was FAR_1 which was omitted from our final NMDS analysis because it was considered an outlier, but *P. palustris* had an importance value of 11 %, while other *Pinus* sp. had an importance value of 18 %, and hardwoods had an importance value of 70%. The other four sites were in contrast to this plot with significantly higher importance values for *P. palustris* ranging from 44 % to 99 % in importance value and aspects ranging from 276° to 331°.

Our species area curve indicated that encountering a new tree species when adding 100 m^2 tapered out at around 31 plots. The standard deviation was less than one at 31 plots. The standard deviation approached zero at 54 plots, thus the 56 plots that we sampled was adequate in sampling our study area even though our plots were nested within sites (**Figure 2.3**). Species importance values were highly variable across sites, but *P. palustris* was always the dominant tree species 5(**Table 2.4**). *P. palustris* (log abundance = 3.5; relative abundance = 61.4) was the most dominant species followed by *Pinus echinata* (log abundance = 2.5; relative abundance = 6.8) and *Pinus taeda* (log abundance = 2.4, relative abundance = 4.9) (**Figure 2.4**). A variety of hardwoods followed including *Quercus* spp. and *Carya* spp. plus two conifer species, *Juniperus virginiana* L.(eastern red cedar) and *Pinus virginiana* P. Mill. (Virginia pine). Eight species had log abundances less than 1.0 or relative abundances less than 0.25 and were omitted in our final NMDS ordination analyses. These species were *J.virginiana*, *Diospyros virginiana* L. (common

persimmon), *Prunus serotina* Ehrh. (black cherry), *Ilex opaca* Ait. (American holly), *Fagus grandifolia* Ehrh. (American beech), *Quercus nigra* L. (water oak), *Sassafras albidum* (Nutt.) Nees (sassafras), and *Carya cordiformis* (Wangenh.) K. Koch (bitternut hickory).

Our NMDS analysis revealed that the best final solution for our data involved using the fourth set with outlier plots and species with < 5% importance values omitted (**Table 2.5**). This solution revealed that three NMDS axes best explained our community data. Minimum stress was 8.933, was significant at the 0.05 level, and explained 93% of the variance. The third set of NMDS ordinations, keeping all species but omitting outlier plots, could have been used as it was significant and explained 92 % of our community data, but we chose set four because of omissions of outliers at both the plot and species levels. We additionally verified our solution by plotting out stress versus our runs and instability, the standard deviation of our stress, against step length, and the magnitude of the gradient vector from our initial run of set four (**Figure 2.5**). Stress dropped quickly and stabilized smoothly with instability dropping in the same manner, suggesting that this set was stable (McCune and Grace 2002).

We were able to identify six different tree groups or communities while managing to keep 55.8% of the information remaining from our cluster analysis. Indicator species analysis significantly placed certain tree species within our communities based on our groupings (**Figure 2.6, Table 2.6 and Table 2.7**). These groupings were incorporated into our NMDS ordination space with these groupings separated into the following communities (numbered by the program based on our HACA and listed here for efficiency): group 1 = pure *P. palustris*; group 9 = *P. palustris* with *P. echinata*, *Pinus virginiana*, and *Quercus prinus* L. (chestnut oak); group 12 (the most diverse plots) = *P. palustris* with Carya alba, *Pinus* sp., *Quercus* sp., and other hardwood species; group 25 = *P. palustris* with *P. taeda* and *Liquidambar styraciflua* L. (sweetgum); group

36 = *P. palustris* with *Liriodendron tulipifera* L. (tulip poplar), *Quercus stellata* Wangenh. (post

oak), *L. styraciflua*, *Acer rubrum* L. (red maple), and *Quercus flacata* Michx. (southern red oak);

and group 40 = *P. palustris* with *Quercus boyntonii* Beadle (Boynton Sand Post Oak), *Quercus*

marilandica Muenchh. (blackjack oak), and *Carya alba* (L.) Nutt. ex Ell. (mockernut hickory)

(**Figure 2.7**). All plots were also grouped in management classes to compare the differences

between the groups from our cluster analysis (**Figure 2.8**). The management classes revealed

different groupings in our ordination space, not matching with the groupings of our communities.

Species richness was higher at plots 3 and 4 of NICH and plot 2 of HSF, all non-managed,

however sites where only arson fires had occurred and no other prior management did not have

high species richness, these were OMS and BSM. The other sites ranged between OMS and

BSM and NICH and HSF, with some trending closer to OMS and BSM and others towards

NICH and HSF (**Figures 2.7 and 2.8**).

Two axes from our principal components analysis were statistically significant ($\alpha = 0.05$)

explaining 67.7 % of the variance in our soil nutrients. Increased acidity (0.244) and buffered

pH (0.235) followed by decreased soil nutrients except for Iron, Copper, Phosphorus, Potassium

saturation, Magnesium saturation and Boron were the most highly associated variables along the

1st axis while on the 2nd axis all soil nutrients except for Magnesium, Boron, Iron, Phosphorus,

Potassium, Managanese, Calcium, Zinc, and soluble salts followed by decreased cation exchange

capacity and acidity were the strongest (**Figure 2.9**). Both principal components were correlated

with other continuous environmental variables to determine their associations with our NMDS

axes. Alpha diversity, regardless of the diversity measure were all strongly associated to NMDS

Axis 1, the first principal components of our soil nutrients were associated with NMDS Axis 2,

and available water content and elevation were associated or negatively strongly associated

respectively with NMDS Axis 3. Heat load index shared an association with both NMDS Axes 2 and 3 (**Table 2.8**).

Geomorphology classes, landform classes, landform type, landform position, down slope shape, and across slope shape, were all significant (**Table 2.9**). All landforms and their positions and shapes are similar and were classified on some aspect of a slope (side, nose, back), interfluve, or tread pertaining to a hill, ridge, or terrace depending on the ecoregion where the plot was located. The down and across slope shapes were either linear, convex, or a combination of both. Soil classes, soil order, and type, also had significant correlations amongst our groupings and are all related to each other since there is a hierarchy to the classification from order to type (**Table 2.9**). All soils are Ultisols belonging to Aquic or Typic Hapludults or Kanhapludults with the exception of the Paleudults for two plots at FAR. For the soil characteristics, soil depth among our plots was strongly significant (**Table 2.9**). Shallow soils were associated with Berry College (BOC), followed by moderately deep soils for all plots at Oak Mountain State Park (OMS), and deep to very deep soils were associated with pure stands of *P. palustris* to the most diverse sites containing *P. palustris*, other *Pinus* sp., and hardwoods. Drainage and permeability were somewhat significant but not as strong as depth.

4. Discussion

4.1. General observations of <u>Pinus palustris</u> communities

Landform observations indicate that these plots are situated on convex to linear slopes on ridges in the Ridge and Valley, hills in the Piedmont, and terraces in the Coastal Plain with soils that are Ultisols in order and Udults in suborder. The general trends of our soil data indicate that they are acidic in nature with most soil nutrients, such as Calcium, Magnesium, and Potassium

22

for example, leached into the soils. The landform and soil patterns in our sites are similar to other *P. palustris* communities in the southern-mixed Piedmont and Ridge and Valley forests of Alabama and North Carolina (Golden 1979, Varner et al. 2003b, Peet 2006). Our data also show that *P. palustris* can occupy western to northern slopes in the interior portions of its range and is not restricted to southern facing slopes as has been previously observed (Wells 1974, Golden 1979, Peet 2006, Varner et al. 2003a, Womack and Carter 2011). This finding is especially important because it indicates that *P. palustris* can recruit across sites with differing aspects without any issues under a warming climate. Further research examining *P. palustris* communities on similar slope positions at other locations need to be conducted to determine if this trend can be observed in the Ridge and Valley. Reed (1905) may have also observed *P. palustris* forests on a variety of different aspects and slopes at two sites when he intensively surveyed and mapped them, one was in the Piedmont (14, 562 ha) and the other was in the Southeastern Plains (28, 566 ha). Our site, RBN, in the Southeastern Plains was included in Reed's (1905) survey. His other site was west of BSM and probably shared similar vegetation patterns. Both of Reed's (1905) sites were dominated by *P. palustris* occupying 77 % of the forested lands in the Piedmont and 88 % of the forested lands in the Southeastern Plains. *Pinus palustris* mostly existed in pure or mixed forests with other *Pinus* sp. and hardwoods across the majority of the landscape that was surveyed with the exception of the bottomland forests along creeks which were mostly dominated by hardwoods and other *Pinus* sp. sporadically mixed with *P. palustris*. Further examination of the maps produced by Reed (1905) show habitats where longleaf pine was dominant on slopes and aspects that may have been similar to patterns we observed in our study. The data and the maps that Reed developed need to be examined further

to determine if longleaf pine did in fact dominate slopes and aspects other than those that were trending southward.

Composition did also vary throughout our *P. palustris* plots, with plots ranging from pure *P. palustris* to *P. palustris* dominated stands mixed with other *Pinus* spp., *Quercus* spp., and other hardwoods. Forty-two percent of our plots were in pure to almost pure conditions, which is similar to prior research regarding pure to almost pure stands of *P. palustris* in these forests (Campbell and Ruffner 1883, Mohr 1901, Harper 1905, 1910, 1911, 1923, 1928, Reed 1905, Golden 1979, Varner et al. 2003a, Varner et al. 2003b, Frost 2006, Stokes et al. 2010). Forty-two percent of our plots were in pure to almost pure conditions. Our sites contrasted greatly from a management perspective as BSM and OMS has had no management and sites like CGM had heavy management in which all hardwoods in the canopy had been removed to intensely manage and promote *P. palustris* in the canopy and understory.

Alpha (α) diversity increased northeastward in latitude and longitude from Alabama to North Carolina. One exception to this pattern is the intensively managed site CGM. The most diverse plots occurred in the southern-mixed forests of South Carolina and mesophytic forests of North Carolina. Berry College (BOC), in Georgia, also had high diversity possibly due to its proximity (17 km) to the mesophytic forest region. The transition between the southern-mixed and mesophytic forests at BOC might not be as abrupt at a local scale as it is at the regional to continental scale. BOC is also managed for *P. palustris*, but in mixed stands with other *Pinus* sp. and other hardwoods (Cipollini 2005). Elevation was not associated with measures of α-diversity and was slightly perpendicular to it (bent towards α-diversity) when looking at our biplot in NMDS ordination space. The direction of elevation with respect to α-diversity can be accounted for due to the diversity seen at FAR, OMS, and BOC. While elevation in our biplot

was associated with more diverse sites, incorporating other high-elevation *P. palustris* communities from other studies could alter our ordination space, especially for pure *P. palustris* communities found in the Ridge and Valley and communities from the Southwestern Appalachians (Golden 1979; Varner et al. 2003a; Womack and Carter 2011).

Our plots are not the only examples of *P. palustris* communities in the southern-mixed and mesophytic forests in the Piedmont and Ridge and Valley (Varner et al. 2003a, Varner et al. 2003b, Stokes et al. 2010). Forty-one additional community plots have also been identified in the southern-mixed and mesophytic forests (Peet 2006, VegBank 2011, personal communication with Milo Pyne, southeastern senior plant ecologist, NatureServe). The community information came from a database containing almost 900 community plots in which *P. palustris* is associated with throughout its range. While the rest of the sampled plots are located in the Coastal Plains, the amount of plots from Peet's (2006) survey in the southern-mixed and mesophytic forests of the Piedmont, Southwestern Appalachians, and Ridge and Valley provide further evidence that *P. palustris* is of significance in these forest regions, albeit probably in fragmented conditions. The dataset for these communities used different measures for estimating abundance, so we did not use them in our analysis, however research revisiting and incorporating these and other known *P. palustris* communities in these forests with our data could contribute to more information on the occurrence of *P. palustris* and the communities they are associated with in these forests.

4. 2. Suggestions for future management

Many of the *P. palustris* communities we sampled currently exist in fragmented and degraded states. Questions remain on how to manage for these communities and whether they

could serve as a reference for restoration of other sites (Harris 2006, Beauchamp and Shafroth 2011). Many of the land management strategies at our and other sites have incorporated no management or management involving the use of fire, thinning, or herbicide or a combination thereof. Some management has involved incorporating current knowledge and practices from what is being applied in Coastal Plain *P. palustris* communities (Varner et al. 2003a; Peet 2006). Such plans should be reconsidered as the underlying disturbance dynamics, topography, and climate are different for Piedmont and Ridge and Valley communities compared to the Coastal Plain communities. Regarding disturbance dynamics, the fire regime in the southern-mixed and mesophytic forests of our study area varies greatly from what is found in the Coastal Plain. Coastal Plain fire regimes occur every one to three yr, while those in the Piedmont occur every four to six yr and those in the Southwestern Appalachians and Ridge and Valley occur every seven to 12 yr (Frost 2006).

The fire regimes for the southeastern United States were based on natural fire compartments that were broken up by water sources, 1st order and 2nd order rivers and streams (Frost 2006). Fire regimes were longer in interval while moving further inland due to the dissected to heavily dissected nature of the northern Coastal Plain, Southeastern Plains, Piedmont, and Ridge and Valley. The combination of water sources and topography would break up lands into smaller land area units or natural fire compartments thereby requiring a higher number of lightning-induced fires to occur in these ecoregions compared to the Coastal Plain. To further lend support to Frost's (2006) work, *P. palustris* fire scars in the Coastal Plains had an historical fire return interval occurring every 2.2 yr with a range between 0.5 to 12 yr over 200 yr (Stambaugh et al. 2011). Aldrich et al. (2010) have shown that pine-oak stands in the Appalachians of Virginia also have an historical fire every 16 yr, also matching with Frost's (2006) estimates for fire

26

regimes. Both studies, Staumbaugh et al.(2011) and Alridich et al. (2010), highlights the need to examine the historical fire regime throughout our study area, something that has not been done yet. Further efforts should be made to verify if these communities do exhibit fire regimes in the range of four to 12 yr as Frost (2006) estimated. Our plots did not have any *P. palustris* with fire scars to make such an assessment and it is possible that other location at our sites or other sites might have fire scars, however much of the Piedmont and Ridge and Valley were heavily utilized for the timber industry so finding such scars could be elusive. Managing for fire could incorporate the use of Frost's (2006) natural fire breaks in the Southeastern Plains, Piedmont, and Ridge and Valley as a guide for potentially mimicking the historical fire regime. The small but eventually growing body of work on fire in the southeastern landscape suggests that management for fire at intervals mimicking the natural historical fire regime should be incorporated into management plans for forested communities in the southern-mixed or mesophytic forests.

Historical fire regimes would also suggest that other tree species could be associated with *P. palustris* communities to some extent as has been observed in past historical accounts, studies, and in this research (Mohr 1901, Harper 1905, 1923: 1928, Wells 1974; Maceina et al. 2000, Varner et al. 2003b, Frost 2006, Womack and Carter 2011). We assume then, depending on the fire regime at local scales that certain tree species would be associated with *P. palustris* when considering fire regime as a gradient. *Pinus palustris* communities with pure to almost pure stands would experience the shortest fire return intervals, followed by communities containing *P. palustris* with *Q. laevis, Q. marilandica, and Q. prinus* with a slightly longer fire return interval, then *P. palustris* with the prior *Quercus* sp. followed by Q. *alba*, *Q. rubra*, *Q. falcata, Q. stellata*, and *Carya* sp. with a longer fire return interval. Communities probably would transition

27

into other mixed hardwood and pine communities were the fire return interval is long enough

that it might or does not support *P. palustris* in the community. *Pinus* species, *N. sylvatica*, and

possibly other minor hardwood species in these southern-mixed forests would probably integrade

between all of these communities depending on the fire return interval and the ability of these

species to tolerate the intensity of the fire (Abrams 2007). These gradients in fire regimes at the

local level are probably correlated with slope position, with lower elevation slope position

possibly receiving less fire and the higher elevation slopes possibly experiencing more fires.

Further investigations into the dynamics of fire as a disturbance at these local scales are needed

to verify these assumptions. Species such as *A. rubrum*, *A. saccharum*, *L. tulipifera*, and *L.*

styraciflua are not fire tolerant species and with continued fire management could eventually be

reduced in importance at our sites and other sites (Abrams 1998, McEwan et al. 2011). The

application of herbicides or thinning to control these hardwoods could contribute to the

elimination of these particular hardwood species sooner rather than later as has been exhibited at

some of our sites in our study area.

Land records also provide another source of information that could be accessed and yield

information on the historical composition of these forests. Alabama is at an advantage because it

was part of the United States federal government's Public Land Office General Land Survey

which incorporated the Township and Range survey for the state in order to sell land to settlers

in the middle to late 1800s. Historical surveys prior to these land sales used and named tree

species for their survey points and have been used in reconstructing the historical composition of

presettlement forests in Alabama (Shankman and Wills 1995, Black et al. 2002, Foster et al.

2004, Predmore et al. 2007). Historical records for Georgia and North and South Carolina could

be more problematic, but there may be privately or publicly owned lands with a rich collection of

history (Blank 2004). Historical land use coupled with the radial growth of trees, their location, DBH, and heights could provide a better understanding of the effects of human and natural disturbance at large or small scales and could be used to elucidate recruitment patterns from these events (Nowacki and Abrams 1997, Black and Abrams 2004). The locations of these trees could be then be incorporated into a GIS and used to determine recruitment and composition patterns at different spatial scales. A variety of potential data does exist to determine how to manage for these sites based on historical information, integrating future scenarios however will require using both historical and current information to build models which can predict the future compositional changes of tree species with regards to changing climate and land use.

4.3. Possible implications for <u>Pinus palustris</u> communities in the future

In the transitional southern-mixed forests, *P. taeda* is considered the dominant tree species occurring both naturally and in pine plantations (Dyer 2006). Its dominance is attributed to fast-growth and the ability to occupy disturbed lands quickly, such as abandoned lands that were cleared for agriculture over the last two centuries. These characteristics are why *P. taeda* is considered the main species for pine plantations in the southeastern forest industry (Turner 1987, Brown et al. 2005). Tree-climate models indicate that *P. taeda*, along with *P. echinata,* will be the dominant *Pinus* species constituting the southern-mixed forests as it expand northwards into the mesophytic forests with warming temperatures; however, environmental stresses due to competition, insects, and fungi compounded with land use change could have serious implications in what is currently being described as *P. taeda* decline (Iverson and Prasad 2004, Eckardt et al. 2010). While these stressors might reduce *P. taeda,* they could promote the recruitment of *P. palustris*, especially since many of the sites on which *P. taeda* are currently

29

found were historically dominated by *P. palustris* (Eckardt et al. 2010). These stressors which

negatively affect *P. taeda* also seem to have slight to no effect on *P. palustris* due to the natural

and life history traits of *P. palustris* (Komarek 1964, Platt et al. 1988, Boyer 1990, Gresham et

al. 1991, Moser et al. 2003, Frost 2006, Johnsen et al. 2009). If any combination of these future

climate and land-use scenarios hold true, then *P. palustris* might also be more adaptable to such

trends then the other *Pinus* species due to its life and natural history.

Further exploration into what limits *P. palustris* from expanding its range need to be tested.

A combination of low and freezing temperatures, wood decaying fungus, and ice and wind

storms along its northern latitudinal and elevational range margins have been proposed as such

causes (Schmidtling and Hipkins 1998, Varner et al. 2003a, Bhuta et al. 2009). Determining

which of these factors limits *P. palustris* in these communities might be a challenge however as

the origins of *P. palustris* in southeastern forests, particularly in the Piedmont, Southwestern

Appalachians and Ridge and Valley, has never been thoroughly examined. Harper (1905)

offered three ideas, ruling one of them out, on the origins of *P. palustris* in these ecoregions.

The two he favored suggested that *P. palustris* was able to break through the fall-line barrier and

into the mountainous ecoregions from the Southeastern Plains possibly due to climate or to some

significant characteristic in the natural history of *P. palustris* or *P. palustris* populations in the

mountains were refugia created when sea level rose sometime in the geological past. The Fall

Line does represent a barrier to dispersal for many Coastal Plain and Southeastern Plains tree

species; however, the underlying factors contributing to the success of *P. palustris* (a dominant

Coastal Plain and Southeastern Plains species) in crossing the Fall Line barrier remains unknown

(Shankman and Hart 2007). Furthermore, Harper (1905) suggests that *P. palustris* could have

still been moving northward during the time of European settlement, but land use changes after

settlement were altered, preventing *P. palustris* from moving further north. If *P. palustris* was

still moving further north during pre-European settlement times, then perhaps determining the

actual barriers limiting dispersal at *P. palustris'* northern range margins might be hard to

determine and it is more tolerable to the mountainous ecoregions than previously thought. In

which case, *P. palustris* might prosper in the southeastern mountainous ecoregions with a

warming climate. Further genetic analysis coupled with tree ring research and models of past

distributions of *P. palustris* might help to uncover its origins. More than likely the origin of *P.*

palustris occurred further south, based on current genetic knowledge of this species, and *P.*

palustris in the mountainous ecoregions were not refugia as Harper (1905) has suggested

(Schmidtling and Hipkins 1998).

Additionally, *P. palustris* already has higher importance values further south in the

subtropical evergreen and southern portions of the southern-mixed forests where it is considered

the forest dominant along with *Pinus elliottii* Engelm. (slash pine) (Iverson and Prasad 2001,

Dyer 2006). Climate scenarios suggest that *P. palustris* will increase in importance value in

these areas from 28.4 % to 38.8 % up from 14.9 % of the current land area it occupied and could

move between 10 km to 370 km north of its latitudinal or ecological optimum, however the

forests within which it was classified to was reduced in land area (Iverson and Prasad 2001,

Iverson and Prasad 2002). However, these models did not account for *P. palustris* in the

northern portions of the southern-mixed and mesophytic forests and this could be due to

sampling schema or models not incorporating the life and natural history traits of this species or

the abundance of this species on the landscape was not significant enough to be seen regional

scales.

The use of Peet's (2006) survey along with additional community data from the United States Forest Service's Forest Inventory Analysis could contribute to building larger abundance or presence and absence datasets coupled with newer models incorporating life and natural histories, growth and yield curves, soils, topography, land use, and both current and future climate and fire return intervals to determine past occurrence and future projections of *P. palustris* and other tree species on the eastern North American landscape (Toräng et al. 2010, Coops and Waring 2011). Tree rings could also be used to elucidate the relationship between climate and radial growth of *P. palustris* and other species in these forests to determine if warming scenarios favor the climatic response of certain tree species (Schöngart et al. 2006, Pederson et al. 2008, Chen et al. 2010, Huang et al. 2010). The use of such information could help to develop better estimates on the impacts of climate and land use change in association with other environmental stressors on these forests.

Our research examined the tree diversity of these *P. palustris* communities; however, further sampling strategies should incorporate sampling the understory to determine herbaceous and shrub layer diversity in these communities. The variation in this portion of the community is also relatively well studied at the local level, but research at broader scales could help to determine the ability of this layer of the community to handle future climate and land-use changes and to determine how individual species will handles such changes (Golden 1979, Maceina et al. 2000, Varner et al. 2003b, Womack and Carter 2011). The use of permanent plots throughout our study area could contribute to such knowledge, while measuring the impacts of climate and land use change in all layers of these communities in the future. Other studies in North America have already revealed such impacts at site-specific scale and incorporated them to the regional scale albeit in the tropical forest of Mexico, the mixed conifer-hardwood forests

of Wisconsin, and in hardwood forests adjacent to the transitional southern-mixed forests

(Williams-Linera and Lorea 2009, Amatangelo et al. 2011, McEwan et al. 2011).

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Table 2.1. Names and site descriptions within our study area. Slope, aspect, and elevation are based on plot averages.

Sites	Size (ha)	Slope (%)	Aspect (%)	Elevation (m)	Trees ha^{-1}	Land Manager
Reed Brake Research Natural Area (RBNA)	242	22.7	260	140	516	Talladega National Forest (federal government)
Oak Mountain State Park (OMSP)	389	42.0	143	292	774	Alabama Department of Conservation & Natural Resources (state government)
Berry College (BC)	70	34.6	202	298	316	Berry College (private 4 year liberal arts college)
Big Smith Mountain (BSM)	60	35.2	225	181	466	Southern Company (private industrial)
Long Cane Ranger District (LCRD)	21	11.1	173	76	490	Sumter National Forest (federal government)
Harbison State Forest (HSF)	16	9.4	257	51	848	South Carolina Forestry Commission (state government)
Forty Acre Rock (FAR)	30	4.9	175	158	1533	South Carolina Department of Natural Resources (state government)
Clark's Grove/West Montgomery (CGWM)	54	6.9	126	123	208	Uwharrie National Forest (federal government)
Eastern Railroad (ERRD)	32	7.6	136	139	1110	Uwharrie National Forest (federal government)
Nichols (NICH)	34	6.4	130	160	998	Private non-industrial landowner

Table 2.2. Average values derived from soil testing for the first 15 cm of soil by site. P, K, CA, Mg, Zn, Mn, Cu, Fe, and B in parts per million.

Site	P (mg kg^{-1})	K (mg kg-1)	Ca (mg kg-1)	Mg (mg kg-1)	Zn (mg kg-1)	Mn (mg kg-1)	Cu (mg kg-1)	Fe (mg kg-1)	B (mg kg-1)
BC	2.03	26.73	114.93	18.43	0.80	5.83	0.14	25.19	0.14
BSM	2.33	19.35	77.25	18.33	0.62	2.68	0.28	45.73	0.10
CGWM	2.00	29.55	131.45	22.00	0.63	7.82	0.14	30.32	0.11
ERRD	2.00	22.40	75.95	15.30	0.39	3.27	0.15	20.52	0.10
FAR	2.75	12.40	43.25	11.50	0.32	1.33	0.19	27.94	0.10
HSF	2.67	30.60	246.38	48.87	1.07	17.06	0.24	33.80	0.14
LCRD	2.40	27.95	119.55	38.65	0.45	4.75	0.26	28.82	0.13
NICH	2.00	19.90	113.75	23.65	0.53	4.75	0.19	47.93	0.11
OMSP	2.03	32.59	450.54	42.26	3.75	17.14	0.11	22.84	0.15
RBNA	2.03	24.45	104.53	23.08	0.68	8.33	0.23	49.83	0.11

Site	pH	BpH	CEC (meq 100g-1)	Acidity (%)	Base Sat (%)	Ca Sat (%)	Mg Sat (%)	K Sat (%)	OM (%)	SS (ppm)
BC	4.63	5.72	4.85	81.86	18.15	13.19	3.43	1.54	4.57	47.55
BSM	4.74	5.85	3.86	84.03	15.97	10.50	4.12	1.35	3.81	32.43
CGWM	4.75	5.75	4.76	79.82	20.19	14.41	4.11	1.66	5.35	51.75
ERRD	4.71	5.82	3.98	85.39	14.62	9.86	3.26	1.51	3.83	35.90
FAR	4.40	5.99	2.81	86.05	13.96	8.96	3.75	1.23	1.71	35.30
HSF	4.51	5.45	7.36	77.68	22.32	15.91	5.27	1.15	13.33	63.91
LCRD	4.96	6.00	3.35	68.02	31.98	19.40	10.15	2.45	3.77	34.05
NICH	4.68	5.79	4.42	80.55	19.46	13.52	4.74	1.22	4.02	42.40
OMSP	4.62	5.38	8.75	70.53	29.47	24.67	3.86	0.92	18.27	76.31
RBNA	4.66	5.72	4.82	82.68	17.32	11.79	4.18	1.34	3.58	32.13

Table 2.3. Landform and soil classes referenced from the overlay of soil field data in a GIS with the U.S Department of Agriculture's National Resources Conservation Service's Soil Survey Geographic Database.

Geomorphology			
Across slope shape = ASLP	Down slope shape = DSLP	Landform = LF	Landform position = LFP
linear = 1	linear = 1	hill slope = 1	interfluve = 1
convex = 2	convex = 2	Hill = 2	side slope = 2
	convex and linear = 3	ridges = 3	tread = 3
		interfluve = 4	nose slope = 4
		marine terrace = 5	interfluve/side slope = 5
		hillslope on ridge = 6	back slope = 6

Soil classification			
Soil series = SS	Soil order = SO	Soil class = SC	Soils type = ST
Tiding =1	Aquic Hapludults/Typic Hapludults = 1	fine, kaolinitic = 1	Clay = 1
Tallapoosa/Fruithurst = 2	Aquic Hapludults = 2	fine-loamy and loamy, mixed, semiactive = 2	Silty Clay = 2
Herndon = 3	Typic Hapludults = 3	fine, mixed, semiactive = 3	Clay Loam = 3
Georgeville = 4	Typic Kanhapludults = 4	fine-loamy, siliceous, subactive = 4	Silt Clay Loam = 4
Blanton = 5	Arenic Hapludults/Fragic Kanhapludults = 5	fine, mixed, subactive = 5	Loam = 5
Vaucluse/Blaney = 6	Grossarenic Paleudults = 6	fine, mixed, subactive/fine-loamy, siliceous, subactive = 6	Silt Loam = 6
Blanton = 7	Rhodic Kanhapludults = 7	fine-loamy, kaolinitic/loamy, siliceous, semiactive = 7	Silt = 7
Nason = 8		loamy, siliceous, semiactive = 8	Sandy Loam = 8
Hiawassee = 9			Loamy Sand = 9
Towney = 10			Sand = 10
Maubila = 11			Sandy Clay Loam = 11
Maubila/Smithale = 12			Sandy Clay = 12

43

Table 2.3 (continued).

Soil characteristics			
Soil depth = SD	Drainage = DRAIN	Parent material = PM	Permeability = PERM
shallow = 1	not well drained = 1	clayey marine sediments = 1	slow = 1
moderately shallow = 2	moderately well drained = 2	sandstone with strate of siltstone and shale = 2	slowly moderate = 2
moderatley deep =3	well drained = 3	mica schist = 3	moderate = 3
deep = 4	moderately well drained/well drained = 4	cretaceous shale = 4	
very deep = 5		precambrian metavolcanic = 5	
very deep/deep = 6		loamy marine deposits = 6	
		sandy marine deposits = 7	
		schist and other metamorphic = 8	
		felsic and mafic = 9	
		slate = 10	

Table 2.4. Importance values for all live stems by site surveyed in this study. To distinguish the species with the highest importance values at each site, the bolded, italicized and underlined value had the highest importance value, the bolded and italicized value had the second highest value, and the bolded value had the third highest value.

STATE	Alabama			Georgia	South Carolina			North Carolina		
ECOREGION (LEVEL III)	Coastal Plain	Ridge & Valley	Piedmont	Ridge & Valley	Piedmont	Piedmont	Piedmont	Piedmont	Piedmont	Piedmont
SITE: IMPORTANCE VALUES (LIVE STEMS)	RBNA	OMSP	BSM	BC	LCRD	HSF	FAR	CGWM	ERRD	NICH
Acer rubrum L. (red maple)	2.47	0.73	1.85	4.51	2.50	***10.33***	1.07	---	5.42	**8.69**
Acer saccharinum L. (silver maple)	---	---	---	1.78	---	---	---	---	---	---
Carya alba (L.) Nutt. ex Ell. (mockernut hickory)	1.26	11.78	---	3.76	---	5.63	2.67	3.16	---	0.82
Carya cordiformis (Wangenh.) K. Koch (bitternut hickory)	---	---	---	---	---	---	---	---	---	1.48
Carya glabra (P. Mill.) Sweet (pignut hickory)	---	0.85	---	1.80	---	---	1.51	---	1.54	2.28
Cornus florida L. (flowering dogwood)	2.86	0.74	---	3.31	3.03	4.12	---	---	**6.48**	3.48
Diospyros virginiana L. (common persimmon)	---	0.73	3.39	---	---	---	2.31	---	---	1.54
Fagus grandifolia Ehrh. (American beech)	---	---	---	---	---	3.40	---	---	---	---
Ilex opaca Ait. (American holly)	---	---	---	---	---	---	---	---	2.55	1.68
Juniperus virginiana L. (eastern red cedar)	---	---	---	---	---	---	1.99	---	---	2.92
Liquidambar styraciflua L. (sweetgum)	1.32	2.32	---	---	**7.81**	4.26	1.85	5.29	3.01	6.57
Liriodendron tulipifera L. (tulip poplar)	---	---	---	---	---	---	---	3.70	2.65	5.84
Nyssa sylvatica Marsh. (blackgum)	1.42	***14.12***	7.28	0.87	2.27	**5.89**	4.37	---	1.23	2.48
Oxydendrum arboreum (L.) DC. (sourwood)	***7.56***	---	---	3.83	---	2.90	---	---	4.13	2.61
Pinus echinata P. Mil. (shortleaf pine)	3.54	3.49	---	***23.25***	5.97	3.69	7.12	---	---	8.28
Pinus palustris P. Mill. (longleaf Pine)	***<u>66.08</u>***	***<u>39.61</u>***	***<u>76.54</u>***	***<u>33.16</u>***	***<u>42.24</u>***	***<u>35.29</u>***	***<u>25.18</u>***	***<u>66.30</u>***	***<u>44.81</u>***	***<u>24.53</u>***
Pinus taeda L. (loblolly pine)	3.59	0.88	***9.25***	---	***33.04***	5.62	11.78	2.65	6.35	4.03
Pinus virginiana P. Mill. (Virginia pine)	---	---	---	5.37	---	---	---	---	---	---
Prunus serotina Ehrh. (black cherry)	---	---	---	1.80	---	2.17	---	---	---	---
Quercus alba L. (white oak)	**4.09**	---	---	4.50	---	4.50	1.03	**5.36**	6.17	4.09
Quercus boyntonii Beadle (Boynton sand post oak)	---	4.57	---	---	---	---	---	---	---	---
Quercus falcata Michx. (southern red oak)	1.40	---	---	1.28	3.13	3.76	1.25	***5.76***	***7.13***	***9.92***
Quercus laevis Walt. (turkey oak)	---	---	---	---	---	---	***12.97***	---	---	---
Quercus marilandica Muenchh. (blackjack oak)	3.17	**13.78**	1.69	---	---	1.18	***13.68***	3.89	1.23	---
Quercus nigra L. (water oak)	---	---	---	---	---	---	2.34	---	---	---
Quercus prinus L. (chestnut oak)	---	1.74	---	**6.98**	---	---	---	---	---	---
Quercus rubra L. (northern red oak)	---	0.74	---	1.21	---	4.96	0.99	---	5.84	2.41
Quercus stellata Wangenh. (post oak)	---	---	---	---	---	2.30	6.93	3.89	---	4.57
Quercus velutina Lam. (black oak)	1.24	1.73	---	2.60	---	---	0.97	---	1.46	1.76
Sassafras albidum (Nutt.) Nees (sassafras)	---	2.20	---	---	---	---	---	---	---	---

Table 2.5. Results of non-metric multidimensional scaling (NMS) when considering 1) all plots and all species; 2) all plots but omitting species with an average importance value less then 5% (when accounting for zero's in the data); all species but omitting plots considered outliers using an outlier analysis; and omitting both species and outlier plots. The fourth choice was used in the selection of our optimal NMS solution.

NMS analysis	Axes	Minimum stress	Minimum stress (Monte Carlo test)	p-value	% variance explained
All plots & all species kept	2	13.981	13.617	0.0080	0.868
All plots but omit species < 5 % IV	2	13.993	10.775	0.0239	0.871
All species but omit outlier plots	3	8.648	10.773	0.0040	0.924
Omit outlier plots & species < 5 % IV	3	8.933	11.092	0.0040	0.930

Table 2.6. Maximum phi coefficients, maximum group designation, and phi coefficients for tree species amongst our groups. *Pinus palustris* occurred on all sites so it was not included in the analysis.

Species	MaxPhi	MaxGrp	Group 1	Group 9	Group 12	Group 25	Group 36	Group 40
QURU	0.25	12	-0.15	0.04	0.25	-0.16	-0.16	0.04
COFL	0.29	12	-0.29	0.13	0.29	0.12	0.26	-0.04
QULA	0.35	12	-0.11	-0.09	0.35	-0.08	-0.08	-0.09
OXAR	0.40	36	-0.20	0.07	0.31	-0.15	0.40	-0.15
QUAL	0.41	12	-0.21	0.09	0.41	-0.24	0.22	-0.25
CAGL	0.44	36	-0.18	0.10	0.09	-0.14	0.44	0.10
PIVI	0.45	9	-0.13	0.45	0.03	-0.10	-0.10	-0.11
PIEC	0.46	9	-0.54	0.46	0.20	0.17	0.42	0.18
PITA	0.46	25	-0.01	-0.36	0.16	0.46	0.07	-0.21
QUPR	0.47	9	-0.20	0.47	-0.07	-0.15	-0.15	0.28
NYSY	0.48	40	-0.21	-0.37	0.14	0.18	0.05	0.48
CAAL	0.59	40	-0.41	-0.14	0.45	-0.28	-0.28	0.59
QUFA	0.61	36	-0.15	-0.08	0.32	-0.24	0.61	-0.25
ACRU	0.61	36	-0.21	-0.25	0.32	0.08	0.61	-0.08
LIST	0.66	25	-0.13	-0.23	0.07	0.66	0.64	-0.23
QUMA	0.67	40	-0.18	-0.26	0.03	0.06	-0.24	0.67
QUST	0.75	36	-0.23	-0.18	0.44	-0.18	0.75	-0.18
LITU	0.78	36	-0.15	-0.17	0.25	-0.16	0.78	-0.17
QUBO	0.79	40	-0.16	-0.12	-0.14	-0.12	-0.12	0.79
Averages	0.50		-0.19	-0.02	0.19	-0.01	0.21	0.07

Table 2.7. Tree species and their significance (α = 0.05) to our groups as determined by a cluster analysis and indicator species analysis for all tree species in *Pinus palustris* communities of the southern-mixed and mesophytic forests of eastern North America.

Species	Maximum Group	Indicator Value (Observed)	Mean	Standard Devation	p-value
CAAL	40	0.59	0.25	0.13	0.001
QUMA	40	0.67	0.26	0.14	0.002
NYSY	40	0.48	0.25	0.13	0.005
QUBO	40	0.79	0.27	0.15	0.006
LIST	25	0.66	0.26	0.13	0.012
PIEC	9	0.46	0.26	0.13	0.017
LITU	36	0.78	0.28	0.14	0.024
QUST	36	0.75	0.27	0.14	0.033
ACRU	36	0.61	0.26	0.13	0.058
QUFA	36	0.61	0.26	0.14	0.077
PITA	25	0.46	0.25	0.13	0.078
QUAL	12	0.41	0.26	0.14	0.079
QUPR	9	0.47	0.27	0.14	0.081
PIVI	9	0.45	0.28	0.14	0.173
CAGL	36	0.44	0.27	0.14	0.236
OXAR	36	0.40	0.28	0.14	0.263
QULA	12	0.35	0.29	0.14	0.278
COFL	12	0.29	0.26	0.13	0.343
QURU	12	0.25	0.27	0.13	0.407
Averages		0.50	0.25	0.13	0.109

Table 2.8. Pearson's correlation coefficients between non-metric multidimensional scaling and our continuous environmental variables across our 53 plots in *Pinus palustris* communities of the southern-mixed and mesophytic forests of eastern North America.

Axis 1	r	r^2	tau	Axis 2	r	r^2	tau	Axis 3	r	r^2	tau
D'	0.83	0.68	0.82	PCA1	-0.51	0.26	-0.39	AWC	0.55	0.30	0.47
E	0.81	0.66	0.82	HLI	-0.32	0.10	-0.22	Elev	-0.10	-0.62	0.38
H	0.81	0.65	0.77	AWC	0.31	0.10	0.08	HLI	0.35	0.12	0.19
S	0.58	0.33	0.58	D'	0.26	0.07	0.21	PCA2	0.27	0.07	0.12
Elev	-0.45	0.26	0.07	H	0.24	0.06	0.23	MAXDW	0.03	0.00	0.05
AWC	-0.34	0.12	-0.23	S	0.21	0.05	0.21	PCA1	0.38	0.14	0.01
MAXDW	0.24	0.06	0.21	E	0.21	0.04	0.17	S	0.05	0.00	-0.01
PCA2	0.15	0.02	0.16	MAXDW	0.19	0.04	0.19	PDIR	-0.01	0.00	-0.04
PDIR	0.15	0.02	0.08	PCA2	0.08	0.01	0.03	D'	-0.17	0.03	-0.08
HLI	0.05	0.00	-0.03	PDIR	0.05	0.00	-0.02	H	-0.09	0.01	-0.08
PCA1	0.02	0.00	0.07	Elev	0.14	-0.14	0.02	E	-0.20	0.04	-0.11

Table 2.9. Multi-response permutation procedures statistics for geomorphology, soil classification, and soil characteristic classes used in determining if our plots were significantly grouped by them. A is the chance-corrected within-group agreement, T is the test statistics, and p-value is at the 95 % confidence level.

Geomorphology	A	T	p-value
Paren Material	0.34	-11.01	0.000000
Landform	0.10	-4.31	0.000600
Landform position	0.13	-5.64	0.000040
Down slope shape	0.09	-5.94	0.000080
Across slope shape	0.10	-10.86	0.000002
Soil classifcation			
Soil series	0.32	-10.35	0.000000
Soil order	0.14	-5.44	0.000040
Soil class	0.15	-5.80	0.000019
Soil type	0.14	-5.92	0.000014
Soil characteristics			
Depth	0.19	-9.41	0.00000005
Drainage	0.02	-1.48	0.084
Permeability	0.02	-1.74	0.062

Table 2.10. Tree species scientific names, authority, common name, and four-letter look up code used in the tables and figures (Integrated Taxonomic Information System 2011).

Scientific name	Authority	Common name	Species code
Acer rubrum	L.	red maple	ACRU
Acer saccharinum	L.	silver maple	ACSA
Carya alba	(L.) Nutt. ex Ell.	mockernut hickory	CAAL
Carya cordiformis	(Wangenh.) K. Koch	bitternut hickory	CACO
Carya glabra	(P. Mill.) Sweet	pignut hickory	CAGL
Cornus florida	L.	flowering dogwood	COFL
Diospyros virginiana	L.	common persimmon	DIVI
Fagus grandifolia	Ehrh.	American beech	FAGR
Ilex opaca	Ait.	American holly	ILOP
Juniperus virginiana	L.	eastern red cedar	JUVI
Liquidambar styraciflua	L.	sweetgum	LIST
Liriodendron tulipifera	L.	tulip poplar	LITU
Nyssa sylvatica	Marsh.	blackgum	NYSY
Oxydendrum arboreum	(L.) DC.	sourwood	OXAR
Pinus echinata	P. Mill.	shortleaf pine	PIEC
Pinus palustris	P. Mill.	longleaf Pine	PIPA
Pinus taeda	L.	loblolly pine	PITA
Pinus virginiana	P. Mill.	Virginia pine	PIVI
Prunus serotina	Ehrh.	black cherry	PRSE
Quercus alba	L.	white oak	QUAL
Quercus boyntonii	Beadle	Boynton sand post oak	QUBO
Quercus falcata	Michx.	southern red oak	QUFA
Quercus laevis	Walt.	turkey oak	QULA
Quercus marilandica	Muenchh.	blackjack oak	QUMA
Quercus nigra	L.	water oak	QUNI
Quercus prinus	L.	chestnut oak	QUPR
Quercus rubra	L.	northern red oak	QURU
Quercus stellata	Wangenh.	post oak	QUST
Quercus velutina	Lam.	black oak	QUVE
Sassafras albidum	(Nutt.) Nees	sassafras	SAAL
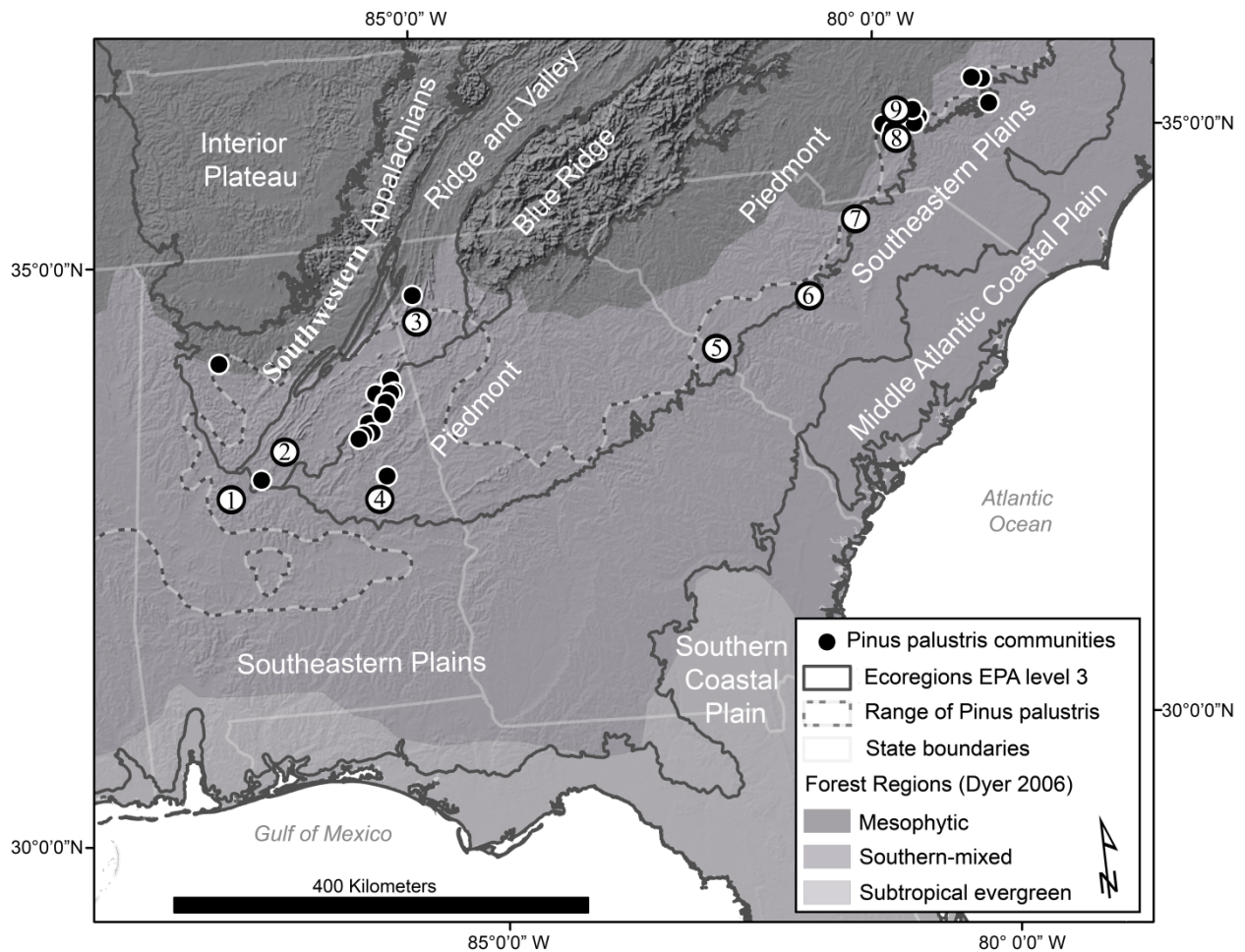
Figure 2.1. The location of our ten study sites and 56 plots in *Pinus palustris* communities of the southern-mixed and mesophytic forests of eastern North America. Site numbers are as follows: one is Reed Brake Natural Area; two is Oak Mountain State Park; three is Berry College; four is Big Smith Mountain; five is Long Cane Ranger District; six is Harbison State Forest; seven is Forty Acre Rock; eight is Clark's Grove/West Montgomery and Eastern Railroad; and nine is Nichols. Forest regions are from Dyer (2006), while EPA Level III ecoregions are from Griffith et al. (2002a; 2002b). Additional locations of *Pinus palustris* communities are from Peet (2006) and VegBank (2011). The area south of the *Pinus palustris* boundary is the range for this species.
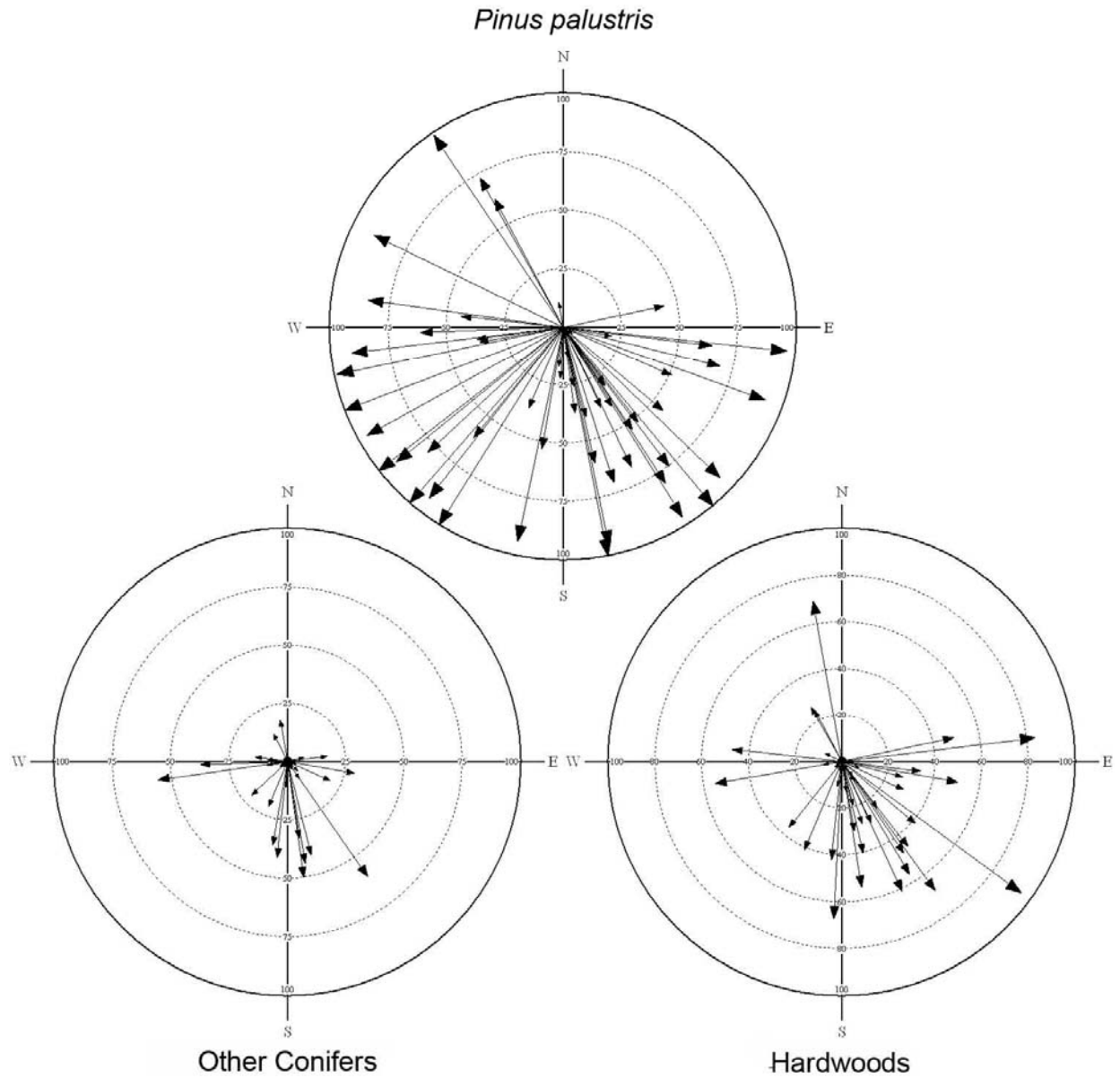
Figure 2.2. Wind rose plot showing the importance values of *Pinus palustris*, other conifers, and hardwoods plotted out by aspect for all 56 plots in *Pinus palustris* communities of the southern-mixed and mesophytic forests of eastern North America.
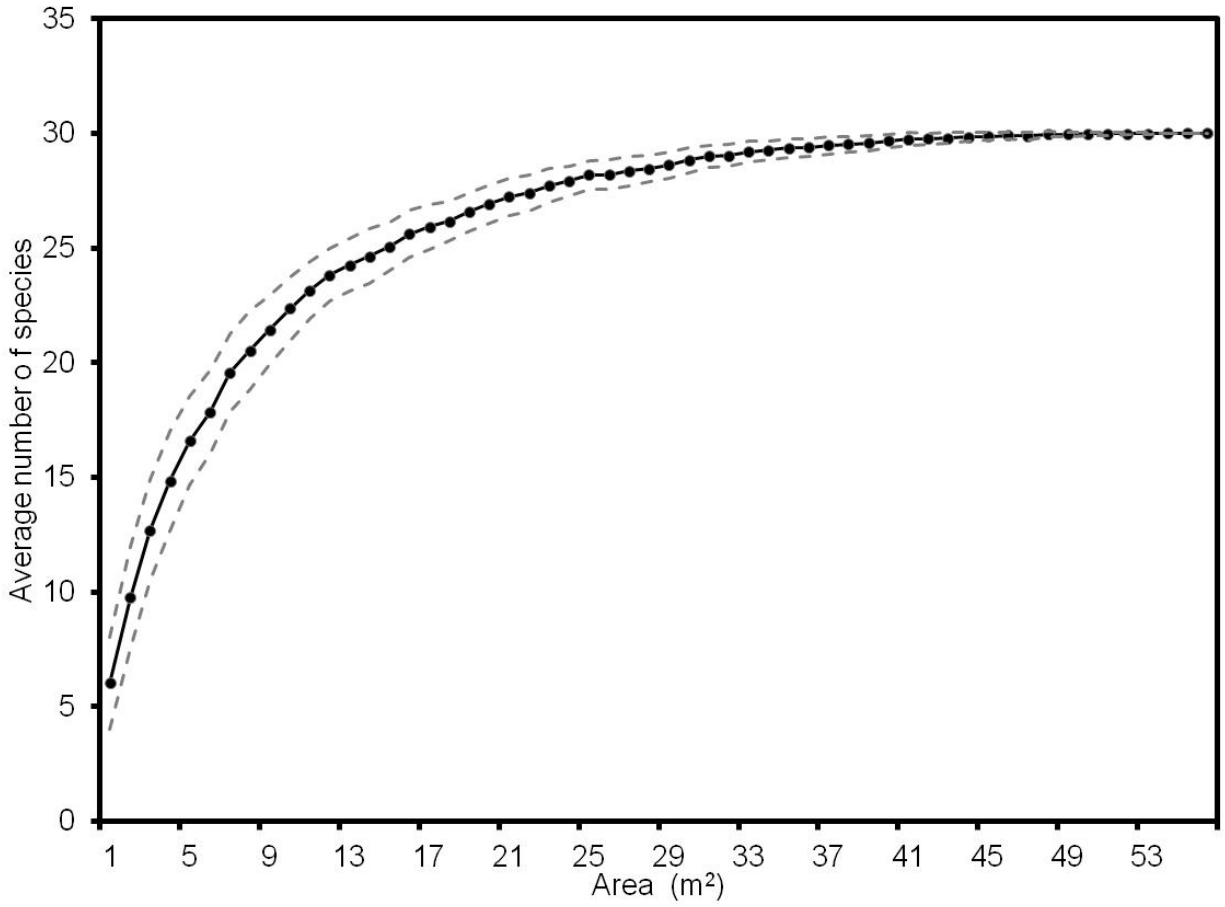
Figure 2.3. Species area curve for all surveyed tree species in *Pinus palustris* communities of the southern-mixed and mesophytic forests of eastern North America. Gray dashed lines are the standard deviation at 95% associated with the curve.
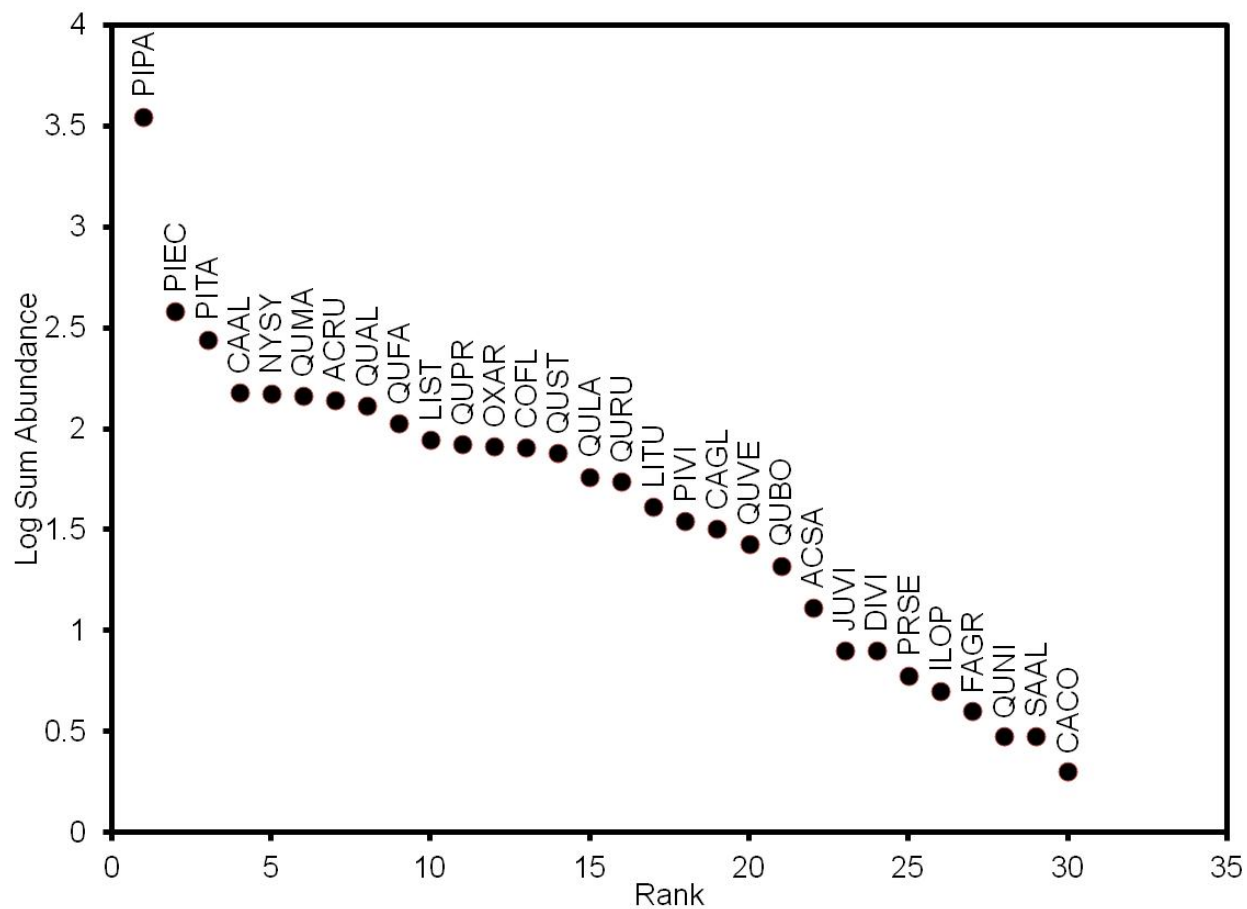
Figure 2.4. Log abundance for all tree species in *Pinus palustris* communities of the southern-mixed and mesophytic forests of eastern North America. Abundance values are based on importance values estimated across all plots. See Appendix T1 for species codes.

A)
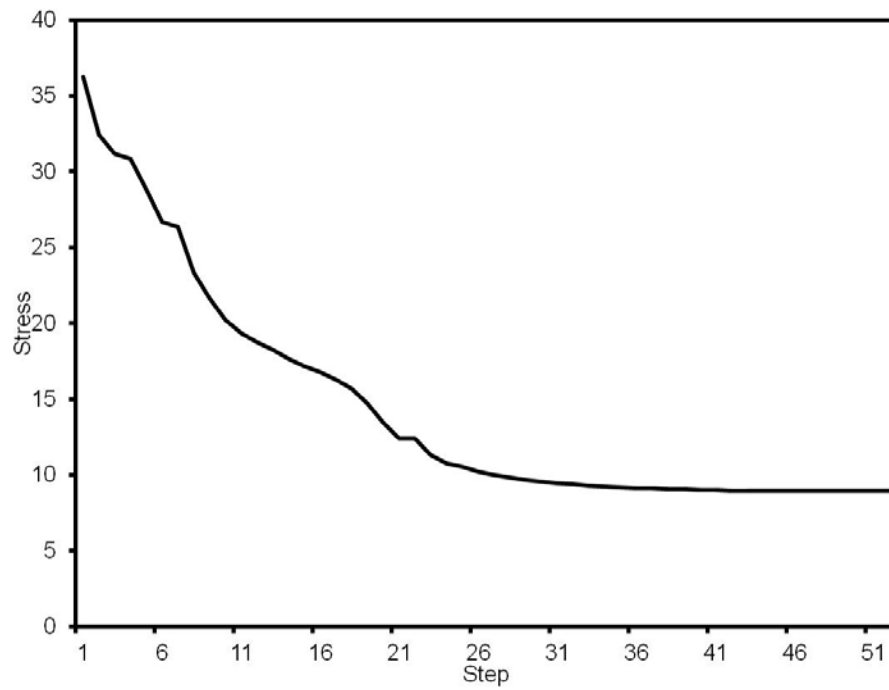
B)
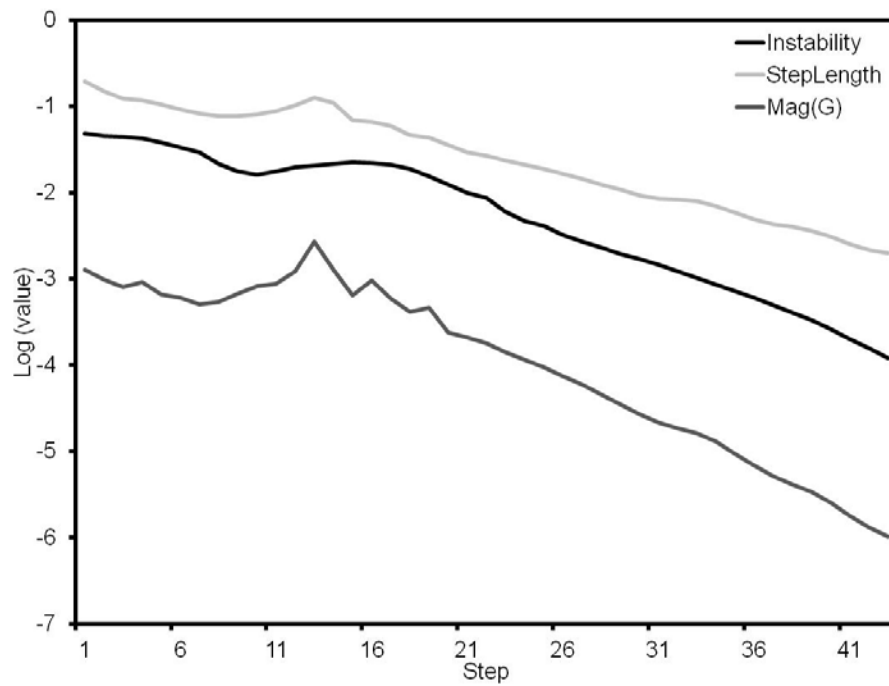
Figure 2.5. Verification of non-metric multidimensional scaling ordination based on stress (A) and instability (B).

56
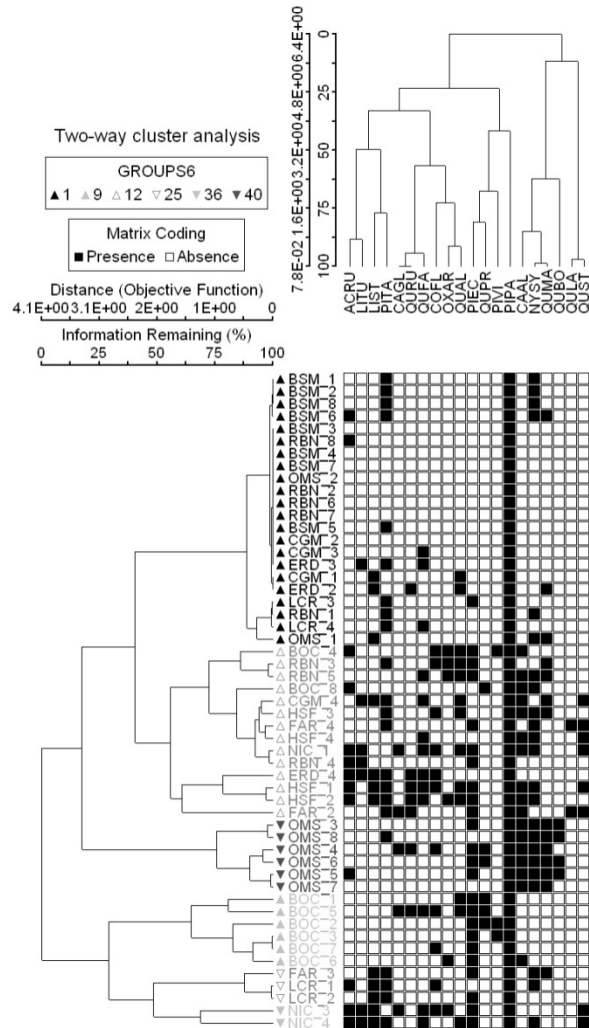
Figure 2.6. A two-way dendrogram and a matrix of presence and absence for 21 species used in our analysis for *Pinus palustris* community variation in the southern-mixed and mesophytic forests of eastern North America. The six groups retained 55.8 % of the information remaining to the right of the left dendrogram with species grouping appearing in the top dendrogram. These groups formed our tree associations and were designated as the following (see Appendix T1 for species code): 1) pure PIPA; 9) PIPA, PIEC, PIVI, and QUPR; 12) PIPA, CAAL, *Pinus* sp., *Quercus* sp., and other hardwood species; 25) PIPA, PITA, and LIST; 36) PIPA, LITU, QUST, LIST, ACRU, and QUFA; and 40) PIPA, QUBO, QUMA, and CAAL. See Table 2.10 for species code.
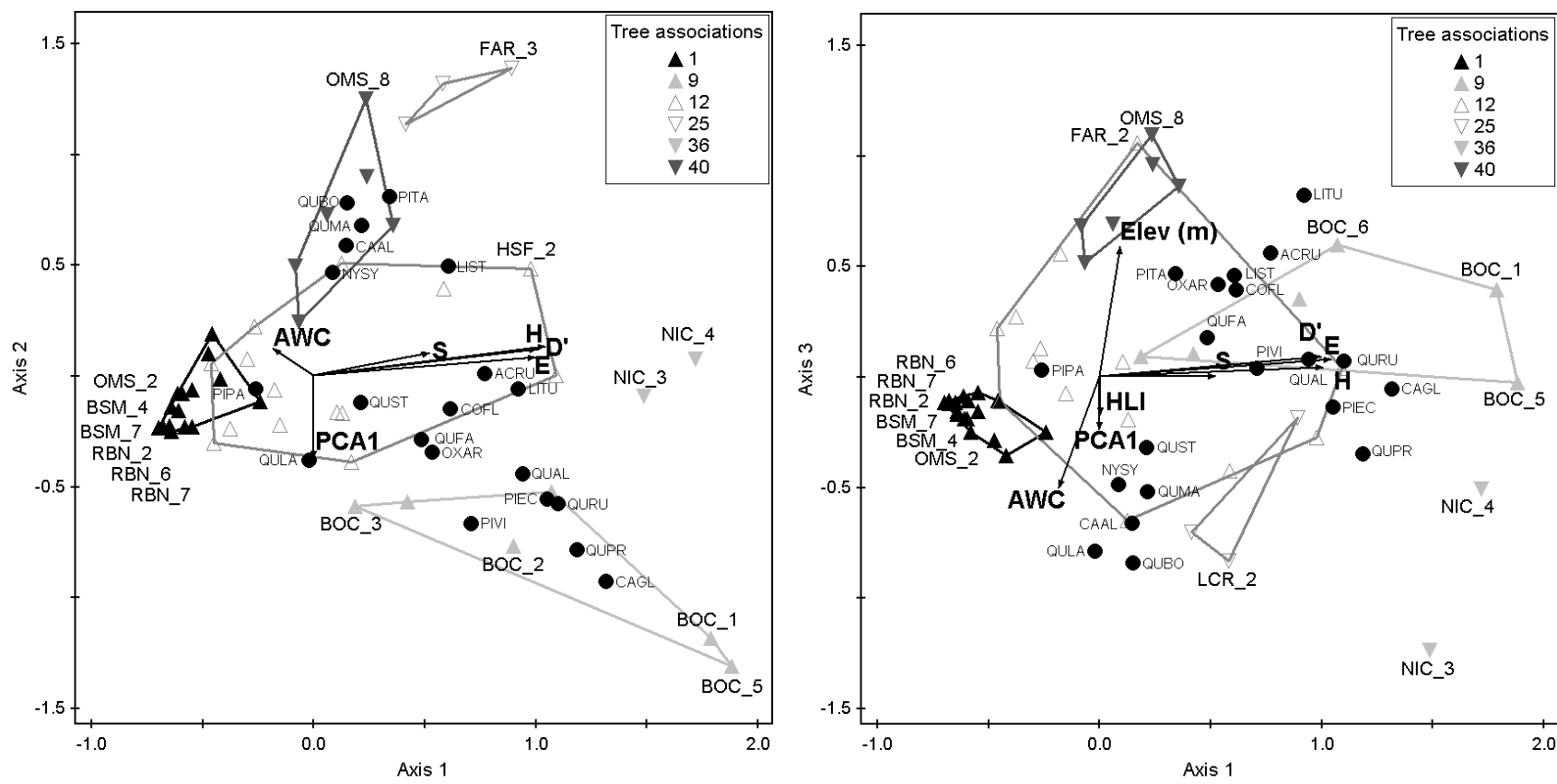
Figure 2.7. Non-metric multidimensional scaling ordination and space along three axes for 53 plots grouped by tree associations through cluster analysis and indicator species analysis throughout *Pinus palustris* communities in the southern-mixed and mesophytic forests of eastern North America. Tree associations were designated as the following: 1) pure PIPA; 9) PIPA, PIEC, PIVI, and QUPR; 12) PIPA, CAAL, *Pinus* sp., *Quercus* sp., and other hardwood species; 25) PIPA, PITA, and LIST; 36) PIPA, LITU, QUST, LIST, ACRU, and QUFA; and 40) PIPA, QUBO, QUMA, and CAAL. See Table 2.10 for species code.

Figure 2.8. Non-metric multidimensional scaling ordination and space along three axes for 53 plots grouped by land management throughout *Pinus palustris* communities in the southern-mixed and mesophytic forests of eastern North America. Management classes were designated as: 1) no management, 2) management with fire, 5) management with fire and thinning, and 7) management with fire, herbicide, and thinning; management classes 3, 4, 6, and 8 were not classified in our plots.
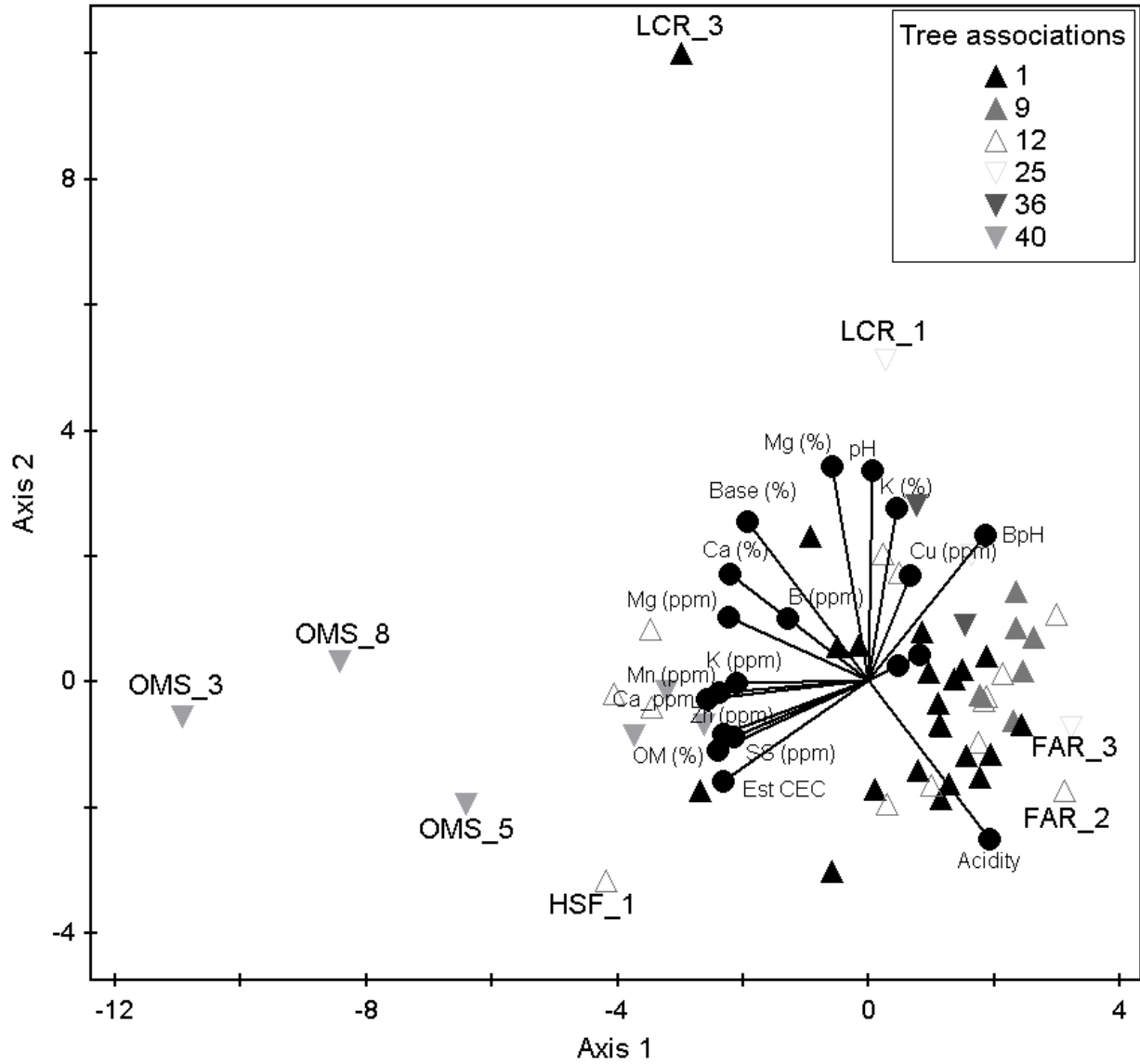
Figure 2.9. The first two principal component axes relating soil nutrients with the 53 plots used in our analysis of *Pinus palustris* community variation in the southern-mixed and mesophytic forests of eastern North America.

60

Chapter 3: Geographical variation of radial growth-climate relationships for an historical dominant conifer species along multiple gradients in the southeastern United States

Note: This chapter was prepared for submission to the Journal of Biogeography

ABSTRACT

Aim An understanding of the variation of radial growth-climate relationships across the landscape is lacking for many species, especially the southern yellow pines, the dominate trees species of the southeastern United States. We explored this variation for one of the southern yellow pines, the historically dominant longleaf pine (*Pinus palustris* P. Mill.) across two gradients, one south to north and the other from southwest to northeast across longleaf pine's northern range margin, to understand how current climate is associated with radial growth and if temperature is the limiting factor for this species as it approaches its range margin.

Location This study was conducted throughout a heterogeneous landscape, which spanned the subtropical evergreen, southern-mixed, and mesophytic forest types that were located in the Southern Coastal Plain, Southeastern Plains, the Piedmont, and the Ridge and Valley ecoregions from Alabama to Virginia.

Methods We developed longleaf pine tree-ring chronologies from 16 sites, grouped them through a hierarchical cluster analysis, while using a principal components analysis to determine their variances from each other and redundancy analyses to relate them to latitude, longitude, and elevation. A correlation analyses was used to determine longleaf pine radial growth-climate

associations for each site and a redundancy analysis was used to determine how these

associations are distributed throughout our study area.

Results The sixteen chronologies were placed into six groups as defined by the hierarchical

cluster analysis. The ordination space and the axes of our redundancy analyses significantly

placed the groupings from the cluster analysis and latitude, longitude, and elevation were

significant in explaining these groupings. Our correlation and redundancy analysis showed that

longleaf pine was limited by monthly minimum winter to early spring temperatures at its

northern range margin however monthly mean total precipitation and monthly mean drought

from late spring to early summer were also associated with these sites. Minimum temperature

was not significantly associated with sites in the southernmost range, while precipitation was not

significantly associated with sites at the most northern elevational, latitudinal, and longitudinal

extremes of longleaf pine's range margin.

Main conclusions Longleaf pine was not only constrained by winter temperatures along its

northern range margin, as precipitation and drought also play a role in this limitation. This

suggests that either our sites are not at the true northern range limit of longleaf pine or that a

more narrow band exists along this northern range margin in which only temperature is the only

variable that limits longleaf pine growth. This research suggests longleaf pine might be a

valuable species for inferring historical drought and precipitation across the southeastern United

States.

Dendrochronology, species range margin, hierarchical cluster analysis, principal components analysis, redundancy analysis, moisture balance, drought index

1. Introduction

The composition, structure, and dynamics of forests in the southeastern United States will be impacted by a variety of ecological and climatological events, including changes in climate and land-use patterns (Hansen *et al.*, 2001; IPCC, 2007; Drummond & Loveland, 2010; Napton *et al.*, 2010). Possible scenarios related to these changes include an alteration in fire frequency, rising temperatures, changes in precipitation and drought, a higher frequency of hurricanes, and an increased pervasiveness for some non-native species and pathogens (Flannigan *et al.*, 2000; Dale *et al.*, 2001; Seager *et al.*, 2009; Eckhardt *et al.*, 2010). Tree species with ranges restricted to the southeastern United States might expand northward or could contract depending on their ability to adapt to such changes (Iverson & Prasad, 1998; 2001; 2002; Beckage *et al.*, 2006; McKenney *et al.*, 2007).   Evidence supporting these future shifts in tree species ranges can be found by examining their historical shifts due to climate change in the geological past (Watts, 1983; Delcourt & Delcourt, 1987; Delcourt & Delcourt, 1988). Bioclimatic and land-use models used in predicting the range expansion or contraction of tree species to climate change have been examined in this region, but have not utilized tree species radial growth and climate relationships in these models. Furthermore, radial growth-climate relationships have been examined for only a few species at broad spatial scales in the southeast. For example, the relationship between radial growth and climate has been used to investigate the effects of temperature and drought on oaks in the Blue Ridge (Speer *et al.*, 2009), to reconstruct a millennia long record of precipitation from bald cypress (*Taxodium distichum* L.) along coastal Georgia and North and South Carolina (Stahle & Cleveland, 1992), and to determine loblolly pine (*Pinus taeda* L.) radial growth-climate associations across its range (Cook *et al.*, 1998).

While the effects of climate on the radial growth of trees across broad scales in the southeastern United States is limited to only a few tree species, further research of the effects on other trees in this region is warranted. This is in contrast to other areas of North America where a large sample size of chronologies exist from which radial growth-climate associations, response, reconstruction, and predictions of future climate change have been analyzed (Cook *et al.*, 1999; Chhin *et al.,* 2008; Chen *et al.*, 2010; Goldblum, 2010; Huang *et al.*, 2010; Williams *et al.*, 2010). The ability to further examine climatic effects on tree species in southeastern forests at such scales is likely limited by the lack of dendrochronological records. A survey of the International Tree-Ring Database supports this discrepancy (ITRDB, 2011). For forests west of the Mississippi River and irrespective of international boundaries for Canada and Mexico, there were 1,352 site chronologies available for analysis, while only 253 site chronologies were available for eastern North American forests. Of these site chronologies, only 95 site chronologies occurred in southeastern forests, from Mississippi, north to Kentucky, east to Virginia, and south to Florida.

In the southeastern United States, the two dominant forest types are the subtropical evergreen and southern-mixed forests. There are only 40 chronologies from only 36 sites in both of these forest types: 19 chronologies for bald cypress, four chronologies for post oak (*Quercus stellata* Wangenh.), three chronologies for overcup oak (*Quercus lyrata* Walt.), and two chronologies for white oak (*Quercus alba* L.). The other 16 chronologies are from three pine species, shortleaf pine (*Pinus echinata* Mill.) with two chronologies, loblolly pine with four chronologies, and longleaf pine (*Pinus palustris* P. Mill.) with ten chronologies from six sites. There is clearly an underrepresentation of chronologies at the regional scale in the southeastern United States to provide a sufficient understanding of the influence of climate on tree species in these forest

types, especially for conifers. The need for more research in this region is important because the subtropical evergreen and southern-mixed forests are dominated by conifers, specifically the southern yellow pines of natural or commercial origins (USGS, 2011). These southern yellow pines include loblolly pine, shortleaf pine, longleaf pine and slash pine (*Pinus elliottii* Engelm). Slash pine has the smallest ecological amplitude as it is mostly confined to the subtropical evergreen forests; however, the other three pine species exhibit larger ecological amplitude, occurring in both the subtropical evergreen and southern-mixed forests and even some parts of the oak-dominated (mesophytic) forests to the north. While this underrepresentation exists however, radial growth-climate research at the local scale from tree ring data not available from the ITRDB has provided some insight into the relationships between climate and radial growth for loblolly pine (Friend & Hafley, 1989; Grissino-Mayer *et al.*, 1989; Travis & Meentemeyer, 1991), shortleaf pine (Friend & Hafley, 1989; Travis & Meentemeyer, 1991; Grissino-Mayer & Butler, 1993), slash pine (Foster & Brooks, 2001; Ford & Brooks, 2003; Harley *et al*., 2011), and longleaf pine (Lodewick, 1930; Coile, 1936; Schumacher & Day, 1939; Meldahl *et al.*, 1999; Devall *et al.*, 1991; Zahner, 1989; Foster & Brooks, 2001; Bhuta *et al.*, 2008; 2009; Henderson & Grissino-Mayer, 2009; van de Gevel *et al*., 2009). While these studies contribute to a better understanding of how climate affects the radial growth of these species at local scales, elucidating these patterns to regional scales has been problematic possibly due to different methods and time intervals used in assessing climate-growth relationships (Meldahl *et al*., 1999). An understanding of the radial growth-climate relationships of these southern yellow pine species is necessary because they will be affected by future land use and climate change which could have ecological and economical implications for the southeastern United States (Iverson *et al., 1999).

Of the southern yellow pines, longleaf pine historically dominated both subtropical evergreen and southern-mixed forests prior to European settlement (Dyer, 2006; Frost, 2006). Human land-use change after European settlement resulted in the removal of this tree species and its associated communities and ecosystems from the southeastern landscape, with only 3% of the 37 million ha of original longleaf pine ecosystems remaining (Frost, 2006). Significant changes in land-use patterns after European settlement contributed to the demise of this species and included the harvest of old-growth longleaf pine for timber and the naval stores industry, fire suppression, and conversion to agricultural, urbanized, and commercial forest lands (Frost, 2006). While longleaf pine is no longer a forest dominant as it once was in southeastern landscape, there are still fragmented populations found throughout its range from which the variation in the relationship between climate and radial growth can be assessed. Deriving a better understanding from these relationships could contribute to a better understanding of the role of climate for this and other southern yellow pine species in the southeastern United States. Variation in the radial growth of southern yellow pines, especially longleaf pine, in old-growth and second-growth forests of the southeastern United States have never been explored across direct or indirect gradients. For example, the study on loblolly pine radial growth-climate associations was based on populations derived from plantation seed sources throughout loblolly pine's range (Cook *et al.*, 1998).

We explored the variation of radial growth in longleaf pine across such gradients to determine how climate is associated with southeastern pines. Our research is based on sixteen longleaf pine chronologies distributed throughout a heterogeneous environment in the southeastern United States from east of the Tombigbee River in Alabama to longleaf pine's northernmost part of its range in Virginia. The objectives of this study were to (1) investigate the

67

variation in the association between longleaf pine radial growth and climate, (2) determine which

climatic variables contribute to this variation, and (3) examine where these variations occur. Our

chronologies run along what we perceive to be two gradients based on (1) elevation and (2)

latitude and longitude. The first gradient that we created runs from south to north in the states of

Alabama and Georgia and the other gradient occurs roughly along longleaf pine's northern range

margin. We hypothesized that longleaf pine radial growth is associated with compounding

climatic variables at its southern range and will gradually shift to where one climatic variable,

temperature, will influence growth at its northern range. We also hypothesize that temperature

limits longleaf pine radial growth along these gradients, especially towards the northern range

margin of this species. These hypotheses are based on the principle of limiting factors, which

proposes that the distribution and growth of any plant species is influenced by one environmental

factor above others when that species falls below the minimum threshold required to sustain it

(Liebig, 1843; Billings, 1952).

2. Material and methods

2.1. Study area description

Our data were collected from sites within the range of longleaf pine in an area that spans

three forest types: the subtropical evergreen, southern-mixed, and mesophytic; and five

ecoregions: the Southern Coastal Plain, Middle Atlantic Coastal Plain, Southeastern Plains,

Piedmont, and Ridge and Valley of the southeastern United States (Omernik, 1987; Dyer, 2006).

Longleaf pine, throughout this portion of its range, exhibits high ecological amplitude throughout

a variety of habitats where it is associated with a diversity of communities (Omnerik, 1998 Dyer,

2006; Frost, 2006; Peet, 2006; **Figure 3.1**). These longleaf pine communities range from xeric

sand barrens, uplands, and flatwoods of the subtropical evergreen forests in the flat to undulating Southern and Middle Atlantic Coastal Plain (almost at sea level) to the rocky and clayey uplands of the southern-mixed forests in the dissected Piedmont and mountains of the Ridge and Valley and the Southwestern Appalachians of Alabama and Georgia at elevations ~600 m (Wahlenberg, 1946; Meldahl *et al.*, 1999). They are also associated with communities in the mesophytic forests of the North Carolina Piedmont, Georgia Ridge and Valley, and Alabama Southwestern Appalachians. These areas have a humid subtropical climate regime with Ultisols soils that are thermic, udic, and acidic. Elevations ranged from 10–472 m with frost-free days ranging from 180 to 240 days throughout our study area. Precipitation averaged 113.28 mm, ranging from 101.61–126.23 mm along our south to north gradient, while averaging 101.63 mm and ranging from 94.22–114.04 mm along longleaf pine's northern range margin (**Figure 3.2**). Along our south to north gradient, temperature averaged 17.4 °C, ranging from 9.1 C to 26.0 °C, while averaging 16.4 °C and ranging 8.7– 24.3 °C along longleaf pine's northern range margin.

In our study, longleaf pine's range occur over three different forest types, the subtropical evergreen forests, the southern mixed forests, and the mesophytic forests (Dyer, 2006). The subtropical evergreen forests consist of fragmented forests dominated by longleaf pine and plantation or naturally-occurring loblolly and slash pine in the uplands, with bottomland hardwood species along rivers and streams. The transitional southern-mixed forests are positioned between the subtropical evergreen and mesophytic forests containing a mix of either loblolly pine plantations or second-growth mixed stands with loblolly pine, shortleaf pine, longleaf pine, oaks, and hardwoods. The mesophytic forests, the most diverse forest of all eastern United States forests, are dominated by mostly oak and other hardwoods, with pines and other conifers scattered throughout. These three forest types are distributed among the five

69

ecoregions in our study area. The Southern Coastal Plain and Middle Atlantic Coastal Pain are composed of low-lying Tertiary-aged flat plains developed from marine deposits. They border both the Gulf of Mexico and the Atlantic Ocean, have poorly drained soils, and have wetlands consisting of swamps, marshes, and estuaries along their coastlines which are bordered by barrier islands (Omernik, 1987). The main difference between these two ecoregions is the coarser soils in the Southern Coastal Plain versus the finely textured soils of the Middle Atlantic Coastal Plain. The forests of the Southern Coastal Plain dominate the landscape along with wetlands, however recent growth associated with the urbanization of coastal areas have replaced many of these forests and abandoned agricultural lands (USGS, 2011). The Southeastern Plains, the largest ecoregion in eastern North America, consists of irregularly-dissected, Cretaceous-Tertiary aged plains bordering the southern portions of the Interior Plateau, the Piedmont, the Ridge and Valley, and the Southwestern Appalachians. Around half of the lands are composed mostly of southern-mixed forests followed by agriculture, and developed lands and wetlands (Napton *et al.*, 2010).

The Piedmont is a transitional Precambrian to Paleozoic-aged metamorphosed to igneous ecoregion between the Southeastern Plains and the Ridge and Valley. The Piedmont consists mostly of second-growth southern-mixed and mesophytic forests that were abandoned after the original forest were utilized for timber and the land utilized for agriculture (Mohr, 1901, Brender, 1974, Golden, 1979, Cowell, 1995). These forestlands makeup over half of the Piedmont while around less than a quarter of the land is agriculture followed by urban/suburban lands (Napton *et al.*, 2010). The Paleozoic-aged folded and faulted mountains of the Ridge and Valley border the Piedmont in the south and then the Blue Ridge throughout the rest of its range. The folding and faulting has created low valleys and parallel ridges where greater than half of the

lands are forests, followed by agriculture which takes up about a third of the land and finally developed lands which comprise just under ten percent of the land (Napton *et al.*, 2010).

2.2. Chronology acquisition

Site selection in the study area was based on personal communication with landowners who knew of forests where longleaf pine was naturally occurring and forms a component of the canopy. We located multiple sites in four states: Alabama (three sites: Reed Brake Natural Area (RBN), and Oak Mountain State Park (OMS), and Big Smith Mountain (BSM)); Georgia (one site: Berry College (BOL)): South Carolina (three sites; Forty Acre Rock (FAR), Harbison State Forest (HSF), and Long Cane Ranger District (LCD)); and North Carolina (one site: Clarkes Grove/West Montgomery (CAG)). BOL is managed by a four-year liberal arts college, while BSM was managed by a private industrial landowner, and the other sites are either managed by state or federal natural resource agencies. RBN is in the southern-mixed forests of the Southeastern Plains, BC and OMSP are in the southern-mixed forests of the Ridge and Valley, BSM, LCR, HSF, and FAR are in the southern-mixed forests of the Piedmont, and CAG is the mesophytic forests of the Piedmont.

Cores at these sites were collected from longleaf pines that were surveyed for height, diameter at breast height (DBH), and location in 20 m x 50 m permanent plots. Longleaf pines > 5.0 cm DBH within a 20 m x 20 m subplot and > 15.0 cm DBH outside of the subplot, but within the plot, were cored 30 cm above the ground, parallel to the contour, and perpendicular to the slope to account for compression wood. Large diameter longleaf pines outside of the plot were also selectively cored using the same methods, with the assumption that they could be old-aged individuals.

71

In addition to the chronologies we collected, we also obtained chronologies from other sources. While these chronologies were developed to serve other purposes in dendrochronological research, they still provide useful information for looking at the relationship between climate and longleaf pine radial growth and overlapped in years with our chronologies (Kush, unpublished data; Meldahl *et al.*, 1999; Knight, 2004; Ortegren, 2008). The ITRDB contained three chronologies, the first site, Flomaton Natural Area (FNA), is a site in the subtropical evergreen forests of the Alabama Southern Coastal Plain. Its chronology was used to assess the influence of climate, specifically temperature, precipitation, and drought, on longleaf pine radial growth at that site (Meldahl *et al.*, 1999). The second chronology is from Weymouth Woods (WYM), located in the southern-mixed forests of the North Carolina Piedmont. The purpose of this chronology was to reconstruct drought in the Piedmont from 1690–2006 (Ortegren, 2008). The third chronology was from the Joseph W. Jones Ecological Research Center (ICH) and was derived from five separate chronologies listed on the ITRDB. These chronologies were used in assessing disturbance dynamics, recruitment, and the influence of climate on these factors in the southern-mixed forests of the Southeastern Plains in southwest Georgia (Pederson *et al.*, 2008).

We also acquired two chronologies, Sprewell Bluffs (SPB) and Greenwood Plantation (GNW), used in reconstructing the streamflow of a Georgia River in the southern-mixed forests of the Southeastern Plains (Knight, 2004). Two other chronologies, Red Tail Ridge (RTR) and Horn Mountain (HMT), were developed from tree cores used in quantifying stand age. These sites were collected in the southern-mixed forests of the Ridge and Valley in Alabama (Kush, unpublished data). The final chronology is from Seacock Swamp located in the southern-mixed forests of the Middle Atlantic Coastal Plain in southeastern Virginia. This chronology was used

in determining the effects of disturbance on and the relationship between climate in longleaf pine at its northernmost range margin (Bhuta *et al.*, 2008; 2009). This gave us 16 longleaf pine chronologies representing wide ecological amplitude from multiple forest types and ecoregions from Alabama to Virginia.

2.3. Chronology and climate development

Cores we collected in the field were dried, mounted, and sanded using successively finer-grit sandpaper to better discern the annual rings per core based on cell structure (Stokes & Smiley, 1996; Orvis & Grissino-Mayer, 2002). A stereo-zoom microscope was used on all cores to visually crossdate their annual rings using the marker-year list method and to measure them at a resolution of 0.001 mm using the program Measure J2X (VoorTech Consulting, Holderness, NH, USA) as an interface between our Velmex measuring system and the computer (Phipps, 1985; Yamaguchi, 1991). From these sites, we chose the oldest longleaf pines to develop our chronologies. All trees dated back to pith or the innermost ring; however, our ages could be offset by 3–20 years or more, since this species can persist in the grass stage while it is a seedling, thereby underestimating an individual's true age (Pessin, 1934; Nelson, 1985; Boyer, 1990). Crossdating was statistically verified using COFECHA and site chronologies were used in developing master site chronologies (Holmes, 1983; Grissino-Mayer, 2001). We also chose older individuals from our other sources in developing chronologies and their crossdating was verified using COFECHA. These raw chronologies were standardized using ARSTAN software (Tree-Ring Laboratory; Lamont-Doherty Earth Observatory; Cook, 1985; Cook & Krusic, 2011). We applied an adaptive power transformation to all chronologies to account for stability in their variation prior to proceeding to a two-step interactive detrending procedure for our

standardization (Cook & Peters, 1997). This procedure allowed for the removal of age and size-related allometric growth trends, thereby equalizing growth between earlier and later segments of individuals while retaining the long-term variability likely associated with climate (Fritts, 1976; Cook & Peters, 1997; Pederson *et al.*, 2004). To account for allometric growth patterns in all chronologies, the first set of detrending standardized all chronologies into a dimensionless index using a negative exponential curve or a linear regression if the negative exponential curve did not fit to a series correctly. For the second set of detrending, we accounted for the effects of tree-tree competition that individuals may experience during the dynamics of closed-canopy forests by applying flexible cubic smoothing splines (Cook & Peters, 1981). We then used a biweight robust mean function to average and create a mean series. Residual chronologies were developed from autoregressive modeling, which removed any autoregressive properties and autocorrelation associated with the standard chronologies (Cook, 1985). The expressed population signal (EPS), rbar, and subsample signal strength (SSS) for each chronology were segmented by 30-year windows with15-year overlaps to assess the quality of our final chronologies (Wigley *et al.*, 1984; Briffa, 1995). EPS values are a function of rbar and the total series in the chronology which explains on a 0.0 to 1.0 scale how well the series in our chronologies related to the overall population. The chronology is compared to a theoretical chronology with an infinite number of trees (Cook & Kairiukustis, 1990) with EPS values > 0.85 considered suitable for further radial growth-climate relationships (Wigley *et al.*, 1948). The rbar is the average correlation or is an indicator of the common variance between series and ranges from 0.0 to a 1.0 scale. The SSS at values > 0.85 indicates the number of trees that represent the common signal of the chronology, highlighting how strong a chronology is while

utilizing the least amount of trees in the chronology. The common interval analyzed for our chronologies was from 1938–1995.

We obtained our climate data, gridded monthly mean total precipitation and maximum and minimum temperature; from 1895–2010 from the Parameter Regression of Independent Slopes Model (PRISM) group at Oregon State University (Daly *et al.*, 2002; Daly *et al.*, 2008; PRISM, 2011). The spatial resolution for the gridded data are 2.5 arc min (~4 km), thereby providing more detailed spatial resolution for this region of the southeast than the National Climate Data Center climate division (NCDC-CD) climatological data. The climate division data spans multiple counties within a state and is an average of climatic data within those counties across the division. We scaled our PRISM data to the county level instead of the site level to account for the spatial uncertainty associated with chronologies that we did not collect in the field. The chronologies not collected by us in the field may only be accurate to within minutes of latitude and longitude, which could create accuracy issues when trying to relate climate to a site, which may be offset by a minimum of 1.85 km of longitude or latitude or more depending on how the position of a site was recorded. PRISM climate data has been used for a variety of sites, at the local, regional, and continental scale, where the influence of climate on radial growth was being studied and is highly applicable to our study (Chen *et al*., 2010; Williams *et al*., 2010). From our PRISM minimum and maximum temperatures, we also calculated mean temperature and compared the quality of the mean monthly temperature and total precipitation from the PRISM and NCDC-CD climate datasets using a paired *t*-test to determine if the means differ significantly from each other. The paired *t*-tests conducted on the PRISM and NCDC datasets for monthly mean temperature and total precipitation revealed that the mean differences for both temperature and precipitation were significantly different between

the datasets (**Table 3.1**). The reason for these differences could be attributed to the scale issue at the county and division level; however, we felt that the PRISM data were representative of climate at the county level.

PRISM precipitation data and the derived mean temperature were used to calculate an hydroclimatic index called the Moisture Balance Drought Index (MBDI). The MBDI is based on the difference between precipitation (P, the supply side) and estimated potential evapotranspiration (PE, the demand) of drought and is derived from the percentiles by month of the P-PE values. The Hamon equation was used to derive PE (mm/month) and is calculated using the following equation, $PE = 13.97 \, dD^2 W_t$, where d is the number of days in a month, D is the mean monthly hours of daylight (12 h units), and W_t, the saturated water vapor density term which is calculated using the following equation, $W_t = 4.95e^{0.062T}/100$, where T is the mean monthly temperature (Hamon, 1961) . The MBDI was used as a substitute to the Palmer Drought Severity Index (PDSI) as MDBI is easier to interpret across spatial and temporal scales, does not require a complex set of bioclimatic variables to calculate, can be applied across a heterogeneous landscape, and is not biased to the Midwest Region of the United States or other similar regions where this method was developed (Palmer, 1965; Ellis *et al.*, 2010). The MBDI is also not affected by actual evapotranspiration, which requires detailed knowledge on the soil characteristics, specifically moisture and type, for an area because it assumes that all soils are at field capacity and unlike PDSI does not require prior values of PDSI to estimate current PDSI (Ellis *et al.*, 2010). The only disadvantage to this index is that the PE could give the appearance that drought is more severe when compared to other indices (MBDI 2011).

2.4. Chronology comparisons and radial growth-climate analysis

We used a hierarchical agglomerative cluster analysis (HACA), principal components analysis (PCA), and redundancy analysis (RDA) to identify groups, ordinate our residual chronologies and to determine variation in radial growth across sites using the program PC-ORD (version 6.0; McCune & Grace, 2002; McCune & Mefford, 2011). These analyses allowed us to assess the variation amongst our site chronologies and to determine if the chronologies were grouped along the gradients. We used HACA to group our residual chronologies using correlation as a distance measure with the flexible beta method, $\beta = -0.25$, as a grouping linkage, thereby allowing us to better visualize and possibly explain our chronologies in our HACA dendrogram, PCA, and RDA. Both PCA and RDA are well suited analyses for linear variables; however, PCA is an indirect or free form ordination analysis which is not driven by explanatory variables, while RDA is a guided ordination analysis and the canonical form of PCA which utilizes environmental variables in explaining the variation in our chronologies (ter Braak & Prentice, 1988; ter Braak, 1994; McCune & Grace, 2002). The PCA and RDA were developed from a variance/covariance cross-products matrix and a distance-based biplot was used to calculate their PCA and RDA scores, which were all in the same units and were on the same order of magnitude (Legendre & Legendre, 1998). Monte Carlo permutation tests were incorporated in both the PCA and RDA, with 999 permutations per analysis and significance at $p < 0.05$. To explore the variation in our residual chronologies without the influence of other explanatory variables, we analyzed our chronologies using PCA to determine the level of variation from each other (Peters *et al.*, 1981; Tardif & Conciatori, 2006; Tardif *et al*., 2006). All chronologies were transformed into uncorrelated variables along axes and their redundancy was summarized, highlighting the maximum variance that they exhibit from their untransformed selves. We then used RDA, to determine how our transformed chronologies matched with our

environmental variables, which for this study was elevation, latitude, and longitude, by examining their linear relationships through multiple regressions (ter Braak, 1994; Legendre & Legendre, 1998). Both PCA and RDA allowed us to determine if our residual chronologies existed along gradients without the influence of climate.

To assess longleaf pine radial growth-climate associations at the local scale, we ran correlation analyses on monthly minimum temperature, mean monthly total precipitation, and monthly MBDI derived from our PRSIM dataset against our residual chronologies using DENDROCLIM2002 (Biondi & Waikul, 2004). This program utilizes a bootstrapping method highlighting correlation coefficients exceeding the 95% significance level (Guiot, 1991). All correlations were calculated from the previous year May to current year October of ring formation using the common analysis period used in developing our residual chronologies from 1938–1995. Since we wanted to understand those climate variables that limit growth for longleaf pine across its range, we focused on positive relationships between the climate variables and radial growth in this analysis (Pederson *et al.*, 2004; Cook & Pederson, 2011). Across our sample sites, we assessed radial growth-climate associations from the significant positive correlations from our correlation analysis against environmental variables (elevation, latitude, and longitude) using RDAs to determine if any gradients could be discerned. We conducted multiple RDAs to examine the effects of monthly minimum temperature, mean total precipitation, and MBDI across our study area. Monte Carlo permutation tests, with 999 permutations per analysis and significance set at $p < 0.05$, were incorporated in these RDAs using the program PC-ORD.

3. Results

3.1. Chronology development, standardization, and ordination

The longleaf pine chronologies varied in ages from 82–316 years with two chronologies dating back to the 1690s (WYM and GNW), SPB dating back to the 1700s, and the rest of the chronologies dating back to between as early as 1802 (BSM) and as late as 1927 (FAR) (**Table 3.2**). Our residual chronologies all had EPS values well above the 0.85, ranging from 0.857 (FAR) to as high as 0.975 (CAG). Rbar values were > 0.278, ranging from 0.278 (BAI) to 0.576 (RTR) and the lowest SSS was for eight trees at 0.851 for RBN and the highest for two trees was 0.875 at FAR. The percent variation explained in the first PCA vector for our residual chronologies ranged from 31.0% to as high as 70.7%. The descriptive statistics derived from ARSTAN for our residual chronologies indicated to us that they would be well suited for further chronology comparisons and climate-radial growth analyses (**Figure 3.3**).

The HACA grouped our 16 residual chronologies into six groups while retaining 68.4% of the information in our chronologies (**Figure 3.4**). The groupings of our residual chronologies from the HACA matches with the ecoregions described in our study area. The Southeastern Plains and Piedmont sites were split into two groups based on their geographic distance between each other. The CAG, LCD, FAR, and HSF chronologies, located in South and North Carolina, were placed into one group one while BSM, SPB, and the site from the Southeastern Plains, RBN, were in group three and were from Alabama and Georgia. Group two was from the Ridge and Valley and included RTR, OMS, and BOL. Group four was from the Southern Coastal Plain and included ICH, FNA, and GNW. The two sites that did not fit into these groupings and were designated in their own individual groups were HMT (group five) and BAI (group six).

The chronologies were further analyzed using PCA, which revealed that two axes were significant, at the 0.001 level, in explaining 44.1% of the variation in our residual chronologies,

26.8% for axis one and 17.3% for axis two (**Figure 3.5**). Elevation was significantly associated

with the second axis (r = 0.743; r^2 = 0.552; p = 0.001), longitude was associated with axis one (r

= 0.389; r^2 = 0.151), and latitude was associated with both axes (r = 0.431; r^2 = 0.186 and r =

0.432; r^2 = 0.179 respectively), but not significantly. Furthermore Spearman's ρ, a non-

parametric test, indicated that elevation was significantly correlated (at 0.0004) for axis two,

while latitude and longitude were not correlated with our two PCA axes.

To better understand the relationship between our chronologies and the environmental

variables, the RDA significantly explained 32.7% variance (p = 0.003) in our chronologies

across three axes with axis one at 15.7%, axis two at 11.5%, and axis three at 5.5% (**Figure 3.6**).

The correlations between each axis and the three environmental variables indicated that elevation

and latitude were associated with axis one (66.9% and 70.6% respectively). Elevation was

negatively associated with both axes two and three, while longitude was strongly associated with

axis 2 (93.1%) and so was latitude (48.4%). The associations for latitude and longitude were

reversed, but not as strong for axis three at 42.6% and 29.1% respectively. Randomization tests

for our eigenvalues for each axis indicated that they were significant at p = 0.0470, with

eigenvalues for individual axes explaining variation at 22.9% for axis 1, 16.8% for axis two, and

8.0% for axis three. The randomization tests between the axes and environmental variables were

also significant at p = 0.001, with chronology-environmental variable correlations at 95.5% for

axis one, 86.7% for axis two, and 91.1% for axis three.

3.2. Tree-ring and climate analysis

Correlation coefficients for monthly minimum temperature, precipitation, and MBDI were

graphed by the groupings returned from the HACA and further examined in the PCA and RDA.

Monthly minimum temperature was not significantly correlated for group four and for one

chronology in group one (LCD). For the remaining 13 chronologies, winter and early spring

monthly minimum temperatures from previous year December to current year March were

significantly correlated (**Figure 3.7**). Prior year summer months were also significant for the

chronologies from Virginia and North and South Carolina (group one and six). Monthly mean

total precipitation was not significant for HMT and BAI (groups five and six), however it was

significant for the other 14 chronologies mostly during current year March to September (**Figure**

3.8). Previous year September precipitation was significant for all North and South Carolina

sites (group one), with the exception of LCD and previous year December precipitation was

significant for RTR in group two. Similar patterns were seen for MBDI, but MBDI was not

significantly associated with BAI, significantly associated with previous year monthly June and

July MBDI at HMT, and were significant for the other 14 chronologies from current year March

to September (**Figure 3.9**). Previous year September MBDI was also associated with all North

and South Carolina chronologies, with the exception of LCD. Precipitation and MBDI for LCD

were mostly associated with current year February and current year spring and summer months.

MBDI was also significant for previous year August and September.

Monthly minimum temperature correlation coefficients were best explained across three

RDA axes (23.0%), with 13.8% for axis one, 5.1% for axis two, and 4.0% for axis three (**Figure**

3.10). The eigenvalues for individual axes and relationships between the axes and the

environmental variables were not significant, but elevation was positively correlated with axes

two and three (0.761 and 0.585 respectively), latitude was positively correlated with axes one

and three (0.841 and 0.149 respectively), and longitude was positively correlated with axis one

(0.887). Three RDA axes significantly explained 41.5% of the variation in monthly total

precipitation correlation coefficients (p = 0.003), axis one (19.9%), axis two (18.5%), and axis three (3.1%; **Figure 3.11**). The eigenvalues for individual axes and relationships between the axes and the environmental variables were significant (0.04 and 0.007, respectively). Correlations between precipitation and the environmental variable were 93.8% for axis one, 90.6% for axis two, and 62.7 percent for axis three. Elevation was positively associated with axes two and three (0.501 and 0.476 respectively) while latitude and longitude were all negatively associated with the three axes. Three RDA axes explained 39.6% of the variation in monthly MBDI correlation coefficients, but were not significant, with axis one explaining 17.9%, axis two explaining 15.7%, and axis explaining 6.0% (**Figure 3.12**). The eigenvalues for individual axes and relationships between the axes and the environmental variables were not significant, but elevation was positively associated with axes two and three (0.623 and 0.557 respectively) and axes one and two associated with latitude (0.451 and 0.889 respectively) and longitude (0.976 and 0.210 respectively) positively associated with axes one and two.

4. Discussion

4.1. Grouping and ordinations of residual chronologies

The PCA and RDA ordination graphs of the residual chronologies show that there are significant gradients, which explain the variation in the distribution. For the PCA ordination graph, there is a strong linear association with PCA axis two which, when a joint biplot is applied to the PCA ordination space, is strongly associated with a gradient of elevation. Longitude and latitude do explain why BAI is so far removed from the other chronologies as it is the site farthest east and north for all chronologies, but the axes and the joint biplot do not contribute in explaining the variation of latitude and longitude of the chronologies as they

proceed up in elevation along the second PCA axis as well as explaining why HMT is also farther out along the first PCA axis between the cluster of chronologies to the left and BAI to the right.

The RDA exploring the variation in longleaf pine radial growth-climate association also significantly explained the variation along latitudinal, longitudinal, and elevational gradients. This can be supported by the similarities between the RDA ordination space and the information in our study area map and the table description of the chronologies in our study area. The RDA ordination space illustrates that elevation is more closely associated with RDA axis one, while longitude is associated with RDA axis two, and latitude is associated with both axes. In both PCA and RDA, HMT and BAI are at the extremes for all the chronologies in our study as they are both associated with the extremes for elevational and longitudinal and latitudinal gradients of the joint biplot. BAI represented the extreme of latitude (farthest east) and longitude (farthest north) while HMT was associated with elevation (472 m). These two residual chronologies may differ from the other chronologies because of their extreme locations in our study area. Both of these chronologies showed significant differences in their residual chronologies from the other chronologies; however, would they show significant differences in their radial growth-climate associations?

One other note needs to be commented upon regarding our analyses between the longleaf pine residual chronologies and their relation to environmental variables. Due to limited information on the chronologies that we were able to retrieve from other individuals or the ITRDB, our research was restricted to elevation, latitude, and longitude, and the opportunity to determine if other environmental variables contribute to explaining the variation of the chronologies could not be assessed, however slope, aspect, and tree-tree competition could also

account for the variation in the chronologies throughout our study area (Pederson *et al*., 2008; Huang *et al*., 2010; Bunn *et al*., 2011). Since the chronologies that we developed from our own study sites were located on different slopes and aspects throughout our sites and their locations were recorded, site-specific differences in our chronologies related to topography should be analyzed in the future to determine if topography and tree-tree competition contribute to any observed differences in the association between our chronologies and climate (Bunn *et al.*, 2011).

4.2. Radial growth-climate associations

Prior research exploring longleaf pine radial growth-climate associations has been mostly concentrated along the southern coastal range margins of this species, however the majority of our chronologies were located in the interior and along the northern range margins (with the exception of FNA, GNW, and ICH) of longleaf pine's range. The incorporation of chronologies from FNA, GNW, and ICH, which are closer to longleaf pine's southern coastal range margins, allowed us to further compare our data with past research in this area. The FNA, ICH, and GNW chronologies were not significantly associated, positively, with winter monthly minimum temperatures, while all other chronologies from our study were. Radial growth-climate associations for these three chronologies supports prior studies of sampled populations along longleaf pines southern coastal range margins in Alabama, Georgia, Mississippi, Florida, and South Carolina that either no or negative relationships exist between radial growth and monthly mean winter to early spring temperatures (Lodewick, 1930; Coile, 1936; Devall *et al.*, 1991; Henderson & Grissino-Mayer, 2009; Foster & Brooks, 2001; Henderson & Grissino-Mayer, 2009). The findings from the re-analysis of FNA chronology are also in agreement with Meldahl

et al. (1999) analysis of FNA, which showed no significant association between radial growth and minimum temperature.

The chronologies from our other sites showing a significant association with winter and early spring monthly minimum temperatures, e.g. previous year December for BAI and HMT to current year January, February, and March for the others, is new ecological information for populations in the interior and along the northern range margins of longleaf pine. Only one study has shown that longleaf pine was responding to winter temperatures, specifically monthly mean February temperature (Bhuta *et al.*, 2009). Our analysis for BAI, which was also studied by Bhuta *et al.* (2009), differed from their results, with our analysis showing a significant association with minimum monthly previous year December, May and June temperature. Several reasons can be offered which could explain the reason for the disparity between the results of the analysis for BAI from our study and the prior study: 1) the use of correlation analysis here versus a response function analysis used in the prior study, 2) minimum temperature was used in this study versus mean temperature in the prior study, and 3) the scale and difference of the climate dataset used between both analyses was different with the NCDC-CD used by Bhuta *et al.* (2009) versus PRSIM county data used for this study. Further examination using PRISM data at the climate division scale for BAI and all other sites needs to be investigated further to see if patterns are the same for the different climate data sets; however both studies do show that longleaf pine radial growth at BAI is associated with winter monthly temperatures (mean or minimum) at its northernmost latitudinal and longitudinal margin.

The other site that showed a similar association to monthly minimum previous year December temperature was HMT in Alabama. The chronology for this site is the highest in elevation for all longleaf pine chronologies ever studied. Recall that both BAI and HMT were

also in their own groups based on the distribution of their residual chronologies in the HACA and were at the extremes in both PCA and RDA ordination space, which suggests that winter temperatures at elevational and latitudinal/longitudinal extremes might play an important role in limiting the distribution of longleaf pine throughout its range. Further examination of these phenomena should be conducted at other sites with similar elevational or latitudinal/longitudinal extremes within longleaf pine's range or for the other southern yellow pines. Prior to our research, the only other southern yellow pine studied was loblolly pine, which was significantly associated with winter temperatures in Arkansas and Maryland at its latitudinal/longitudinal northern range margins (Cook *et al.*, 1998).

The association with winter temperatures with our chronologies could be related to winter photosynthesis, which has been observed for loblolly pines in the Piedmont of North Carolina (Hepting, 1945; McGregor & Kramer, 1963). During frost free days in the winter and early spring, temperate conifers, such as longleaf pine, might take advantage in gaining extra photosynthate and thereby carbon fixation during the non-growing season (Chabot & Hicks, 1982; Havranek &Tranquillini, 1995; Bhuta *et al.*, 2009). This might give conifers an edge in competing with other tree species during the growing season. Another possibility that could explain the association to minimum temperatures for longleaf pine might be attributed to freezing or desiccation events when temperatures fall below 10 °C (Cook *et al.*, 1998). Either of these possibilities needs to be examined further as multiple scenarios could be at play here for longleaf pine along its northern range margin as winter and early temperatures from our study could possibly be affected by both.

Another finding from this research that needs further examination is the influence of previous summer temperatures on all sites in South and North Carolina and Virginia (with the exception

of HSF and LCD). While these interior sites were limited by winter temperatures, previous year summer temperatures had about equal effect on these chronologies as well. This finding has also been observed for longleaf pine in Texas, but not for longleaf pine in coastal South Carolina (Henderson & Grissino-Mayer, 2009). Henderson and Grissino-Mayer (2009) suggested that prior year hot summer temperatures caused longleaf pine to shutdown and use food reserves for the following year in Texas. The same idea could be applied to our chronologies in Virginia and North and South Carolina, however further research to better explain this phenomena is needed to determine if this phenomenon is associated with previous year summer temperatures and radial growth for both the Texas site and our sites (Henderson & Grissino-Mayer, 2009).

With the exception of BAI and HMT, all other chronologies from the interior to near the coastal range margins in our study showed significant associations between radial growth and monthly total precipitation and monthly drought throughout longleaf pine's range. The BAI chronology was not significantly associated, positively, with precipitation and drought and HMT was not significantly associated, positively, with precipitation, but was with previous year summer drought (specifically, June and July). Current year precipitation and drought spanning from March to September was usually the dominant signal across all sites, while previous year September precipitation and drought for four North and South Carolina sites, previous December precipitation and drought for RTR, and previous August drought for OMS were also significantly associated, positively, with annual ring growth. This finding is in support of past research which had found that current year March to October precipitation and drought were associated with longleaf pine chronologies in the subtropical evergreen forests of the Southern Coastal Plain (Lodewick, 1940; Foster & Brooks, 2001; Henderson & Grissino-Mayer, 2009), the southern mixed forests of the Southeastern Plains (Coile, 1936; Schumacher & Day, 1939) from northern

87

Florida to southern Alabama and Georgia, and at a site in the Sandhills of North Carolina (van de

Gevel *et al.*, 2009). Current year summer drought was also associated for a site in the southern

mixed forests of the Alabama Southeastern Plains (Zahner, 1989). Current year August

precipitation and February PDSI were associated with longleaf pine radial growth in the southern

mixed forests of the Southeastern Plains of Mississippi (Devall *et al.*, 1991). Loblolly pine, just

like longleaf pine, was also drought sensitive throughout its range, but more particularly so in the

western part of its range (Cook *et al.*, 1998). These findings from both our research and prior

work reveal that longleaf pine and loblolly pine are strongly associated with a combination of

precipitation and drought across much or all the southeast. Further research needs to be

conducted on these species or on shortleaf, utilizing a range-wide chronology, as these conifers

would contribute to a better understanding of models that seek to understand the effects of

summer drought in the southeast throughout the past, present, and future (Anchukaitis *et al.*,

2006).

4.3. Radial growth-climate gradients and limits to distribution

Our hypotheses that longleaf pine's radial growth would be associated with multiple climatic

variables in the south and only one climatic variable, temperature, in the north along our

hypothesized south to north gradient and that temperature alone, specifically winter

temperatures, would contribute to limiting the range distribution of this species along its northern

range gradient was not supported from our analyses. While all of our interior sites (with the

exception of LCD) did show previous year December to current year March minimum

temperatures limiting longleaf pine growth, all chronologies, with the exception of our extreme

chronologies (HMT and BAI), were also affected by both precipitation and drought during

February to September of the current year. While these other climatic variables are also significantly associated with longleaf pine radial growth along its northern range margin, we still support the hypothesis put forward by Bhuta *et al.* (2009) that winter temperatures are associated with controlling or limiting the range of longleaf pine to some degree along its northern range margin, but that precipitation and drought might also contribute to some degree as well.

The proposed hypothesis by Bhuta *et al.* (2009) suggested that longleaf pine genetic diversity decreased from west to east and from south to north, with growth and survival related to a mean annual minimum temperature which both had a north-south component (Schmidtling & Hipkins, 1998; Schmidtling *et al.,* 2000). The effects of these other climatic variables need to be explored further in context with the genetic diversity of this species to determine if they have also had a limiting effect on longleaf pine like mean annual minimum temperature was proposed to have had roughly throughout the Holocene (Schmidtling & Hipkins, 1998; Schmidtling *et al.,* 2000). Radial growth-climate-gene associations need to be investigated further at local scales, across longleaf pine's range, and perhaps on other southern yellow pines to see if similar patterns are observed.

Another idea that might contribute to explaining the patterns we observed in our data about longleaf pine at its northern range margin was suggested by Harper (1905). Harper (1905) mentioned that longleaf pine may have still been moving northward during the European settlement of North America and alteration in land use change after European settlement may have limited the expanding range of longleaf pine. If this species was still expanding its range northward, perhaps the majority of our sites along our gradients are not at the true northernmost elevational and latitudinal/longitudinal range margins for longleaf pine. Our BAI and HMT chronologies were limited only by winter temperature and additional sites like these might

identify the true northern range margin of longleaf pine. Also, the area in which longleaf pine is affected by just winter temperatures could also be a small leading band along longleaf pine's range margin at elevational, latitudinal, and possibly longitudinal extremes; further investigation into this matter is warranted. For the extreme sites, HMT and BAI, and the chronologies along the northern range margin, our findings show similar agreement with other dendroclimatological studies where winter temperature was significantly associated with the radial growth of other species along its northern range margin in the eastern United States. These tree species were conifers, such as red spruce (*Picea rubens* Sarg.; Conkey, 1982; Johnson *et al.*, 1988), Atlantic white cedar (*Chamaecyparis thyoides* (L.) Britton, Sterns, & Poggenb.; Pederson et al. 2004; Hopton & Pederson, 2005), eastern hemlock (*Tsuga canadensis* (L.) Carrière; Cook & Cole, 1991), and pitch pine (Pederson *et al.*, 2004). Research investigating how other temperate eastern North American conifers responds to winter temperatures needs to be addressed especially for areas in the southeastern United States to determine if there could be a positive growth response to warming at their range margins (Bhuta *et al.*, 2009). Also, while the RDA for the significant monthly minimum temperature and drought correlation coefficients showed no significance and precipitation did show significance between the RDA axes and the biplot data, the ordination spaces for all three climatic variables do help to visualize how the climatic variables in our study are distributed in RDA ordination space and in reality, especially along our hypothesized gradients.

4.4. Implications for climate change

Models examining the effects of future climate change on the range expansion of eastern North American tree species have shown that with temperatures warming across the southeastern

United States, longleaf pine could expand its range from 10 km to 370 km north of its ecological optimum (Iverson & Prasad, 2001; Iverson & Prasad, 2002). With a warming climate occurring along longleaf pine's northern range margin from Alabama to Virginia, we would expect to see a decrease in winter temperature stress on the radial growth of longleaf pine at our current sites, eventually leading to winter temperatures with no significant positive association as this species expands it range northward. The leading edge of longleaf pine's expanding range margin would be constrained by winter temperatures, as we have seen at our sites, especially along any elevational or latitudinal/longitudinal extremes like BAI and HMT.

As the range margins of longleaf pine expand northward and the affects of winter temperatures decreases, drought and precipitation stress during the growing season would increase in association with longleaf pine radial growth at our interior sites. This would be similar in fashion to what has been observed for longleaf pine at FNA, GNW, and ICH and other sites along the southern coastal range margins from prior research. A similar scenario like this has been suggested by Cook *et al.* (1998) for loblolly pine and Bhuta *et al.* (2009) for longleaf pine. Furthermore, climate models investigating the effects of future climate change on fire have suggested that a warming southeastern United States will lead to an increased seasonal severity rating which translates into increased fire activity for the southeast by as much 30% (Flannigan *et al.*, 2000). If increased precipitation and drought stress are associated with increased fire activity, then future climate change could favor longleaf pine instead of other conifers or hardwoods. This could result in longleaf pine dominating interior sites in either a savanna or woodland type habitat and the coastal range margins for longleaf pine maintaining a savanna type habitat or being converted to grassland depending on how tree mortality is affected by both an increase in temperature, droughts, and the frequency of disturbances resulting from fire or

hurricanes that are associated with climate change (Gilliam & Platt, 1999; Beckage *et al.*, 2006; Pederson *et al.*, 2008).

Further analyses need to be conducted which incorporate longleaf pine radial growth-climate patterns, like those studied here, into climate and land-use models, as climate has been shown to drive tree growth rates more strongly than soil fertility and disturbance (Toledo *et al.*, 2011). Understanding how these patterns fit into such models would make these models more robust and significant, while improving the ability in determining the response of longleaf pine to current and past climate and predicting the ability of longleaf pine to adapt to future climate change, especially in areas where longleaf pine's range has been predicted to expand (Graumlich, 1989; Cook & Cole, 1991; Loehle & LeBlanc 1996; Loehle, 1996; Iverson *et al.* 1999; Tardif *et al*., 2006; Pederson *et al.* 2008). Improved models using radial growth-climate associations would also guide and inform land managers in the development of forest management and restoration plans which account for the projected changes in climate and land use patterns across the southeastern United States, not only for longleaf pine, but for other important conifer and hardwood species (Iverson *et al.*, 1999; Harris et al. 2006).

While our research highlights the variability in the association between longleaf pine radial growth and climate across multiple gradients from Alabama to Virginia, there is a need for further research of these radial growth-climate associations for populations geographically isolated from the main range of longleaf pine, such as those in Louisiana and Texas, to determine how they are related to our research. This need can also be extrapolated to areas which are also unknown in the interior of Mississippi and the coastal range margins along Georgia and South and North Carolina. By determining the underlying climatic variables that contribute to limiting the radial growth of longleaf pine, or any other tree species, baseline information could be

92

utilized from which to assess the ability of a tree species to adapt to future changes in climate throughout its range. Filling in these gaps will account for local and regional variation in soils, topography, tree-tree competition, and land use, while providing a more comprehensive view on the spatial and temporal variations for radial growth-climate associations throughout longleaf pine's range. Filling in these gaps would also provide an understanding on how complex interactions between these variables could be impacted by climate change and while furthering the ecological knowledge of this species.

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Table 3.1. Information and chronology statistics for longleaf pine chronologies situated along two hypothesized gradients in the southeastern forests of the United States.

Site	BAI[2]	CAG[1]	WYM[5]	FAR[1]	HSF[1]	LCD[1]	BOL[1]	SPB[3]	GNW[3]	FNA[4]	ICH[8]	RTR[6]	HMT[7]	OMS[1]
Map number	1	2	3	4	5	6	7	8	9	11	10	12	13	14
State	Virginia	N. Carolina	N. Carolina	S. Carolina	S. Carolina	S. Carolina	Georgia	Georgia	Georgia	Alabama	Georgia	Alabama	Alabama	Alabama
Level 3 ecogreion	MACP	Piedmont	Piedmont	Piedmont	Piedmont	Piedmont	R & V	Piedmont	SEP	SCP	SEP	R & V	R & V	R & V
Latitude (°N)	36.57	35.30	35.13	34.68	34.09	33.70	34.33	32.85	30.86	31.02	31.22	33.70	33.30	33.31
Longitude (°W)	-76.90	-79.95	-79.37	-80.51	-81.12	-82.20	-85.25	-84.48	-84.02	-87.25	-84.48	-85.73	-86.07	-86.75
Average Elevation (m)	10	132	140	159	45	78	314	262	72	63	43	350	472	298
COFECHA satistics														
Chronology length	1908–2003	1909–2008	1690–2006	1927–2009	1901–2009	1889–2009	1825–2008	1708–2002	1694–2003	1816–1995	1844–1995	1889–1997	1845–2005	1867–2008
No. of trees/No. of cores	19/36	51/55	21/35	36/38	25/40	30/51	36/51	32/49	31/57	27/43	29/49	40/42	29/29	31/49
First-order autocorrelation	0.513	0.653	0.594	0.553	0.559	0.615	0.568	0.529	0.554	0.603	0.548	0.670	0.596	0.569
Mean segment length	78.2	89.4	264.4	57.2	85.2	105.3	103.7	158.0	191.2	96.3	98.3	55.2	79.9	78.1
Absent rings (%)	0.036	0.253	0.076	0.000	0.029	0.019	0.095	0.181	0.486	0.000	0.104	0.259	0.173	0.026
Segment problems (%)	10.93	1.28	1.85	0.00	2.19	0.46	3.18	4.32	3.96	0.00	3.93	1.25	1.06	3.59
ARSTAN statistics - common interval 1938-1995														
Variance in first PCA vector (%)	31.0	42.4	39.1	70.7	40.4	46.1	37.5	35.0	42.0	46.4	39.1	60.8	53.5	39.7
EPS (no. of trees ? 0.85)[†]	0.927	0.975	0.953	0.857	0.955	0.974	0.957	0.936	0.971	0.958	0.934	0.966	0.912	0.947
Rbar (between trees)[‡]	0.278	0.402	0.364	0.52	0.366	0.439	0.341	0.317	0.395	0.436	0.347	0.576	0.485	0.358
SSS (trees in sample when ? 0.85)	0.856 (10)	0.867 (8)	0.862 (8)	0.875 (2)	0.864 (8)	0.869 (7)	0.864 (9)	0.865 (9)	0.867 (8)	0.861 (6)	0.854 (7)	0.874 (4)	0.866 (4)	0.868 (8)

Chronologies from: [1] = Bhuta, this study; [2] = Bhuta *et al.*, 2008; 2009; [3] = Knight, 2004; [4] = Meldahl *et al.,* 1999; 5 = Ortegren, 2008; 6 = Varner et al., 2003; 7 = Kush, unpublished data; [8] = Pederson *et al.*, 2009; [4, 5, 8] from IT

MACP = Middle Atlantic Coastal Plain; SEP = Southeastern Plains; SCP = Southern Coastal Plain; R & V = Ridge & Valley

[†] Expressed population signal (EPS) is the chronology reliability on a 0.0 to 1.0 scale. An EPS ? 0.85 indicates that the number of trees at that level are acceptable for yielding a common signal (Wigley et al., 1984).

[‡] Rbar is between trees.

[*] Subsample signal strength (SSS) determines the number of trees in a chronology with a strong common signal and aids in assessing the adequacy of replication in the that chronology.

Table 3.2. Paired *t*-test results comparing PRISM and the United States National Climatic Data Center Climate Divisions (NCDC-CD) climate data for temperature and precipitation from 1895–2010.

Precipitation (mm)	PRISM	NCDC
Mean	107.2	105.5
SD	23.77	21.52
SE	1.72	1.55
n	192	
mean difference	-1.71	
t-value	-3.44	
p-value	0.0007	
correlation	0.95827	

Temperature (°C)	PRISM	NCDC
Mean	16.98	16.81
SD	7.21	7.27
SE	0.52	0.52
n	192	
mean difference	-0.17	
t-value	-3.83	
p-value	0.0004	
correlation	0.99665	
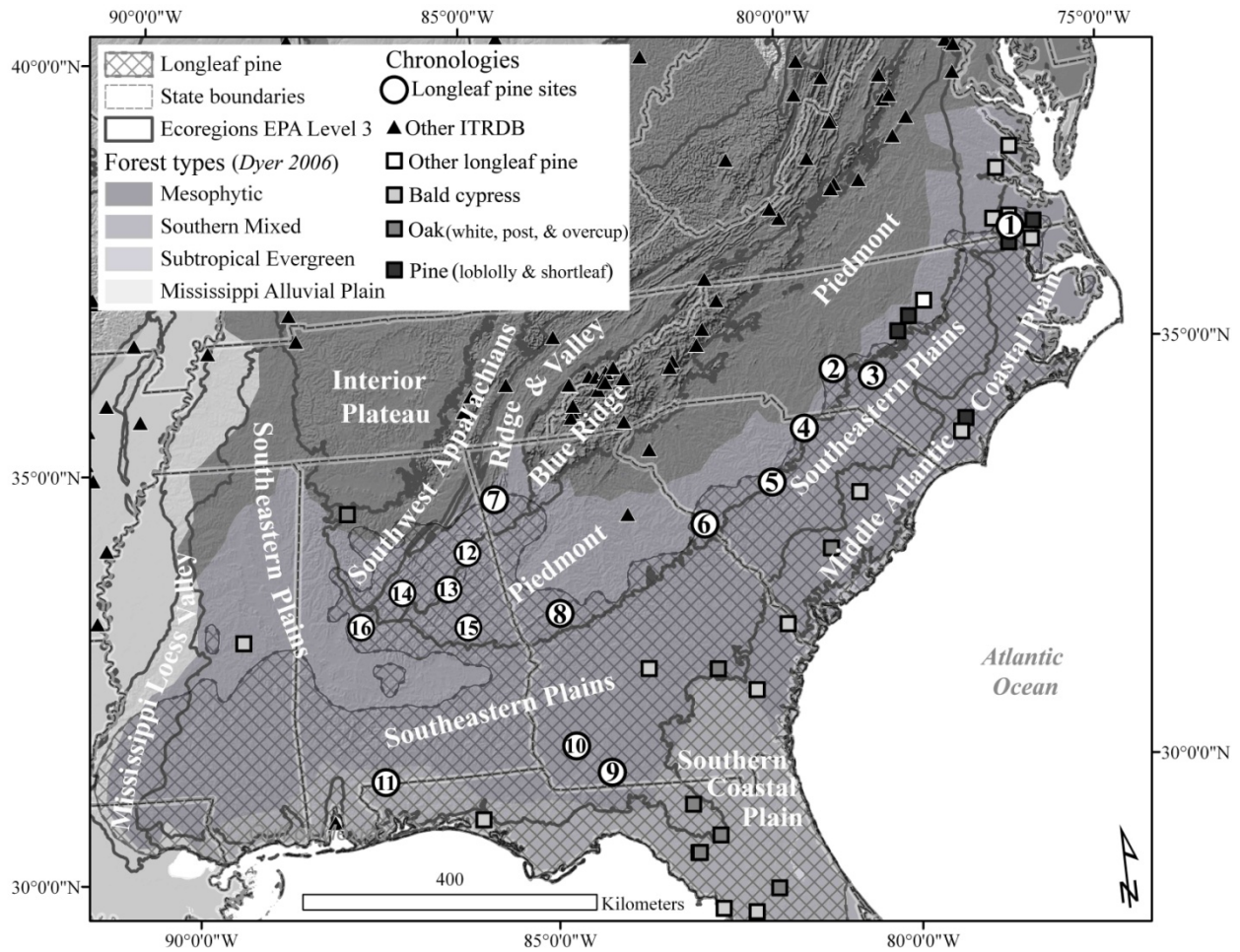
Figure 3.1. Location of longleaf pine chronologies used in this study (numbered circles) across forest types (Dyer 2006) and ecoregions (Omernik 1987). Sites 3, 10, and 11 are from the International Tree Ring Database (ITRDB). Other symbols are chronologies by species from the ITRDB for the southeastern United States. See Table 3.1 for further chronology descriptions.
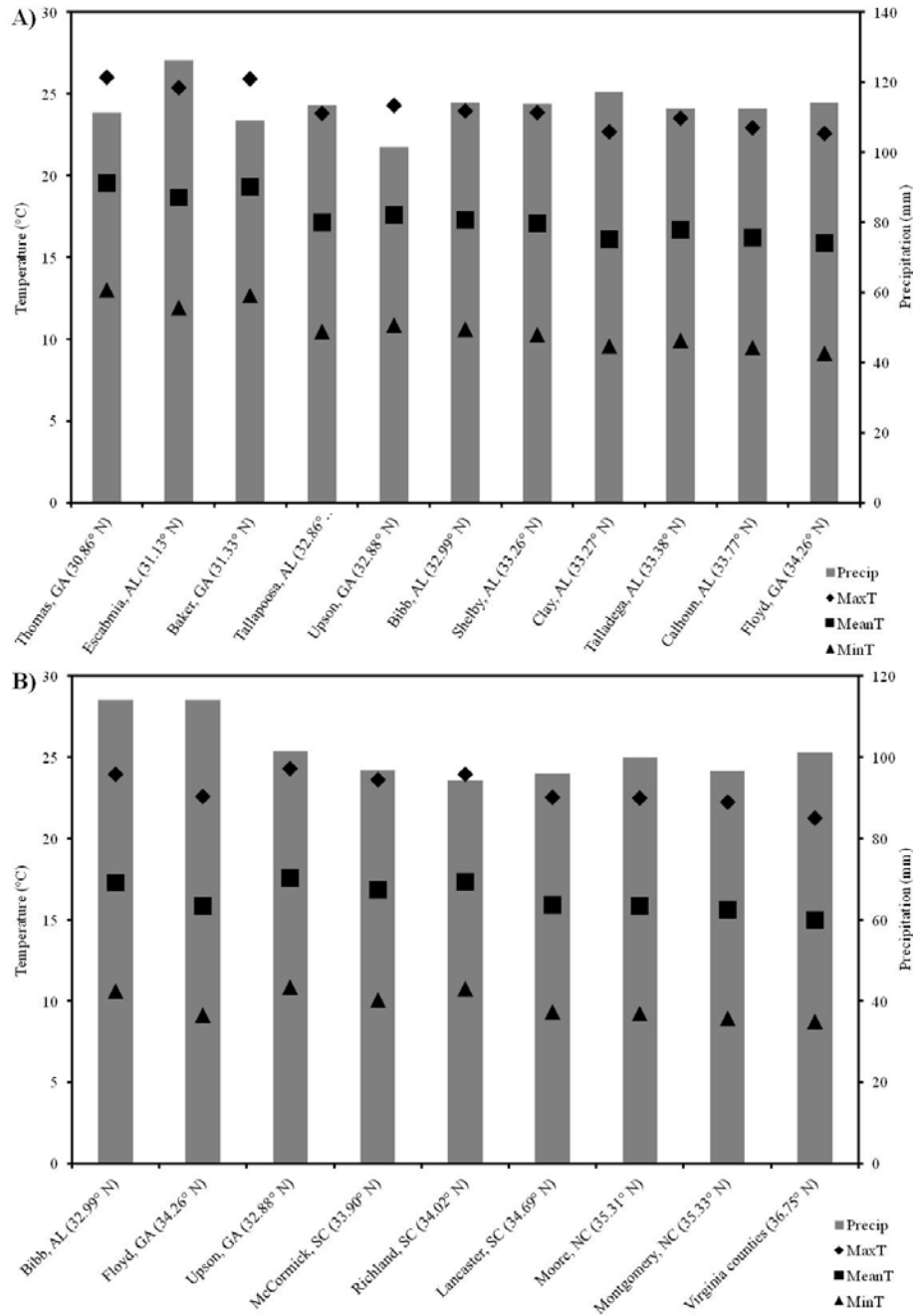
Figure 3.2. Annual maximum, mean, and minimum temperatures and annual mean total precipitation from 1895-2009 derived from Parameter-elevation Regressions on Independent Slopes Model climatological data (PRISM Climate Group 2011) at the county level and arranged by latitude A) along the south to north gradient running in Alabama and Georgia and B) along the northern range margin of longleaf pine.
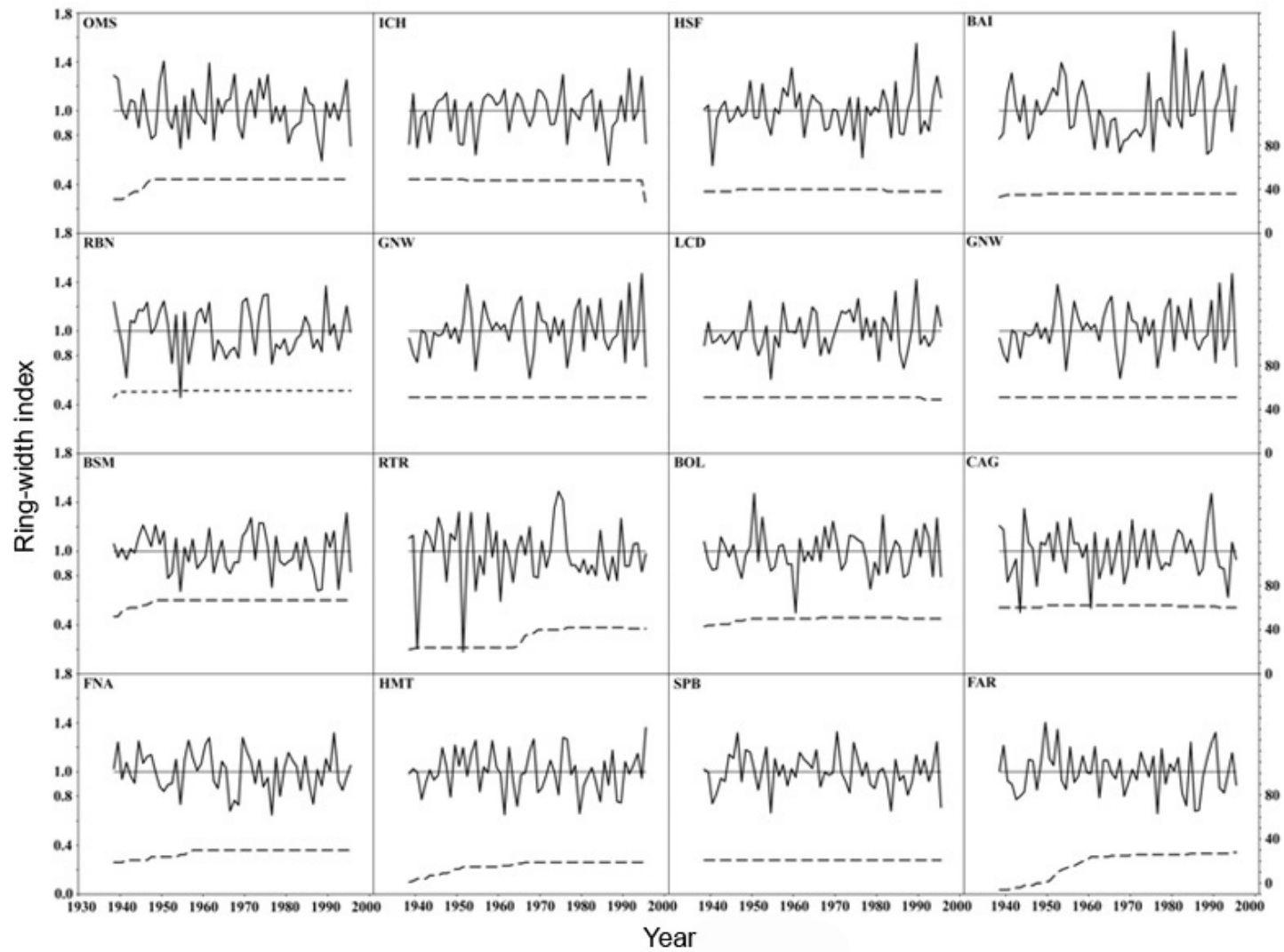
Figure 3.3. Longleaf pine ring-width residual chronologies and their sample size (dash lines) for the period 1938–1995.
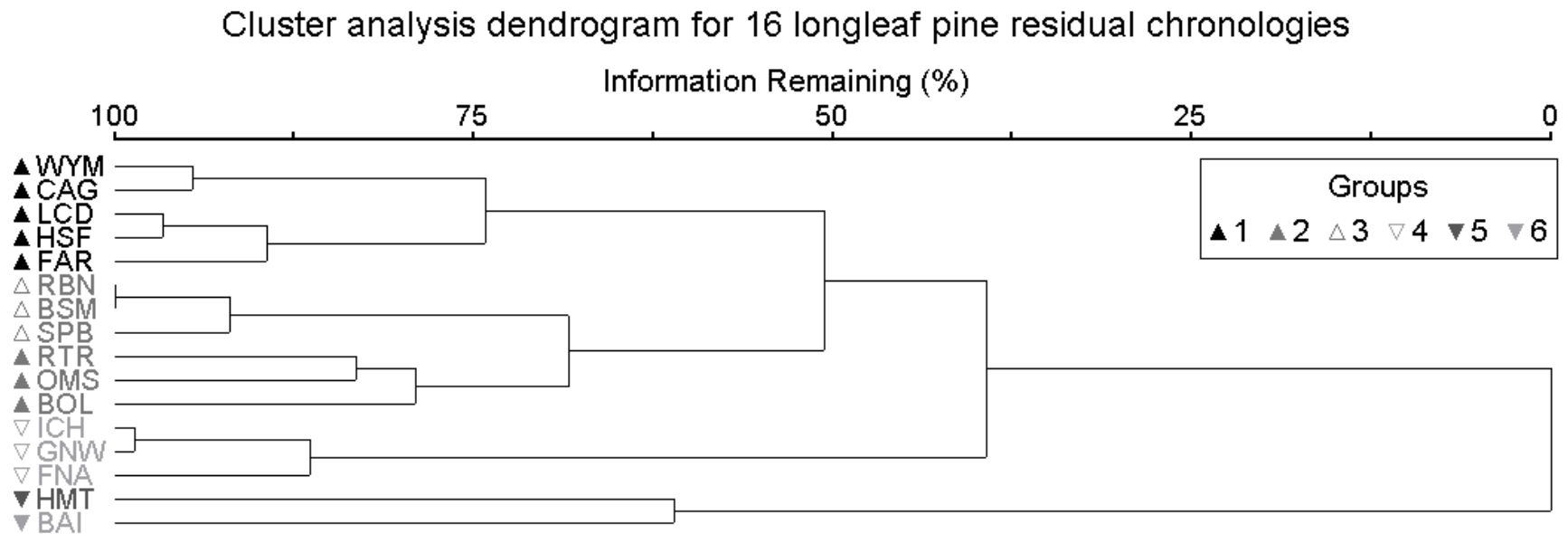
Figure 3.4. Cluster analysis for 16 longleaf pine residual chronologies using correlation as a distance measure and the flexible beta method, β = 0.25, as a group linkage.
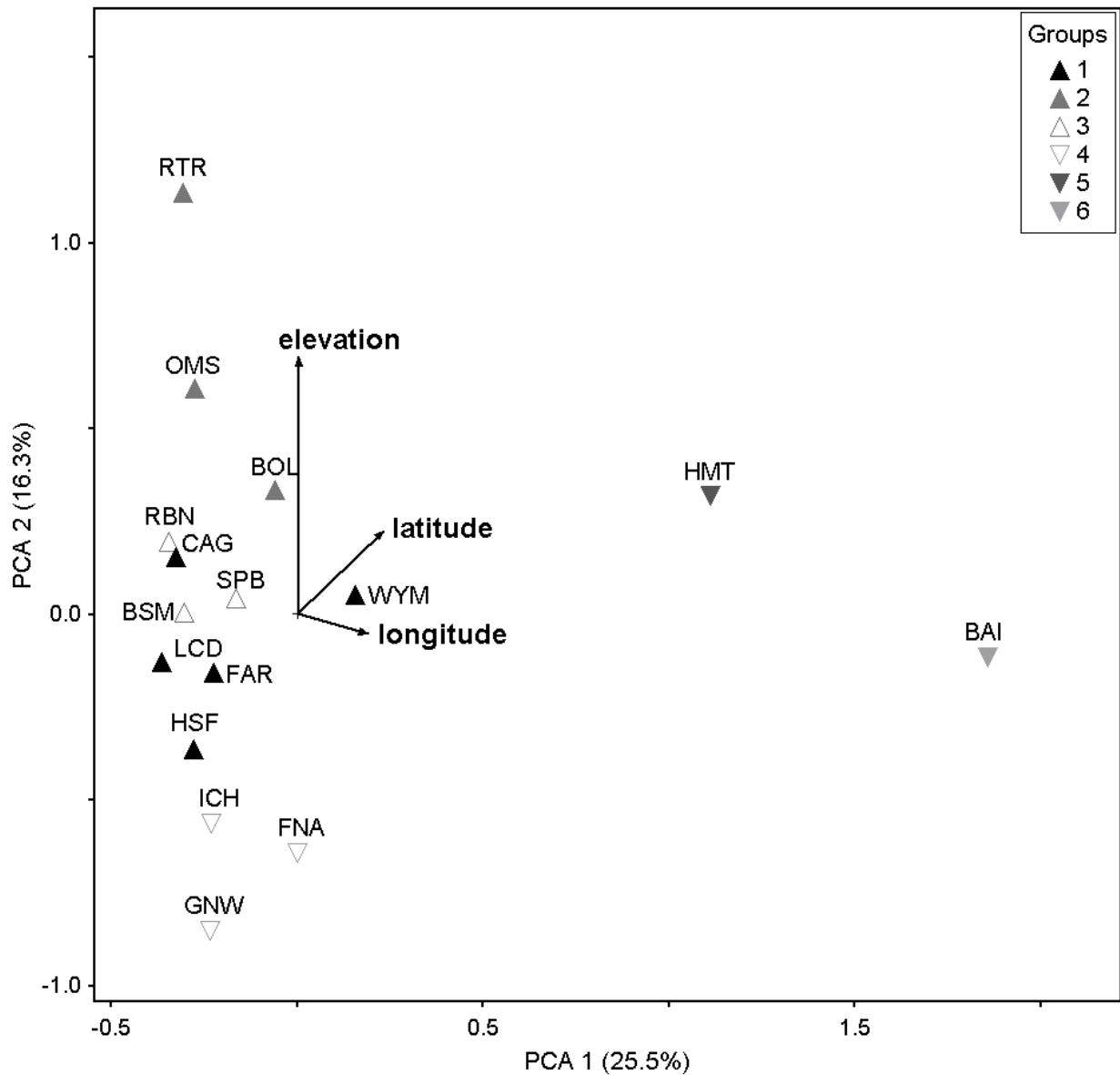
Figure 3.5. Principal components analysis of 16 longleaf pine residual chronologies plotted along two PCA axes with a joint biplot for elevation, latitude, and longitude.
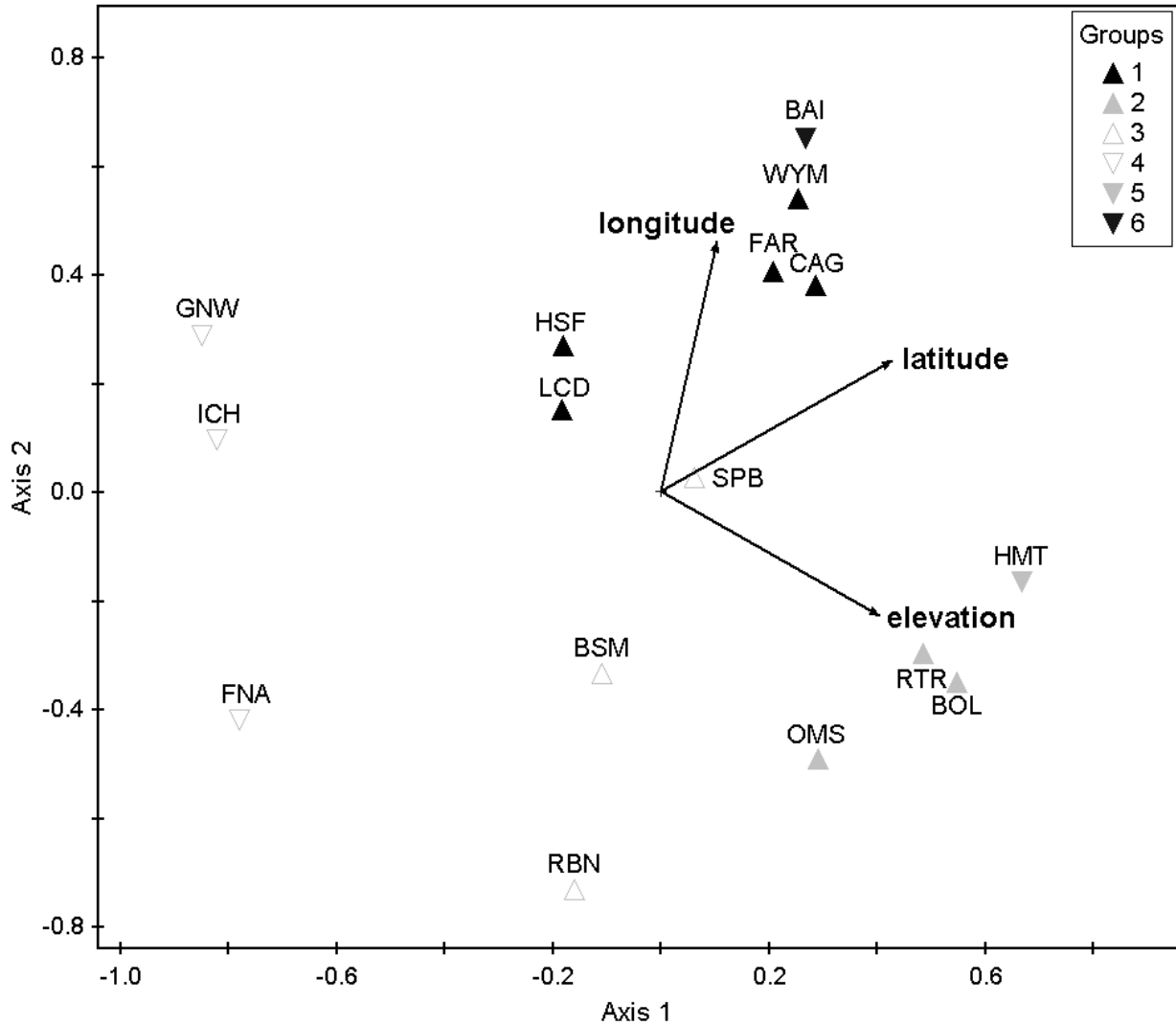
Figure 3.6. Redundancy analysis (RDA) for 16 longleaf pine residual chronologies for the southeastern United States against a joint biplot for latitude, longitude, and elevation. RDA axis three not shown.
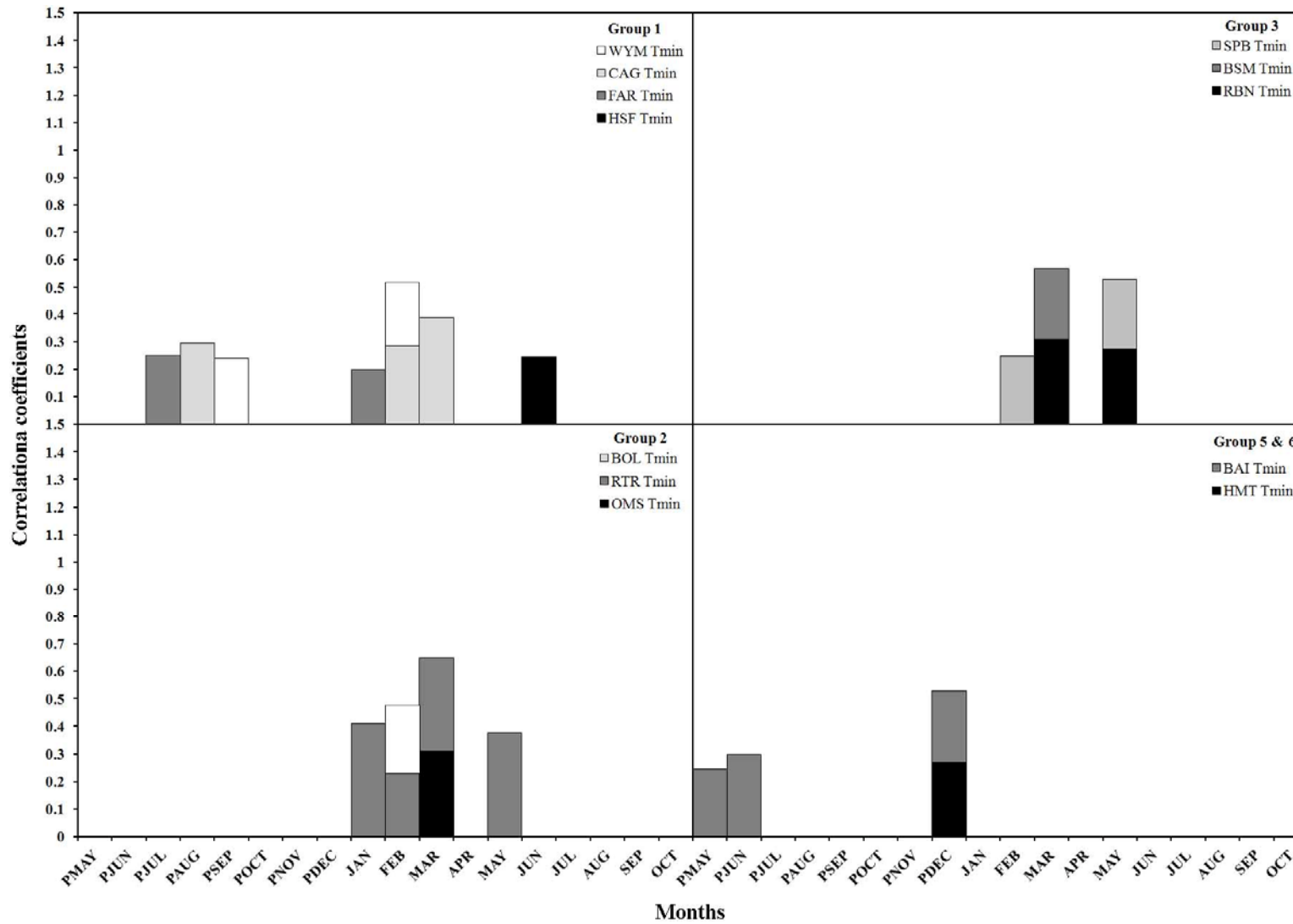
Figure 3.7. Significant correlation coefficients (p = 0.05) between monthly minimum temperature and 16 longleaf pine residual chronologies placed into groups from our cluster analysis. Group 4 (FNA, ICH, and GNW) did not have any significant correlations.

111
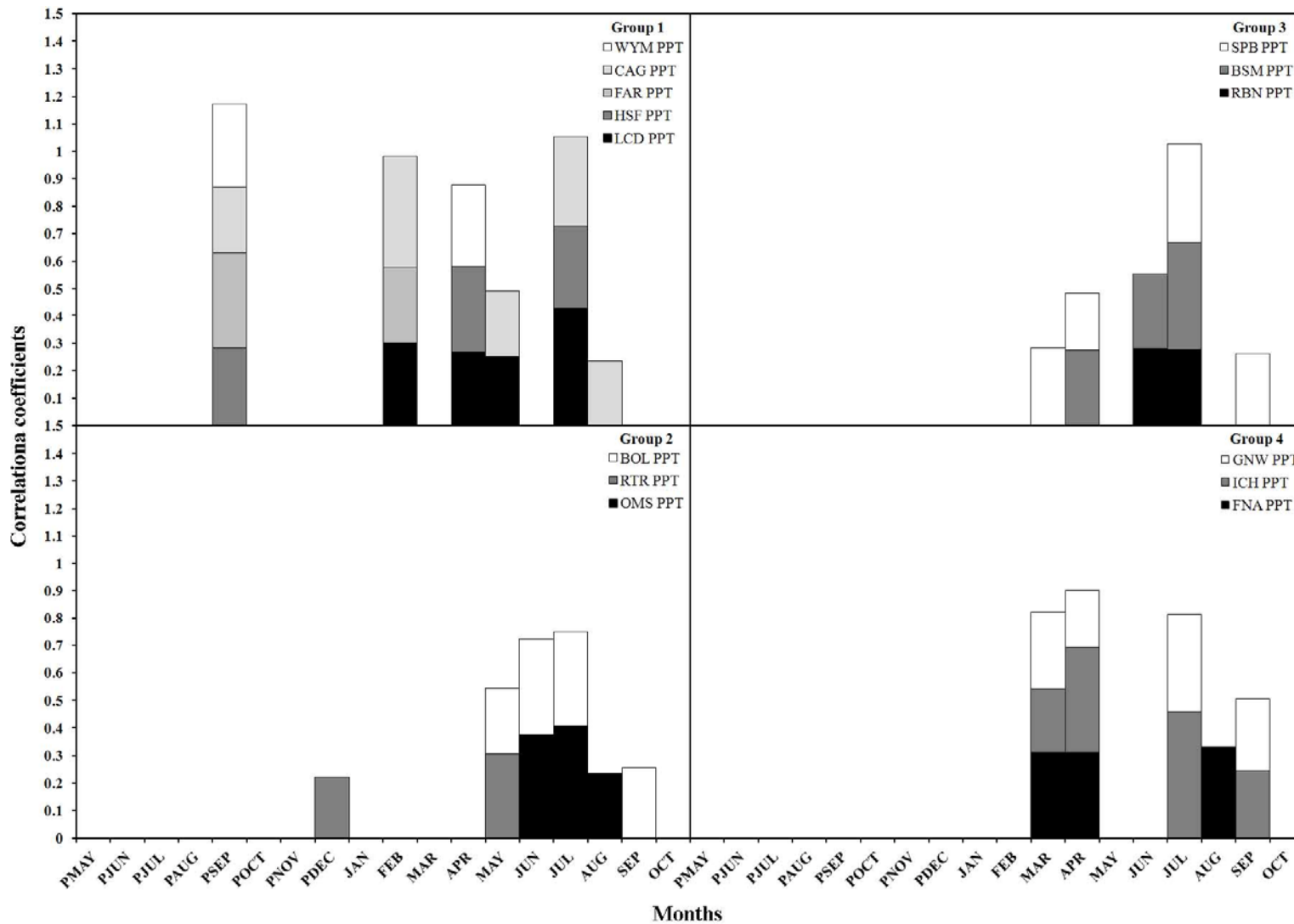
Figure 3.8. Significant correlation coefficients (p = 0.05) for monthly mean precipitation for 16 longleaf pine residual chronologies in the southeastern United States placed into groups from our cluster analysis. Groups 5 (HMT) and 6 (BAI) did not have any significant correlations.
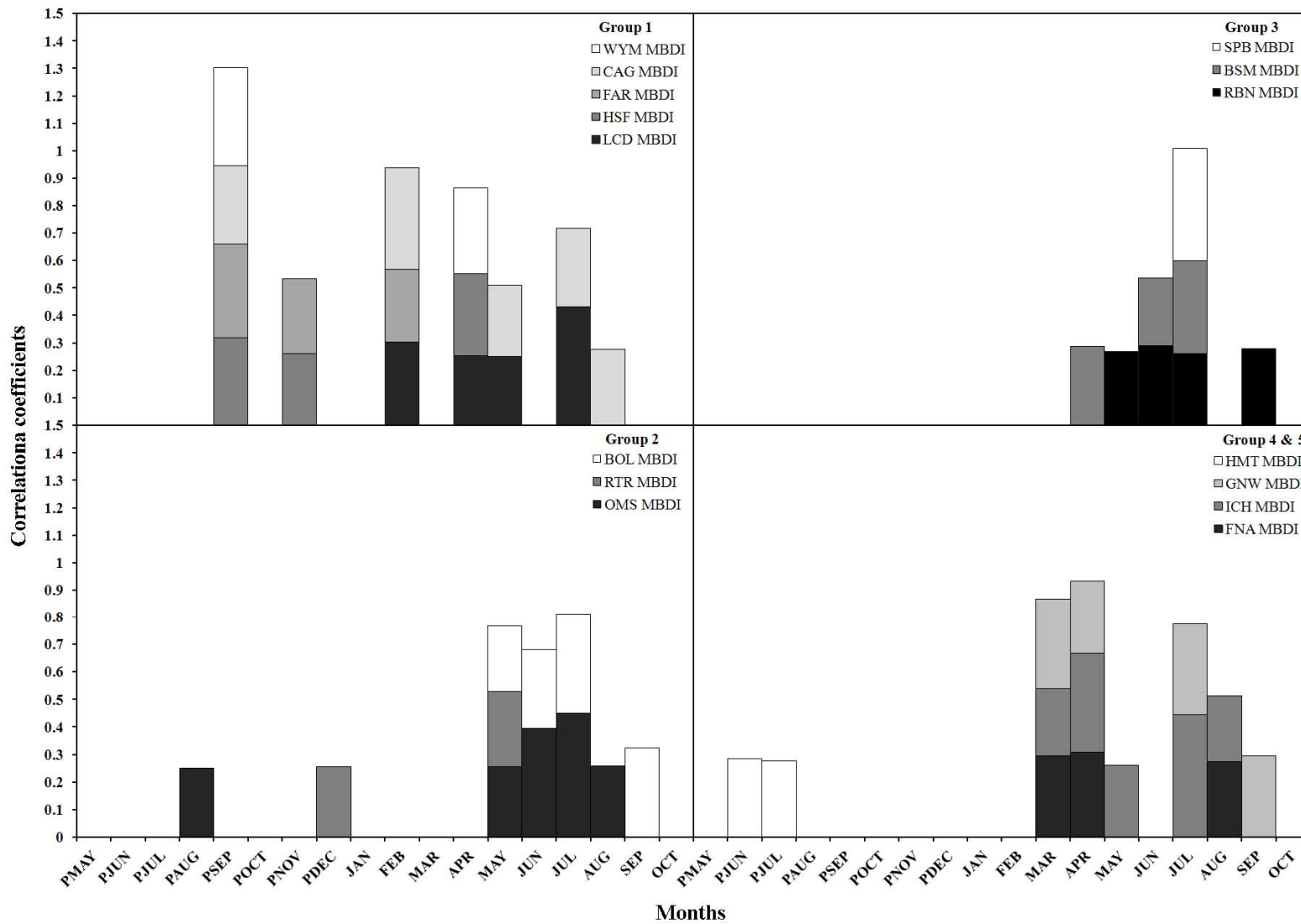
Figure 3.9. Significant correlation coefficients (p = 0.05) for monthly mean moisture balance drought index (MBDI) for 16 longleaf pine residual chronologies in the southeastern United States placed into groups from our cluster analysis. Groups 6 (BAI) did not have any significant correlations.

113
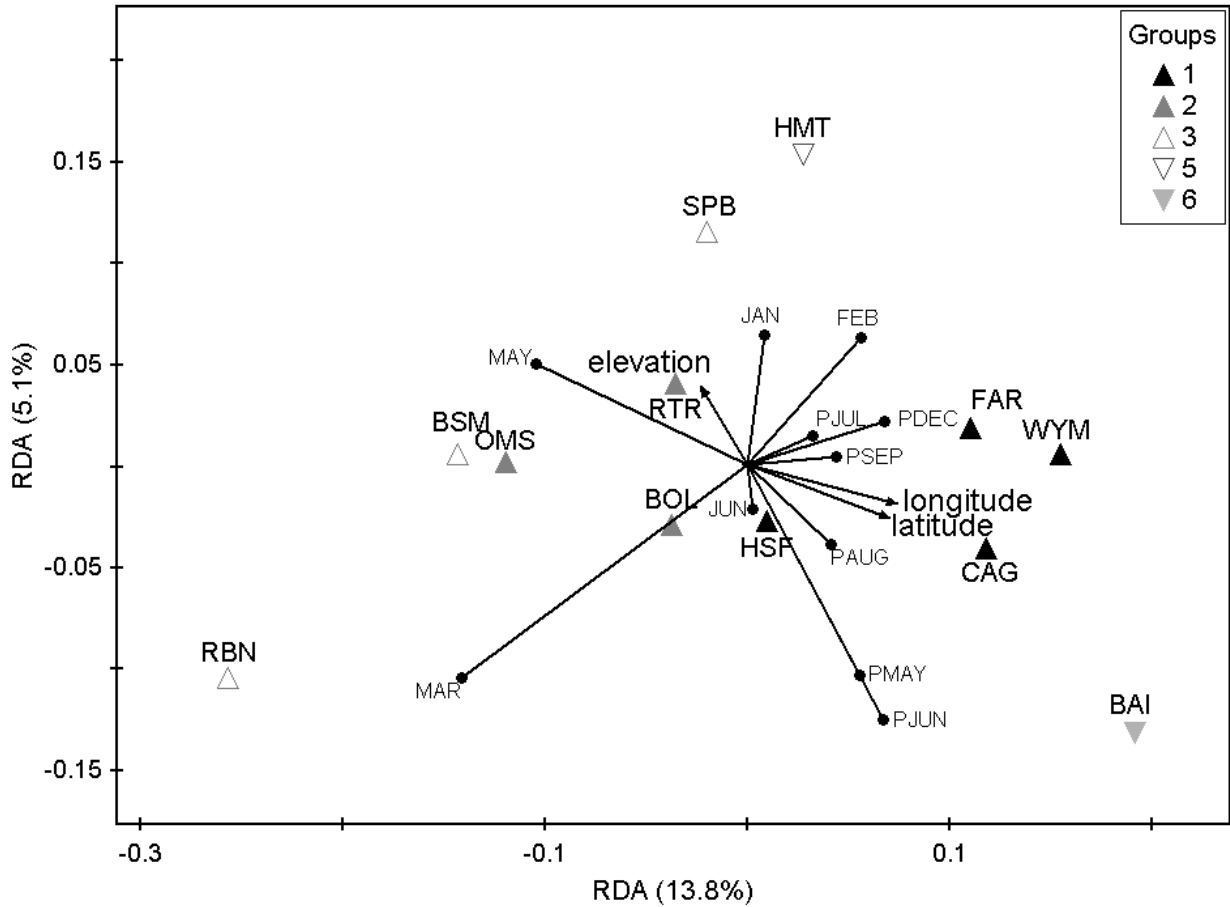
Figure 3.10. Mean monthly minimum temperature correlation coefficients for 16 longleaf pine residual chronologies in the southeastern United States. RDA axis three not shown.
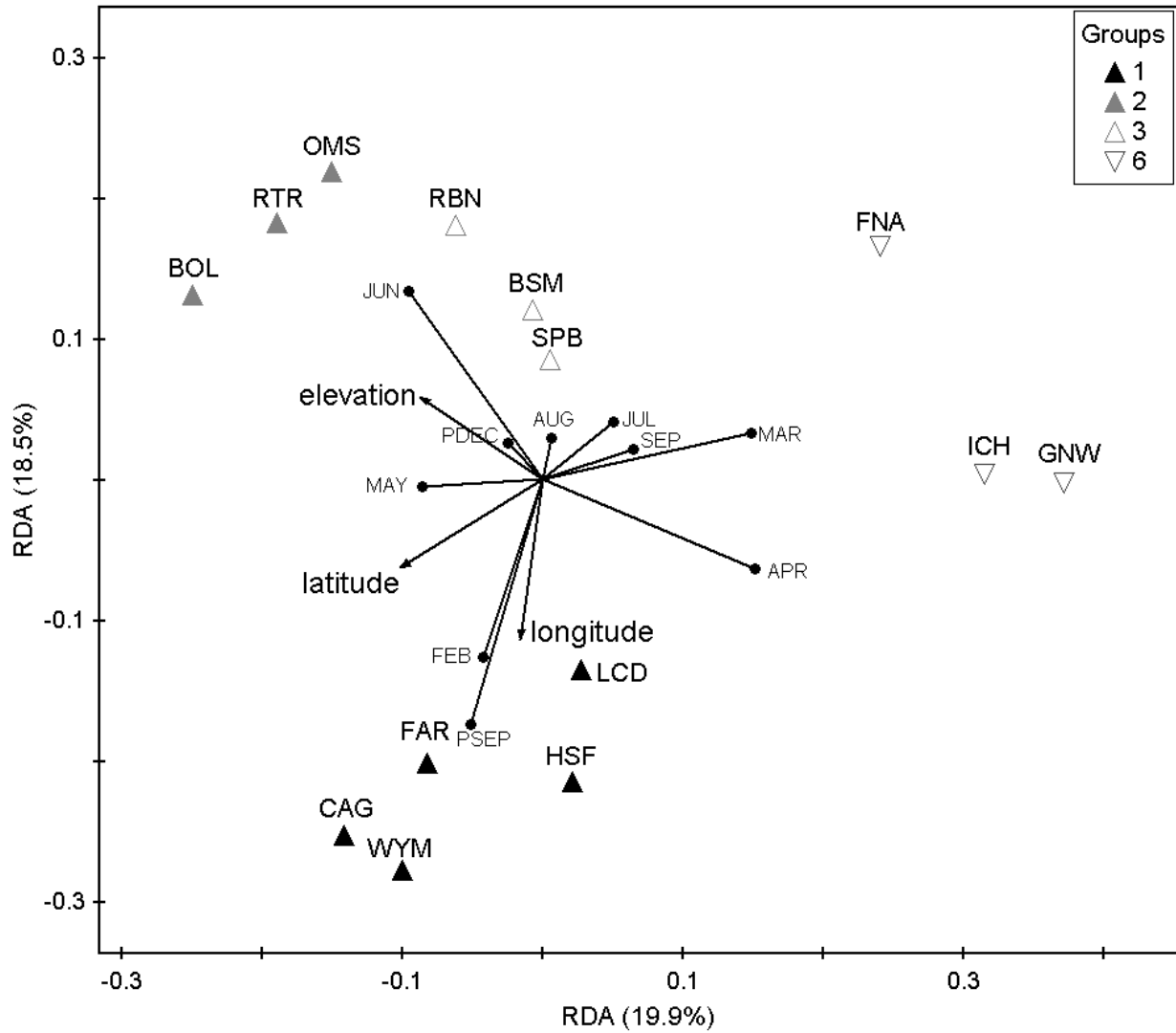
Figure 3.11. Mean monthly total precipitation correlation coefficients for 16 longleaf pine residual chronologies in the southeastern United States. RDA axis three not shown.
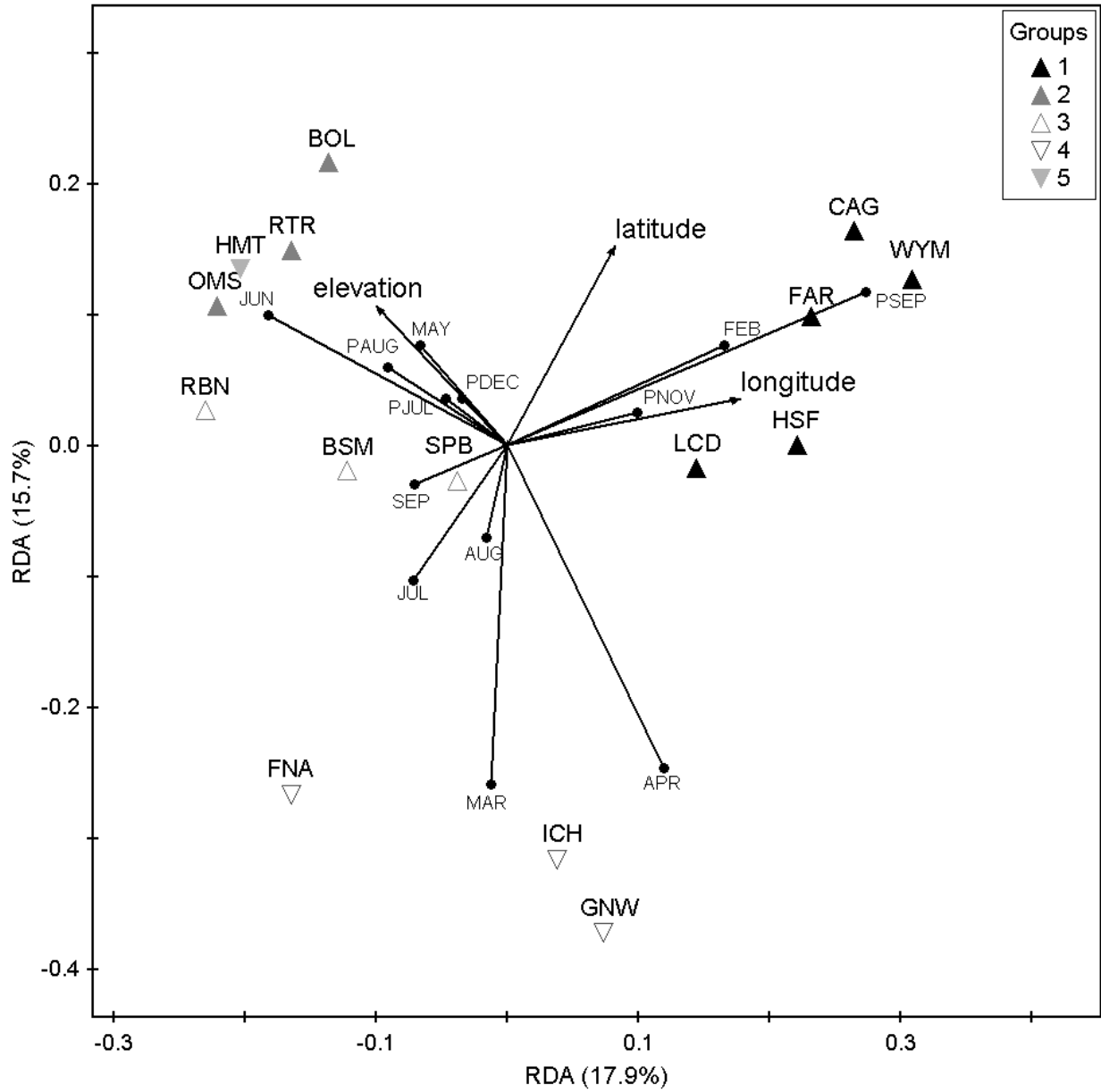
Figure 3.12. Mean monthly moisture balance drought index (MBDI) correlation coefficients for 16 longleaf pine residual chronologies in the southeastern United States. RDA axis three not shown.

116

Chapter 4: Temporal and spatial patterns of canopy trees in a *Pinus palustris* P. Mill. (longleaf pine) woodland community in the Alabama Piedmont

Note: this chapter is formatted for submission to the Journal of Vegetation Science.

Abstract

Question: How do temporal and spatial patterns in structure, composition, and dynamics of the tree canopy in a Piedmont *Pinus palustris* woodland community vary in comparison to other *P. palustris* ecoregions of the southeastern United States?

Location: Big Smith Mountain (BSM), southern-inner Piedmont, Alabama, USA.

Methods: I surveyed all trees at BSM identifying, measuring morphometrics, georeferencing, coring, collecting canopy cover and tallying seedlings and saplings in eight 0.1 ha plots. I synthesized field data, conducted point pattern analyses, and used dendroecological methods to determine disturbance patterns by reconstructing release events at BSM and then compared them to other *P. palustris* communities.

Results: Big Smith Mountain is an upland *P. palustris* woodland community consisting of an almost pure stand of *P. palustris* with a thick ericaceous shrub layer covering all aspects and slopes. *P. palustris* had an importance value of 76%, canopy cover of 54 %, a reverse-J shaped diameter distribution, individual ages dating back to as far as 1669, and a trimodal pattern (1880s, 1940s and 1990s) of recruitment to the canopy. Relationships between release events

and large-scale disturbances were not observed, indicating that unrecorded high-intensity fire events may be the cause for disturbance at BSM. *Nyssa sylvatica*, *Sassafras albidum* and *Prunus serotina* are recruiting into the seedling and sapling class while *N. sylvatica*, *Pinus taeda*, and other hardwoods are recruiting to the canopy in 1990s. Point pattern spatial analysis revealed dispersion by diameter, while showing an opposite trend for some plots when looking at tree age.

Conclusions: *Pinus palustris* at BSM is not restricted to southern aspects and slopes such as in the Ridge and Valley. *P. palustris* individuals persisted in the subcanopy for prolonged periods, responded with increased growth to releases, and did not need large-scale disturbances for recruitment as has been observed in Coastal Plain and Ridge and Valley forests. While *P. palustris* has recruited to the canopy continuously over the last two centuries, other pines and hardwoods have done so over the last two decades probably due to an absence of fire. The BSM *P. palustris* community is unique to the Piedmont however sharing similar descriptions to two communities that have been described in the Coastal Plain, with *P. palustris* in the canopy, a dense herbaceous layer, and little to no midstory layer.

Keywords: disturbance, point pattern analysis, dendroecology, structure, composition, dynamics

Nomenclature: Retrieved 09/12/2011 from the Integrated Taxonomic Information System on-line database, http://www.itis.gov.

1. Introduction

Forested communities and ecosystems, hereafter referred to as systems, where a single foundation tree species is instrumental in ecological structure, function, and processes abound worldwide and include such examples as *Pinus albicaulis* Englem. (whitebark pine); *Tsuga canadensis* (L.) Carrière (eastern hemlock); and mangroves species (*Rhizophora* spp.) (Ellison et al. 2005). These foundation tree species exhibit range-wide geographic variation in their ecology and some are in serious decline due to complex, multi-faceted natural and human-caused impacts. *Pinus palustris* P. Mill. (longleaf pine) is a foundation tree species documented throughout a variety of systems within the southeastern United States (Reed 1906; Golden 1976; Gilliam et. al. 1993; Noel et al. 1998; Gilliam & Platt 1999; Kush & Meldahl 2000; Varner et al. 2003; Frost 2006; Peet 2006; Stokes et. al. 2010). These fire-dependent systems once covered over 37 million ha while exhibiting high ecological amplitude, complexity, and diversity; however, compounding human activities have contributed to the reduction, fragmentation, and dysfunction of these systems leaving only 841,800 ha (Frost 2006). These human activities include multiple commercial uses (naval stores and timber industries), seedling predation by feral hogs, conversion of forests to agricultural and urbanized landscapes, and changes in fire and land management practices (Frost 2006). Fragmented patches of old-growth or second-growth *P. palustris* communities exist throughout the southeastern landscape ranging from well managed to degraded conditions and have been described most

Peet (2006) classified the geographic variation and diversity of *P. palustris* systems based on 135 naturally occurring vegetation associations managed with a history of low-intensity fires, scaled them to six ecological groups based on physiognomy and soil type, and created six *P. palustris* ecoregions: Atlantic Coastal Plain, Southern Coastal Plain, Eastern Gulf Coastal Plain,

Western Gulf Coastal Plain, Fall-Line Sandhills, and Piedmont and Montane Uplands. Of the

900 plots used in his vegetation classification, only nine plots were documented in the Piedmont,

Southwestern Appalachians, and Ridge and Valley ecoregions of the Piedmont and Montane

Uplands (Omernik 1987; Peet 2006). While the majority of the well-studied *P. palustris* systems

occur in the Coastal Plain, much less is known about Piedmont and Montane Upland *P. palustris*,

its associations, composition, structure, and function. Only 20 ha of the remaining 40,000 ha of

Piedmont and Montane Upland *P. palustris* forests are described as old-growth (Varner et al.

2003b; Stokes et al. 2010). Land managers have shown increasing interest in the restoration and

management of these remaining *P. palustris* forests, but have relatively little information on

these forests which they can use as a guide. Some managers may have possibly resorted to using

similar management of Coastal Plain *P. palustris* systems, however such management might not

be appropriate for Piedmont and Montane Uplands systems due to differences in edaphic

characteristics , topography, and fire regimes (Varner et al. 2003; Brockway et al. 2005; Frost

2006; Stokes et al. 2010).

In the Piedmont and Montane Upland ecoregions, *P. palustris* communities are highly

variable within the ecoregion and compared to those in Coastal Plain *P. palustris* communities.

Current knowledge of the Piedmont and Montane Upland *P. palustris* communities are based on

historical accounts, reconstruction of vegetation patterns prior to presettlement and site-specific

studies. In the Southwestern Appalachians, *P. palustris* dominates the canopy in a *P. palustris* -

Pinus virginiana Mill. (Virginia pine) - *Quercus marilandica* Muenchh. (blackjack oak) - *Cornus*

florida L. (flowering dogwood) woodland (VegBank 2011). Several contemporary studies of the

Ridge and Valley focus on the composition, structure, and dynamics of *P. palustris* woodland

communities in the Mountain Longleaf National Wildlife Refuge and the eastern ranger districts

of the Talladega National Forest (Shankman & Wills 1995; Maceina et al. 2000; Varner et al. 2003a; Varner et al. 2003b; Stokes et al. 2010; Womack and Carter 2011). In the Piedmont of Alabama and Georgia, a few studies have reconstructed the composition of pre-European forests and the influence of Native Americans on them (Cowell 1995; Black et al. 2002; Foster et al. 2004). *P. palustris* systems were documented in Alabama (Black et al. 2002; Foster et al. 2004) but not in Georgia (Cowell 1995). Two studies offer an in-depth understanding of the structure, composition, and dynamics of the Piedmont forests, one by Reed (1905) who surveyed 14 562 ha of land in Coosa County, AL, of which 77% were pure or mixed upland *P. palustris* forests and 11% were mixed bottomland hardwood forests with scattered *P. palustris* and a higher abundance of *P. taeda* and *Pinus echinata* Mill. (shortleaf pine). Reed documented a variety of diameter classes for *P. palustris* ranging from 2.54 cm to 106.7 cm and heights up to 34 m. These original, old-growth forests were harvested for their timber after the survey so further information on their current status could only be examined through the second growth forests that recruited after the harvest. The second study, by Golden (1979), examined the forest communities of the Ashland and Opelika Plateaus and the Piedmont Ridge along the Devil's Backbone. He observed two communities with occurrences of *P. palustris* based on three plots: a *Q. marilandica-Pinus* community with *P. palustris* mixed with *P. echinata* as a second dominant and a xeric upland community restricted to ridges and upland slopes with pure stands of *P. palustris*. Community structure using diameter-size classes and counts of seedlings and saplings revealed that both communities had individuals occurring across all diameter-size classes. One pure *P. palustris* community exhibited somewhat of a reverse-J shaped distribution with plentiful recruitment of seedlings and saplings, while the other appeared to have an equal amount of *P. palustris* individuals occurring in almost all size classes, between five to ten

individuals per class, and almost no recruitment of seedlings and saplings. The mixed community had a high recruitment of *Q. marilandica* and *P. taeda* seedlings and saplings, however the trend reversed for *P. taeda* while *Q. marilandica*, *P. echinata*, and *P. palustris* occurred with five or less individuals per size class. *Pinus palustris* was absent however from the 18 to 26 cm size classes, but was found in the larger size classes indicating that perhaps some of these individuals were removed from the community naturally or by humans.

Due to the limited amount of studies on Piedmont *P. palustris* communities, further detailed information is needed on their structure, composition, and dynamics to determine if historical and contemporary studies share similar observations. My study documents the structure, composition, and disturbance dynamics for one such Piedmont *P. palustris* woodland community located in Alabama. I examined the spatial and temporal patterns of the structure, age, and composition of trees in the community and extrapolated recruitment patterns from a tree-ring chronology. Several questions guided this research: 1. How does the composition of a *P. palustris* Piedmont community compare to those described in other *P. palustris* ecoregions? 2. Is forest structure dominated by *P. palustris* or do other species occur in the canopy or seedling and sapling layer? 3. Is recruitment to the canopy or in the seedling and sapling layer connected to large-scale disturbances, such as hurricanes, or local-scale disturbances, such as removal of individuals from the community by fire or timber harvest? 4. Is there a spatial component to recruitment patterns, are they clustered or dispersed by diameter or age? My overall goal for this research is to determine whether differences exist between the canopy trees of this community and its counterparts described in the historical and contemporary literature for the Coastal Plain, the Ridge and Valley, and Piedmont.

2. Methods

2.1. Site description and land ownership

The 59.9-ha Smith Mountain forest is situated on the Piedmont Ridge (Devil's Backbone) and is located on two mountains, Big Smith Mountain (BSM), maximum elevation of 238 meters above sea level, and Little Smith Mountain, maximum elevation of 213 meters above sea level, in Tallapoosa County, Alabama, USA (**Figure 4.1**). The Piedmont Ridge is wedged between the Ashland and Opelika Plateaus in the southwestern portion of the southern-inner Piedmont, a northeasterly-southeasterly ecoregion occurring from east-central Alabama to southwestern North Carolina and located between the Ridge and Valley to the north and the Coastal Plain to the south (Golden 1979; Griffith et al., 2001). Phyllite, quartzite, and sericite schist bedrock of Precambrian and Paleozoic origins make up the parent material for the moderately-eroded Tallapoosa-Fruithurst soil complex of Smith Mountain forest. This soil complex consists of gravelly loam Typic Hapludults found on 15 – 40 % slopes and is composed of the following series: the shallow depth Tallapoosa (60%) found on upper and middle slopes; the moderately deep Fruithurst (30%) found on lower slopes and toeslopes; and minor components of Badin (5%), Cartecay (2%), and Wehadkee (2%) (McGhee 2007). This soil complex is found from 122 to 335 meters in elevation with depth to the high water table being more than 1.83 cm (McGhee 2007). It has low fertility, moderate permeability, low available water capacity, and high organic matter in the surface layer (McGhee 2007). The climate of this portion of the southern-inner Piedmont area is humid subtropical with a mean annual precipitation ranging from 88.9 cm to 147.3 cm, mean annual air temperature ranging from 10.6 to 20 °C, and frost-free periods ranging from 190 to 225 days (McGhee 2007).

The Smith Mountain Forest is part of a 295.1-ha designated general-public use area (GPUA) that borders Lake Martin, a 16,187 ha artificial reservoir with 1,127 km of shoreline. Lake Martin was the largest human-made body of water in the world in 1926 when it was formed from the construction of a hydroelectric dam on the Tallapoosa River (Alabama Power Company 2010a). All GPUAs at Lake Martin are owned and managed by the Alabama Power Company (APC), a subsidiary of the Southern Company, a publicly American-owned electric utility company. These GPUAs border the waters of Lake Martin and are "reserved for the development of parks, boat ramps, concessionaires' facilities and other recreational facilities open to the public (Alabama Power Company 2010a)." The forest is surrounded by Lake Martin along the southwest, while adjacent forested lands surround it on the north to northwest and residential properties border it to the east.

2.2. Land-use history

The first purchases of the lands comprising Smith Mountain forests consisted of US Federal Government land patents administered through the General Land Office. The US Federal Government, based on the PLSS and the township and section survey, split these lands into quarters and sold them to three individuals in 1845, 1858, and 1876 (General Land Office Records 2011). The APC purchased these lands, more than likely not from the original landowners, between 1914 – 1926 to serve as buffers encompassing the hydroelectric dam and lake project. Land-use history prior to the APC acquiring these lands is unknown, but three primitive mining shafts created for obtaining gold at BSM have been unearthed that predate purchases made by current landowners; however, the timing of excavation remains in question (personal communication, E.B. "Skip" Turner, retired AFC forester and Jimmy Lanier, CRATA

executive director). Within Smith Mountain Forest, there is a 4.1 ha square parcel of land which

encloses the summit of BSM and is owned and managed by the Cherokee Ridge and Alpine Trail

(CRATA), a not-for-profit organization dedicated to the promotion of natural areas and foot-only

trails around Lake Martin. In 1939, this 4.1 ha parcel was sold to the Alabama Forestry

Commission (AFC) who monitored the area for human and natural-caused fires through the use

of the only developed area, a 24 meter high fire tower and ranger station which were both built

by the Civilian Conservation Corps (CCC). The fire tower was decommissioned in 1980 and the

AFC sold the land back to the APC in 2006, and the APC sold this land to CRATA in 2010. In

1959, a timber sale for the tract of land containing BSM was recorded, however the slopes of

BSM were not harvested for timber (personal communication, Mark M. Tuggle, APC forester

and William A. Tharpe, APC historian). An intense arson fire in 2007 was thought to have killed

many of the trees at BSM (personal communication, Mike M. Tuggle, APC forester and Jimmy

Lanier, CRATA executive director).

2.3. Field methods

I preliminarily surveyed BSM in 2009 and found that the eastern aspect contained only a few

live trees but was covered mostly by snags, downed trees, and an herbaceous layer of grasses,

rendering the tree community unsuitable for sampling due to die-off after the 2007 fire. The

northern to southeastern aspects of BSM also were affected by the fire, but the density of live

trees on these slopes allowed for sampling of trees in the community. At the BSM summit, I

randomly chose eight compass bearings, which served as transects ranging from northeastern to

southeastern aspects. A random elevation was chosen along the transect serving as the point

where plot center would be. Plots were established parallel to the slope's contour, but were

perpendicular only when topography or elevation appeared to alter a change in tree community composition. All data were collected in summer (August and September) of 2009.

I established eight, 20 x 50 m (0.1 ha) permanent plots based on the methods of Peet et al. (1998), tagging, identifying, and measuring for height and diameter at breast height all trees and snags greater than 5.0 cm diameter at breast height (DBH). Height was measured using an electronic clinometer, while diameter was measured to the nearest centimeter with diameter tape. Permanent survey pins for the plot and all tagged trees were georeferenced using a GPS unit or a combination of a GPS unit, total station, and survey prism. Georeferenced data were postprocessed in the laboratory to correct for any georeferencing field errors using Pathfinder Office 5.1 (Trimble, Sunnyvale, CA, USA) or Leica Geo Office (Leica Geostystems AG, Heerburg, CH) and exported to ArcGIS 9.3.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) for further spatial analysis. Canopy cover was measured at BSM by recording the presence or absence of the vertical projection of a tree's crown in the canopy to the floor via a vertical densitometer at a height ~1.8 m at 5 m intervals along five equally-distanced transects running the 50 m length of the plot (Stumpf 1993). Data recorded for canopy cover was binary, with the absence of tree canopy recorded as no canopy cover and the presence of a tree's canopy recorded with the species providing the canopy cover. A nested 20 m by 20 m subplot between the 20 m and 40 m section of the main plot was used to tally seedlings and saplings by species. Saplings were considered < 5.0 cm DBH but > 1 m in height, while seedlings were < 1m in height. We also cored all trees > 5.0 cm DBH within the subplot and cored all trees > 15.0 cm outside of the subplot, but within the plot. *Pinus palustris* with large diameter sizes adjacent to the plot were assumed to be old-aged individuals and were also cored.

All trees were cored with increment borers 30 cm above the ground, parallel to the contour and perpendicular to the slope to account for compression (pines) or tension wood (hardwood).

2.4. Dendroecological analysis

All tree cores were air dried, affixed to mounts, and sanded to aid in tree-ring analysis. All rings were crossdated using the list year method measured at a resolution of 0.001 mm using a stereo-zoom microscope and a Velmex measuring system (Velmex Inc., East Bloomfield, NY, USA) coupled with Measure J2X software version 4.2 (VoorTech Consulting, Holderness, NH, USA; Yamaguchi 1991; Stokes and Smiley, 1996; Orvis and Grissino-Mayer, 2002). I used COFECHA software for quality assurance and control by statistically verifying my cross-dating (Holmes 1983; Grissino-Mayer 2001). The raw ring widths from this chronology were used in determining minor (> 20 % but < 50 %) and major releases (> 50 %) based on the development of a site-specific modified boundary-line criterion (Black &Abrams 2003). The selection and development of a site-specific boundary line was used because the number of annual rings from BSM compared to the number of annual rings developed from six *P. palustris* sites developed by Bhuta et al. (2008) had a 1:1.81 ratio, 18,174 annual rings from BSM compared to 32,970 annual rings from those six sites. The difference in the sample size of annual rings for BSM compared to the other six sites suggested to me that the other six sites could obfuscate release patterns for BSM because the sum of the six groups were based on populations for Coastal Plain *P. palustris*, which may have different disturbance histories compared to Piedmont *P. palustris* and Ridge and Valley *P. palustris* (Varner et al. 2003).

Instead of using mean percent growth change and mean prior radial growth, I calculated median percent growth change (MPGC) for year *t* of all *P. palustris* in the chronology by taking

the ten year median growth change before (MGCB) and after (MGCA) that year, subtracting MGCB from MGCA, and dividing the difference by MGCB (MPGC = MGCA – MGCB/MGCB), while median prior radial growth (MPRG) is simply MGCB. MPRG was placed into 0.5 mm segment classes and the ten highest MPGC values in each class were used to create a boundary line using an exponential trend line. Use of the median in calculating growth change allows for more statistical robustness in these calculations since tree-ring data could be non-normally distributed (Rubino & McCarthy 2004). Boundary-line criteria were not developed for *Pinus taeda* L. (loblolly pine) and *Nyssa sylvatica* Marsh. (blackgum) since samples were only a few in number, dated to 1987 at the earliest, and the calculation of MPGC would not provide enough data for developing a boundary line and releases for these species. *Acer rubrum* L. (red maple) boundary-line criteria were not developed as well because only one core was taken.

 Pinus palustris individuals experiencing minor or major releases using the boundary-line criteria were used in the development of a minor (20%) and major (50%) release chronology based on mean yearly MPGC (Nowacki and Abrams 1997; Black and Abrams 2003). These modified chronologies were analyzed using a number of superposed epoch analyses (SEAs; EVENT software: Holmes & Swetnam 1994) to determine statistically if any recorded disturbance events such as hurricanes, the 1959 logging event, or the construction of the fire tower in 1939 influenced any release events seen in these chronologies. Hurricanes used in this analysis include the following: 1) unnamed hurricanes in 1881 (category 2), 1887 (category 2), 1893 (category 4), 1902 (category 2), 1915 (category 2), and 2) named hurricanes in 1950 (Hurricane Easy, category 3), 1975 (Hurricane Eloise, category 3); and 1995 (Hurricane Opal, category 4). Using ArcGIS, hurricanes greater than a category 2 on the Fujita scale were chosen

128

for this analysis and were based on their tracks which passed within and around the counties that surround Tallapoosa County, AL. The intensities given for the hurricanes listed are their intensities before landfall; they were more than likely not as severe when they reached the study site area. For the SEAs, I tested for the effects of all events, the effects of hurricanes only, and the effects of human disturbances only on release patterns for the 20% and 50% chronologies. I ran two superposed epoch analyses per each category with a twelve year window, spanning one year prior to the event through to the current year of the event and ten years after. The first SEA had no segments, while the second SEA was processed by 50 year segments with 25 year overlaps.

2.5. *Geospatial analysis*

Plot metrics and geospatial analysis of tree distributions were carried out in ArcGIS 9.3.1. I derived slope (%), aspect (%), and elevation (m) from 1/3 arc-second digital elevation model (United States Geological Survey, 2011) for the Smith Mountain forest area and specifically calculated slope, aspect, and elevation for all plots based on georeferenced trees or plot pin locations. Georeferenced trees were also used in determining Ripley's K-function (Ripley, 1981) using the Spatial Statistics toolbox in ArcGIS. Ripley's K-function is a point pattern cluster analysis used in determining the dispersion or clustering of individual points over multiple distances from each other by comparing them to Monte Carlo simulations to determine if the observed dataset significantly deviates from the expected along a gradient of distance. If the observed K exceeds the higher confidence interval produced from the Monte Carlo simulation, then the trees at BSM are clustered. However, if the observed K exceeds the lower confidence interval produced from the Monte Carlo simulation, then the trees at BSM are dispersed. The

129

trees mapped at the plot level were weighted by DBH, ran against 999 simulations with 100

distance bands using Ripley's edge correction formula, a correction method appropriate for

square and rectangular study areas. An output was created in ArcGIS with an expected and

observed dataset and upper and lower confidence intervals to determine if the spatial relationship

was significantly clustered or dispersed along a gradient of distance. Two plots were not

included in both of these analyses due to field errors that could not be corrected with GPS

software.

3. Results

3.1. Plot, tree canopy, and seedling and sapling characteristics

The study plots ranged in elevation from 157 m to 206 m, had slopes ranging from 27.2 % to

41.7 %, and southeasterly aspects (134°) to almost north-northwestern aspects (296°; **Figure**

4.1). Within these plots, data on 436 stems were collected, including 21 *P. palustris* cored

adjacent to the studied plots that were chosen for their large diameter size. Diameter distribution

for all trees at BSM shows a reverse-j shaped distribution with 493 *P. palustris* stems across all

size classes ranging from 5.0 to 50.0 cm DBH. *Pinus taeda* only occurred between the 5.0 to

15.0 cm DBH classes.   All hardwood species appeared in the 5.0 and 10.0 cm DBH classes, with

A. rubrum having one individual in the 20 cm DBH class and *N. sylvatica* having one individual

in the 10.0 cm DBH class (**Figure 4.2**). Canopy cover consisted either of *P. palustris* (53.6 %)

or an open canopy (45.0 %), with *P. taeda* and *N. sylvatica* hardly contributing to cover, 1.2 %

and 0.2 % respectively (**Figure 4.3**). *Pinus palustris* also had the highest importance values for

both live trees and snags, 76.5 % and 82.7 % respectively, followed by a combination of *P. taeda*

(1.2 % live and 0.7 % snags), and *N. sylvatica* (0.9 % live and 2.5 % snags; **Table 4.1**).

Sassafras albidum (Nutt.) Nees (sassafras) seedlings dominated live seedlings and *N. sylvatica* and *Prunus serotina* Ehrh. (black cherry) saplings dominated live saplings (**Table 4.2**). *Pinus palustris* seedlings and saplings were tallied in the seedling and sapling classes, however, were not the dominants like they were for dead saplings.

Based on DBH, the spatial point pattern analysis for trees at Big Smith Mountain showed that only plot eight had trees that were significantly dispersed than a random distribution along the first three-quarters of the distance, while the other plots leaned toward being dispersed but were not significant (**Figure 4.4**). Since age values existed for some trees in these plots, I also analyzed point patterns using age as a weight and found that only plot one was significantly clustered across the plot, while plot seven was significantly clustered at greater distances, the four other plots show variation between clustering and dispersion, but with no significance (**Figure 4.5**).

3.2. Age distributions, recruitment, and disturbance patterns inferred from annual rings

I determined the ages of 322 trees at BSM based on an individual's innermost tree ring or the pith: 302 live *P. palustris* (203 with no pith, 78 with pith, and 21 from outside of my plots); eight *P. palustris* snags; two fallen *P. palustris*; eight live *P. taeda*, one live *N. sylvatica*, and one live *A. rubrum*. Nine live and three standing dead *P. palustris* could not be dated since their cores were damaged. The oldest tree established in 1669 while the most recent tree established in 2003 both were *Pinus palustris*. All of the *P. taeda* dated between 1987–2000, the *N. sylvatica* dated to 1995, and the *A. rubrum* dated to 1962. The year dating back to the pith or the innermost ring for all live *P. palustris* was compared to DBH and height with *P. palustris* approaching a maximum DBH of 50.0 cm and a maximum height of 25.0 m (**Figure 4.6**). The

131

largest *Pinus palustris* at BSM was 48.2 cm DBH and had an innermost date of 1908, however it

was not the oldest live individual, which was 38.0 cm DBH and dated back to 1802. The

majority of *P. palustris* dated back to the 1860s based on their innermost ring, with only five

individuals dating beyond that decade. On the other end of the spectrum, some *P. palustris*

below 15 cm DBH dated beyond 50 years and older and appeared to be heavily suppressed in the

mid or understory. One individual dates back to 1891 and was only 6.2 m in height and 12.2 cm

in DBH It is important to note that capturing the true age of *P. palustris* at any site, even BSM,

is elusive since this species can persist as a seedling, also termed the grass stage, from 3–20

years or possibly more after germination. As a result, no annual rings are produced and no

height growth is observed (Pessin 1934; Nelson1985; Boyer 1990). Regardless, the age for *P.*

palustris at BSM is age at coring height and is definite since the series per core and per tree at

BSM were crossdated (Fritts 1976). Age-class distributions with five year increments were

developed from my dated samples (n=388) and showed three noticeable peaks for recruitment

occurring in the 1880s (11 tree ha^{-1}), 1940s (33 trees ha^{-1}), and 1990s (30 tree ha^{-1}) (**Figure 4.7**).

Of the 23,606 annual rings measured, 18,174 rings were used to calculate MPGC and MPRG

while developing a site-specific boundary line for BSM, with 17,286 rings indicating no release,

782 annual rings with a release between 20–50% (122 *P. palustris*), and 107 annual rings with a

release greater than 50% (21 *P. palustris*). Disturbance patterns revealed two peaks that

occurred over the history of the site with the majority of releases for BSM occurring from 1985–

1995 and the second peak occurring in 1915, tapering out until 1945 (**Figure 4.8**). The

superposed epoch analysis that was performed on both the 20% and 50% disturbance

chronologies revealed no statistical significance for the events that occurred in proximity to the

study plots (**Figure 4.9**).

A *P. palustris* chronology for BSM originally consisting of 362 cores from 302 individuals was developed however, 76 of the cores running from 1984–2008 were omitted from my release analysis leaving me with 286 *P. palustris* cores from 261 individuals running from 1670–2008. The series intercorrelation for the chronology was 0.500, a mean length series of 82.5 years, a standard deviation of 0.477, and an average mean sensitivity of 0.296.

4. Discussion

4.1. General observations

Two important observations can be made from this study that applies to the current knowledge of *P. palustris*. The first is that historical accounts and recent studies suggest that Piedmont and Upland *P. palustris* woodland communities are located on exposed ridges, upper portions of slopes, and south-facing aspects (Mohr 1901: Varner et al. 2003; Peet 2006; Womack & Carter 2011). This however was not the case at BSM. *Pinus palustris* dominated the tree canopy on all slopes and aspects of BSM, with the exception of the eastern aspect due to the arson fire. *Pinus palustris* did dominate the canopy there at one time (personal communication, Mark M. Tuggle, APC forester and Jimmy Lanier, CRATA executive director) and future observations of the few live, snags, and fallen *P. palustris* as well as recruitment patterns on this aspect would be informative. To lend historical support to my observations at BSM, Reed's (1905) survey and mapping indicates that *P. palustris* was found on multiple aspects and slopes, not just those that were south facing, on tracts of lands in adjacent Coosa County to the east. Reed's survey on 14,562 ha indicated that *P. palustris* dominated the landscape (11,252 ha). *Pinus taeda* and other hardwoods were more dominant along rivers and creeks (1605 ha). While

133

the original forests surveyed by Reed (1905) were harvested by the timber industry in the first quarter of the 20th century and then replaced by second-growth forest, perhaps any remnants of old-growth *P. palustris* that were not cut in addition to the resulting second-growth forests on that property might show similar patterns where *P. palustris* occupies slopes and aspects that are not restricted to the south like at BSM. Contemporary research overlaid on Reed's (1905) old forest survey area needs to be conducted to determine if this still can be observed on the landscape for those sites, however, historical records and mapping from those tracts of land still support my observations at BSM.

The second observation is that individual BSM *P. palustris* show patterns that are contrary to classifying this species as shade-intolerant. *Pinus palustris* has been considered a shade-intolerant due to the dependence of seedlings and saplings needing large canopy gaps with minimized tree species competition for successful recruitment (Wahlenberg 1946; Platt et al. 1988; Palik et al. 1997; Brockway and Outcalt 1998). Individual *P. palustris* at BSM show annual increment patterns, beginning from their pith or innermost date that are indicative of suppression while they are currently in the subcanopy or that they had been suppressed below the canopy at one time, but were now canopy dominants. These suppression patterns spanned a couple of years to over 50 years as can be seen for individuals currently below the canopy when comparing the relationship between age to height and DBH.

To further illustrate this phenomenon, I compared the annual increment patterns of eight *P. palustris*, four individuals below the canopy, < 10 cm DBH, < 10.5 m in height, and with ages ranging from 52–91 years and four individuals that were or are canopy dominants. These four canopy dominants were over 100 years in age and > 40.0 cm DBH (**Figure 4.10**). Three of these individuals were > 20.0 m in height and one, a broken snag, had a height of 8.4 m. All four

subcanopy *P. palustris* exhibited bolting patterns which are attributed to rapid growth during the first few years of this species as a sapling (Pederson et al., 2008). They rarely exceeded beyond 1.0 mm in growth year^{-1} after their individual bolting and maintained low annual incremental growth at a minimum of 52 years for one individual (BSM 400) and at a maximum of 91 years for another (BSM 291). While I was only able to date back to the innermost ring for the four canopy dominants, thereby missing their bolting patterns, the annual increment patterns of two individuals from this group show evidence of suppression in their younger years where annual incremental growth was less than 2 mm year^{-1} for at least 50 years for one individual (BSM 209) and almost 90 years for the other individual (BSM 305). The other two canopy dominants exhibit annual increment patterns suggesting that they could have recruited in open conditions, as their growth appears to show a bolting trend, then decreasing in growth for a couple of years, but then reversing this trend, possibly maintaining a negative exponential growth pattern typical of aging trees. The suppression patterns observed in the four subcanopy *P. palustris* and in the two canopy *P. palustris* are similar to observations for *P. palustris* individuals experiencing suppression from southern Alabama (Meldhal et al. 1999), southwestern Georgia (Pederson et al. 2008), and southeastern Virginia (Bhuta et al. 2008). Annual increment patterns from the Alabama, Georgia, and Virginia sites showed that *P. palustris* could remain in suppressed states for multiple decades until a reduction in overstory competition allowed for individuals to release, especially if they previously resided below the canopy. Evidence from my site and the other three sites in Alabama, Georgia, and Virginia, highlights the importance of rethinking the shade-intolerability of *Pinus palustris* and how annual increment patterns can clarify the ability of a tree species to tolerate shade and thereby competition from adjacent trees.

4.2. Composition

Pinus palustris was the dominant tree species (relative dominance of 97.5 % and an importance value of 76.5 %). While not quantified within the plots, I did observe *Symplocos tinctoria* (L.) L'Hér (common sweetleaf); *Kalmia latifolia* L. (mountain laurel); *Rhus copallinum* var. *latifolia* Engl. (winged sumac); *Vaccinium arboreum* Marsh. (tree sparkleberry); and *Rhododendron minus* Michx. (Piedmont rhododendron) in these plots. These species were below 5.0 cm DBH and I considered them to be part of the shrub layer. I did not make any observations of species in the herbaceous layer. More research is needed to determine the dominance of the observed species in the shrub layer and to identify additional species in both the shrub and herbaceous layer in order to fully define the BSM community. However, based on the tree layer, this community can be considered a *P. palustris* woodland community. Similar tree and shrub composition described at other *P. palustris* woodland communities locally (Golden 1979) and at a broader scale (Peet 2006) are similar to my observations at BSM.

At the local scale, Golden (1979) described communities similar to BSM as xeric uplands with an ericaceous shrub layer with *V.arboreum*, *V. stamineum* L. (deerberry), *V. pallidum* Ait. (Blue Ridge blueberry), *Gaylussacia dumosa* (Andr.) Torr. & Gray (dwarf huckleberry) and *K. latifolia* and a poorly defined herbaceous layer with a thick layer of *P. palustris* needles. The relative dominance of the six *P. palustris* plots surveyed by Golden (1976) indicate that *P. palustris* dominated the canopy (86 %), while *S. albidum* (8 %), *N.sylvatica* (7 %), and *Cornus florida* L. (flowering dogwood; 5 %) had a higher presence in these plots than other canopy trees. At BSM, the relative dominance for *P. palustris* (97.6 %) was slightly higher than the mean of Golden's (1979) survey and there were different species associated with the BMS tree community: *P. taeda* (9.2 %) and *N. sylvatica* (7.3 %), *Diospyros virginiana* L. (persimmon)

(3.4%). While *A. rubrum* was surveyed at BSM, it did not occur in any of the *P. palustris*

communities surveyed by Golden (1979) and was mostly dominant in more mesic communities.

Peet (2006) mentions two woodland communities that are relegated to clayey and rocky

uplands, one in the Atlantic Coastal Plain and Fall-line Sandhills of North and South Carolina

and another described from historical accounts of Mohr (1901) and Harper (1943) in the interior

portion of the Eastern Coastal Plain of Alabama and Georgia. The community described by Peet

(2006) in the Atlantic Coastal Plain and Fall-line Sandhills shares some similarities to BSM, as

K. latifolia forms a dense shrub layer with other shrubs typical of the Piedmont and there is

hardly any herbaceous layer. The community in Alabama and Georgia show some similarities to

BSM with *P. palustris* dominating the tree canopy but sharing it with xeric oaks, *Q. marilandica*

and *Quercus laevis* Walt., a shrub layer of *K. latifolia*, and a poor herbaceous layer. The

difference between BSM and these other communities is that there is an absence of *Q. laevis*,

Aristida stricta Michx. (pineland threeawn) and *V. crassifolium* Andr. (creeping blueberry) as the

ranges of these species do not occur in BSM (Burns & Honkala 1990; Peet 2006). Further

examination of the shrub and herbaceous layer at BSM could aid in determining what makes the

woodland community at BSM unique or similar to these other sites found at both the local and

broader scales.

4.3. Structure, dynamics, and recruitment

The density of *P. palustris* at BSM (428 trees ha^{-1}; excluding *P. palustris* cored outside of the

plot) is higher than what has been documented in the Ridge and Valley (two sites, 298 and 283

trees ha^{-1}; Varner et al. 2003), the Coastal Plain (36 – 395 trees ha^{-1}; Schwarz 1907; Platt et al.

19988; Meldahl et al. 1999), and in the Piedmont in Coosa County (131 – 205 trees ha^{-1}; Reed

1905). There also is a higher occurrence of snags at BSM with 55 trees ha^{-1} compared to less

than 20.0 trees ha^{-1} for all the other sites (Varner et al. 2003). It is not easy to explain why

density at BSM is so high compared to other sites, especially since the historical descriptions

from adjacent Coosa County in the Piedmont show lower densities. As for the higher density of

snags at BSM throughout multiple diameter classes, this could be attributed to the 2007 arson

fire and any other high intensity unrecorded fires that may have killed off *P. palustris* in the past.

The BSM diameter-class distribution is indicative of a reverse-J shaped distribution, a pattern

also seen in the structure for old-growth *P. palustris* at the Wade Tract in the Eastern Coastal

Plain (Platt et al. 1988) and at both Caffee Hill and Red-tail Ridge in the Ridge and Valley

(Varner et al. 2003; **Figure 4.3**). One noticeable difference however between these two old-

growth sites and BSM, is that the larger diameter-class size at BSM tapers out at 50 cm DBH,

while those at Wade Tract, Red-tail Ridge, and Caffey Hill taper out at 55 cm DBH or higher. *P.*

palustris also appears to approach a limit of 50 cm DBH, regardless of age, with even the fallen

P. palustris dating back to 1669 reaching an estimated DBH of 46.3 cm (**Figure 4.6**). Plots

studied by Golden (1979) showed that *P. palustris* existed in diameter size classes $\geq$ 30 cm DBH,

however it is not known whether *P. palustris* diameters went beyond this class or if they were

limited to just the 30 cm DBH class. Gilliam et al. (1993) and Peet (2006) have suggested that

geographical variation in vegetation for *P. palustris* systems can be attributed to soil texture and

soil moisture for the Coastal Plain and soil clay and incident solar radiation in the Piedmont and

Montane Uplands. Whether or not these soil characteristics can be translated to limiting basal

area in *P. palustris*, is unclear, but by examining soil characteristics and nutrients at broad

geographical scales throughout the range of *P. palustris*, patterns might begin to emerge that

could help to explain if these soil characteristics contribute to limiting factors in the distribution of the population at BSM.

The reverse-J shaped distribution of the diameter-class is thought to translate to a reverse-J shaped distribution for age-classes (Olive & Larson 1996). This is not the case at BSM. Continuous recruitment of 5-year age classes has occurred since 1860 with a number of individuals dating back between the 1850s–80s, but a trimodal distribution is apparent suggesting that over the past two centuries *P. palustris* has recruited during three periods (**Figure 4.8**). The three most prominent peaks of recruitment for age cohorts at BSM occurred from the 1860s–1890s, the 1930s–1940s, and the 1990s–2000s. These recruitment peaks match up well with 20% and 50% 5-year release event classes which peak from the 1900s –1920s, the 1930s– 1940s, and the 1990s–2000s (**Figure 4.9**). These pulses can also be seen in the 20% and 50% chronologies developed for BSM (**Figure 4.10**). Incorporating the study of tree rings to determine age and disturbance patterns and tying them into the distribution of age and diameter classes at BSM revealed that the utility of the j-shape diameter distribution to understand age distribution might need re-visiting. At BSM, the j-shape diameter distribution would not be a good indicator of the distribution of age due to the ability of *P. palustris* to maintain itself below the canopy for over 20 years or longer.

4.4. Disturbance History Analysis

Since the SEA did not statistically determine that large-scale natural or human-caused disturbances were associated with recruitment patters at BSM, I can only speculate that the cause of the release patterns at BSM could possibly be attributed to two causes, which are probably intertwined with each other to some degree. The first is associated with climate. Release

patterns of *P. palustris* in southeastern Georgia were significantly correlated with increased

temperature and reduced precipitation and have been reported in other forests (Pederson et al.

2008). The climate-disturbance association at that site could have been responsible for

increasing drought stress, reducing vigor, increasing the occurrence of fire intensity, and thereby

increasing mortality for canopy dominant *P. palustris*. There is probably an underlying

connection between climate and release events at BSM as well which should be investigated

further to determine how climate is associated with BSM release events. Also, local-scale

disturbances related to high intensity arson fires, local meteorological events (such as ice storms

or tornadoes or other high wind events), human caused events (such as small scale selective

harvesting of timber for individuals), or a combination of some of these events occurring

simultaneously (not recorded by humans) might contribute to release patterns at BSM. Similar

befuddlement was observed for Ridge and Valley *P. palustris* communities except that those

communities also had incidences of heartwood decay caused by the fungus *Phellinus (Fomes)*

pini (Brot.) Ames, which could have contributed to recruitment and release patterns there

(Varner et al. 2003). Heartwood decay is a common feature for older *P. palustris* throughout its

range, but only one incidence was noted on an individual dating back to 1669. This same

individual showed evidence of three former cavities created by locally extinct populations of

Picoides borealis (Viellot, 1809), red-cockaded woodpecker. Any other evidence of individuals

with heartwood rot may have been removed from the canopy or the herbaceous layer (fallen

individuals) due to high-intensity fires in the past. The lack of wide-scale disturbance could also

explain why spatial patterns of trees weighted by diameter at breast height or age may not have

been significantly clustered for some plots. Another explanation as to why patterns of clustering

for *P. palustris* at BSM were not present could have to do with the scale of my analysis. My

study plots might not be large enough in scale to capture the spatial patterns that are present at BSM and perhaps a survey that encompasses the whole site might yield the clustering of younger individuals related to recruitment on the BSM landscape. One other important note, is that the fallen *P. palustris* dating back to 1669 was not fully intact at its base. It appeared to have fallen due to fire damage possibly from the 2007 arson fire. I assume prior to it falling over, that a cat face may have been present on the tree due to scarring from past fires or the naval stores industry. If a cat face was present it may have allowed for the susceptibility of the tree to succumb to fire and to have fallen over in the manner in which it was found.

   Pinus palustris recruitment has occurred consistently over the last two centuries, but the last three decades has seen increased recruitment of *P. taeda* and *N. sylvatica,* some as large as 20 cm DBH. Other hardwoods are also recruiting into BSM, as seen in the smaller diameter classes and seedling and sapling layers, while *P. palustris* is barely recruiting in the seedling and sapling layer (**Table 4.2**). Even though *P. palustris* might appear to not be recruiting in these layers, its life history as evidenced in this study and others, suggests, that they might be waiting for the opportunity for release, especially if future low-intensity fires control the amount of hardwoods. Even though the density of dead *P. palustris* saplings was the highest compared to the other saplings they were at heights where it is the most susceptible to fire, 0.6 to 0.9 m (Boyer 1990). At the grass stage or beyond this height *P. palustris* is fire resistant (Boyer 1990). The apical meristem of these saplings must have been subjected to the intense arson fire which may have been burning hot enough to not just damage, but kill them. It would appear that perhaps more emphasis should be placed on managing for fire at BSM in order to reduce hardwood competition and promote *P. palustris*. *Pinus palustris* communities in the Coastal Plain Fall-Line Sandhills have been replaced by more shade-tolerant hardwoods due to the disruption of

pre-Europeans settlement fire regimes (Gilliam and Platt 1999). Before European settlement, the

fire regime in this area of the southeastern U.S. occurred every 4 – 6 years (Frost 2006).

Evidence in support of the historical fire regime at BSM cannot be substantiated because any fire

scarred trees may have been removed from BSM during the arson fire of 2007 and possibly other

subsequent fires (Stambaugh et al. 2011). However, possible evidence for future management

incorporating fire is necessary; as there has been continued recruitment of *P. palustris* over the

past two centuries into the canopy without competition from other tree species, which could

mean, that fire was preventing these other tree species from establishing themselves at this site.

Since the arson fire of 2007, another arson fire in 2010 was reported (personal communication,

Jimmy Lanier, CRATA executive director). The effects of this fire coupled with the intense fire

of 2007 may have helped to reduce recruitment by *P. taeda* and hardwoods at this site.

Appropriate fire management should be implemented to promote low-intensity fires at BSM that

do not affect the canopy catastrophically like the 2007 incident did, as it more than likely

contributed to the mortality of *P. palustris* in all diameter classes for snags at BSM.

An in-depth understanding of canopy trees of this unstudied community has revealed new

insights into the ecology and biogeography of *P. palustris*. I found that longleaf pine was not

just restricted to south-facing slopes and that this particular species of longleaf pine does not

adhere to the general perception that age class mimics diameter class. This research highlights

the importance of conducting research on large tracts of forested land owned and managed by

large corporations. These forested lands have ecological value by contributing in a variety of

ways to the ecological structure and function at a regional or local scale and should be

considered for future research. For example, the corporately-managed Lake Martin area in

Alabama currently contains 3053 ha of forested land of which only 7% are in pine plantations

(Alabama Power Company 2010b). Such areas could serve as corridors or parts of a matrix in a

fragmented landscape and as a resource for ecosystem services at the landscape scale

(Chetkiewicz et al 2006; Nelson et al. 2009).

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Table 4.1. Raw Density, relative density, dominance, relative dominance and relative importance for A) live trees and B) snags at

BSM, Alabama.

Species (live)	Frequency (occurrence plots⁻¹)	Relative Frequency (%)	Density (stems ha⁻¹)	Relative Density (%)	Dominance (m² ha⁻¹)	Relative Dominance (%)	Importance Value
Pinus palustris	1.0	38.1	427.5	94.0	17.0	97.5	76.5
Pinus taeda	0.6	23.8	12.5	2.7	0.2	1.2	9.2
Nyssa sylvatica	0.5	19.0	8.8	1.9	0.2	0.9	7.3
Diospyros virginiana	0.3	9.5	2.5	0.5	0.0	0.1	3.4
Acer rubrum	0.1	4.8	2.5	0.5	0.0	0.3	1.9
Quercus marilandica	0.1	4.8	1.3	0.3	0.0	0.0	1.7
Total	2.6	100	455	100	17.4	100	100

Species (snags)	Frequency (occurrence plots⁻¹)	Relative Frequency (%)	Density (stems ha⁻¹)	Relative Density (%)	Dominance (m² ha⁻¹)	Relative Dominance (%)	Importance Value
Pinus palustris	0.9	63.6	55.0	88	1.7	96.4	82.7
Nyssa sylvatica	0.3	18.2	5.0	8	0.0	2.5	9.6
Pinus taeda	0.1	9.1	1.3	2	0.0	0.7	3.9
Diospyros virginiana	0.1	9.1	1.3	2	0.0	0.3	3.8
Total	1.4	100	62.5	100	1.8	100	100

Table 4.2. Frequency, relative frequency, density, and relative density for seedlings, saplings, and dead saplings at Big Smith Mountain, Alabama.
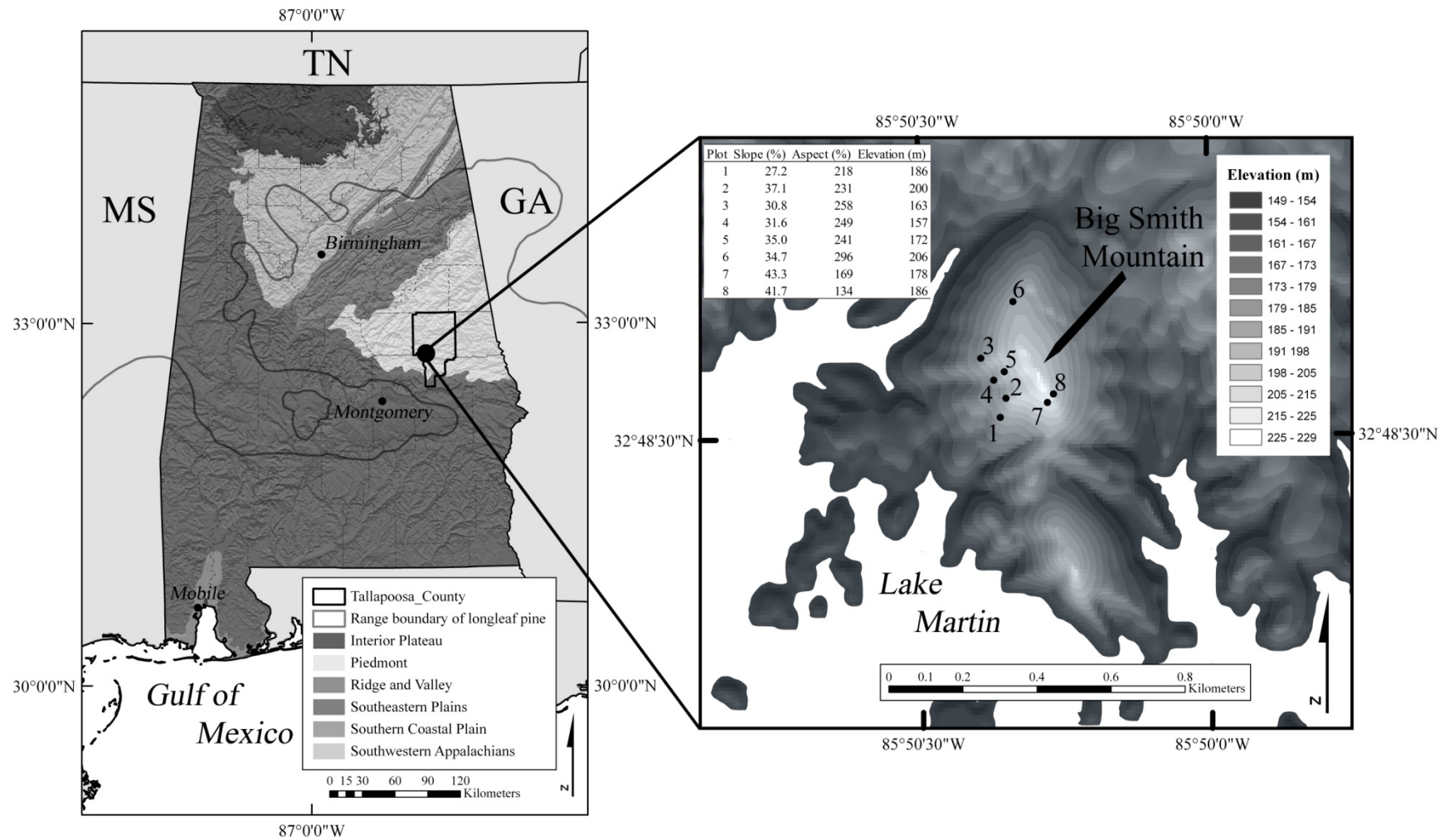
Seedlings	Frequency (occurrence plots^{-1})	Relative Frequency (%)	Density (seedlings ha^{-1})	Relative Density (%)
Sassafras albidum	0.6	16.1	213	35.6
Nyssa sylvatica	0.8	19.4	172	28.8
Diospyros virginiana	0.8	19.4	75	12.6
Quercus marilandica	0.8	19.4	72	12.0
Quercus falcata	0.3	6.5	25	4.2
Pinus palustris	0.4	9.7	22	3.7
Prunus serotina	0.3	6.5	16	2.6
Quercus alba	0.1	3.2	3	0.5
Total	3.9	100.0	597	100

Saplings (live)	Frequency (occurrence plots^{-1})	Relative Frequency (%)	Density (saplings ha^{-1})	Relative Density (%)
Nyssa sylvatica	0.8	22.2	316	47.2
Prunus serotina	0.1	3.7	150	22.4
Diospyros virginiana	0.8	22.2	69	10.3
Pinus palustris	0.6	18.5	63	9.3
Sassafras albidum	0.4	11.1	53	7.9
Quercus falcata	0.3	7.4	6	0.9
Quercus marilandica	0.3	7.4	6	0.9
Acer rubrum	0.1	3.7	3	0.5
Pinus taeda	0.1	3.7	3	0.5
Total	3.4	100	669	100

| Saplings (dead)	Frequency (occurrence plots^{-1})	Relative Frequency (%)	Density (dead saplings ha^{-1})	Relative Density (%)
Pinus palustris	0.4	60.0	34	64.7
Nyssa sylvatica	0.1	20.0	16	29.4
Acer rubrum	0.1	20.0	3	5.9
Total	0.6	100	53	100

Figure 4.1. The location of Big Smith Mountain in the southern-inner Piedmont of Alabama. Numbers on the inset map indicate plot locations.

151
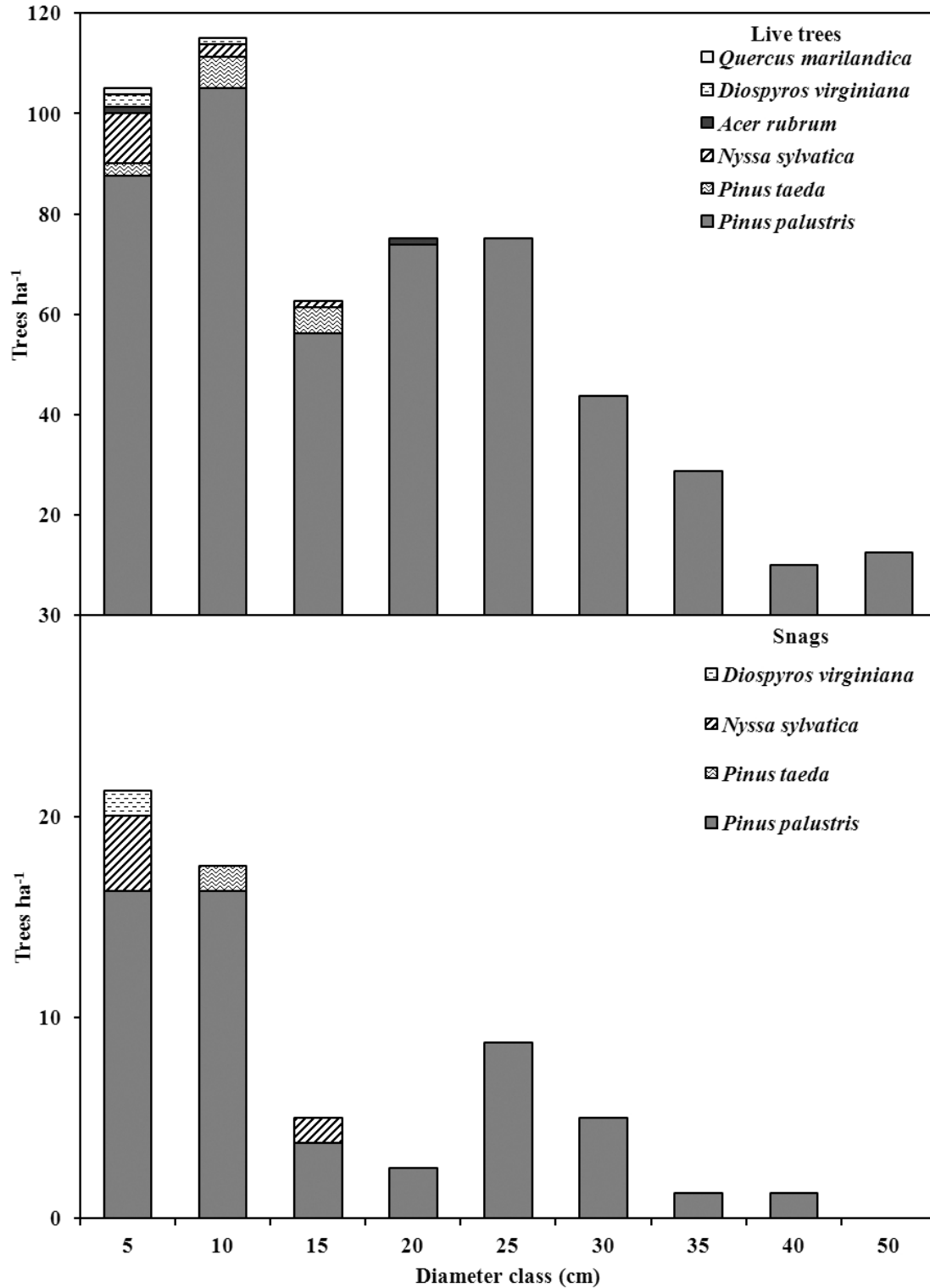
Figure 4.2. Diameter-class distribution for all A) live trees and B) snags observed at eight randomly-located plots in Big Smith Mountain, southern-inner Piedmont, Alabama.
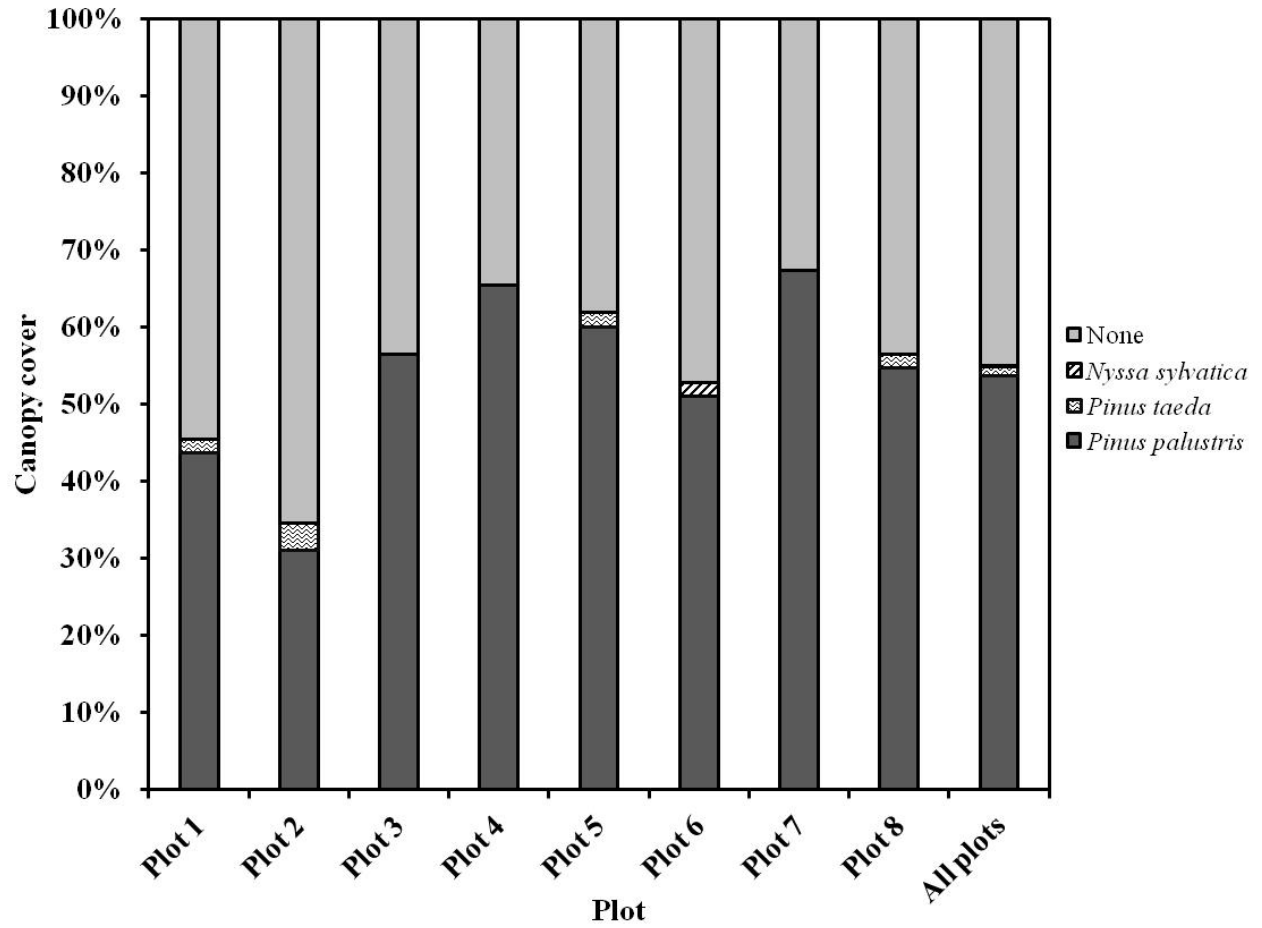
Figure 4.3. Canopy cover for all trees observed in eight random plots at a height of ~1.8 m using a densitometer at Big Smith Mountain, southern-inner Piedmont, Alabama.
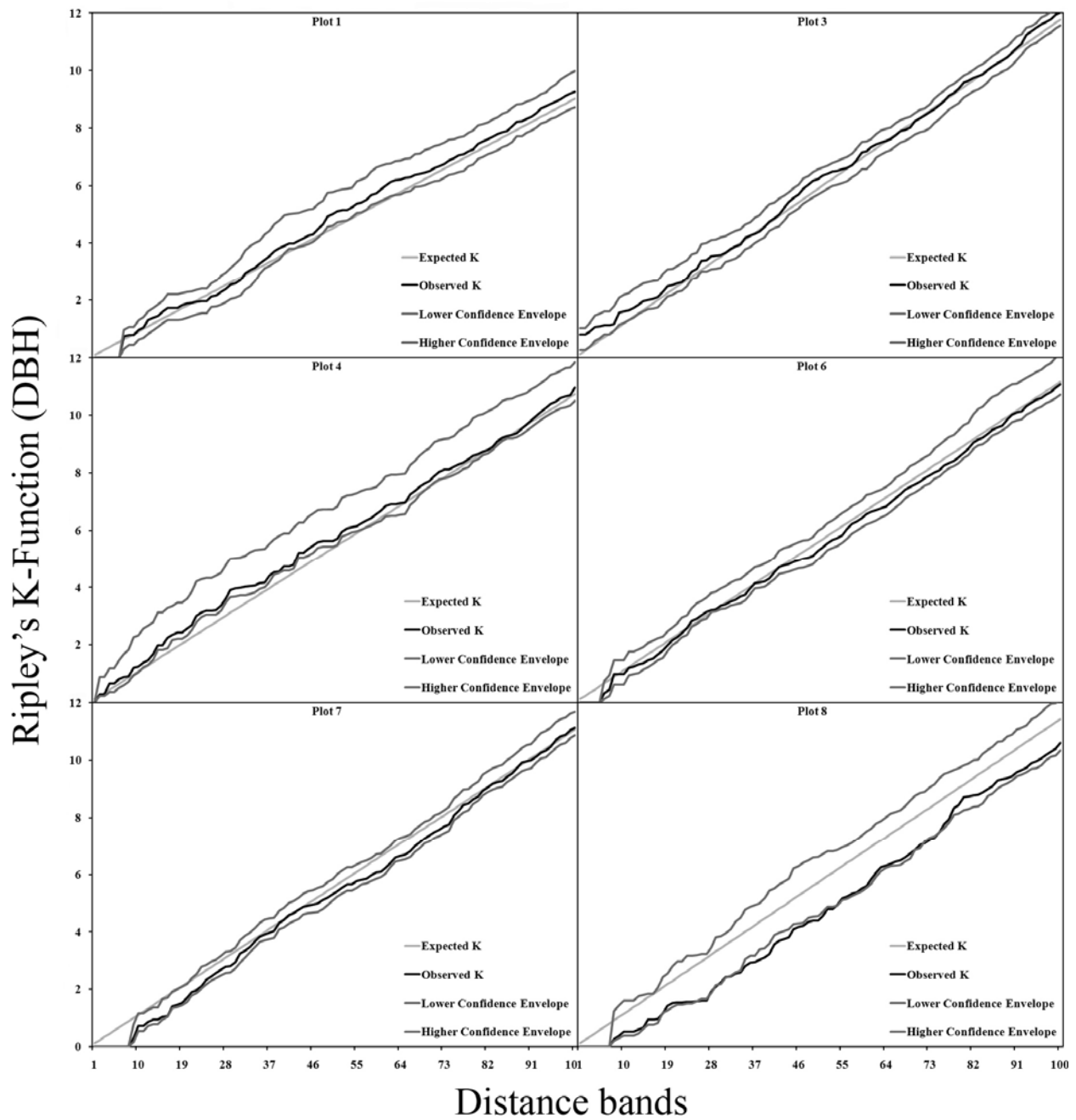
Figure 4.4. Ripley's K function point pattern analysis for all trees weighted by diameter at breast height in plots one, three, six, seven, and eight at Big Smith Mountain, southern-inner Piedmont, Alabama. Plots two and five were not included in this analysis due to GPS collection errors encountered in the field that could not be corrected in laboratory.
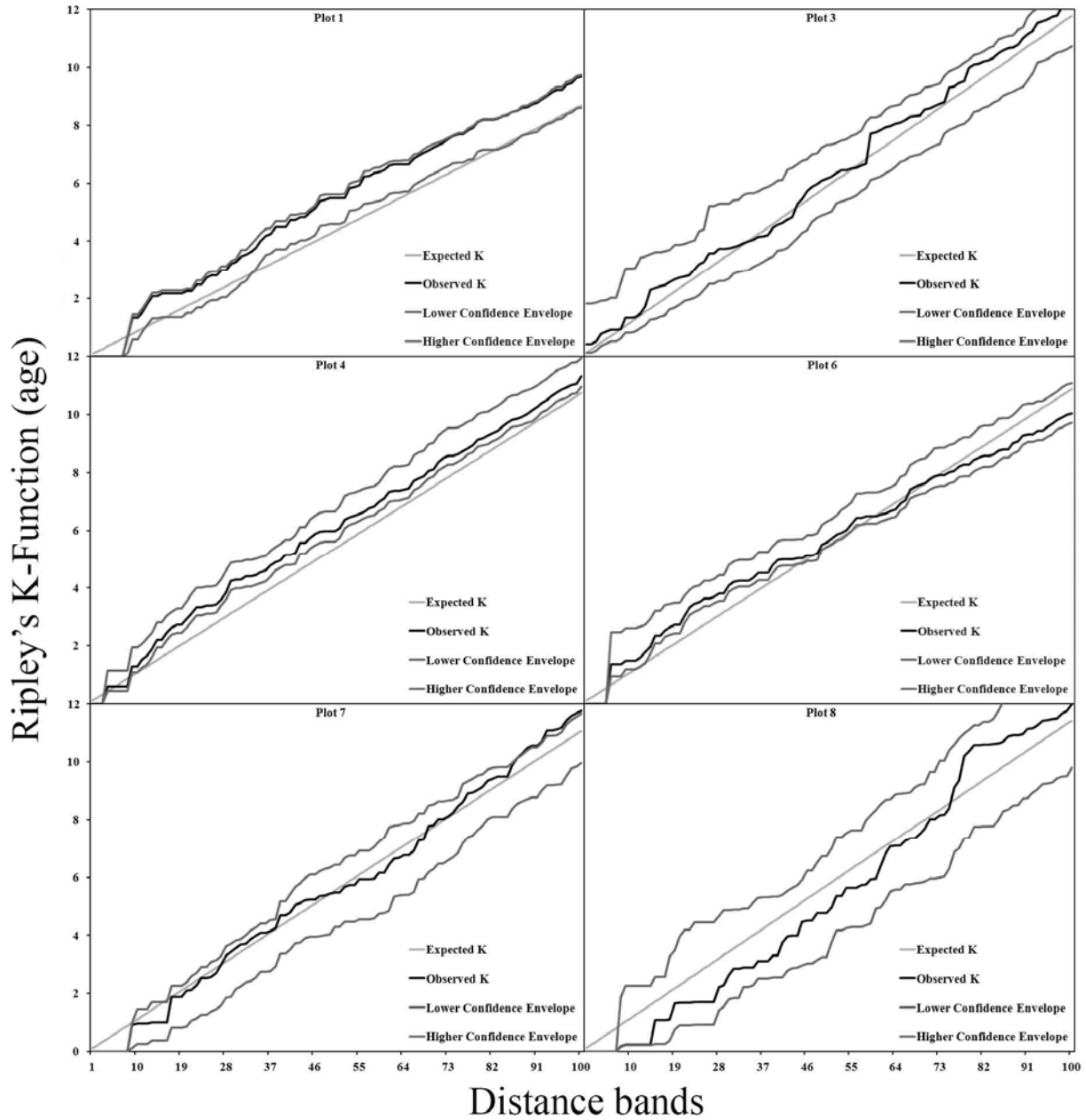
Figure 4.5. Ripley's K function point pattern analysis for all trees weighted by age in plots one, three, six, seven, and eight at Big Smith Mountain, southern-inner Piedmont, Alabama. Plots two and five were not included in this analysis due to GPS collection errors encountered in the field and which could not be corrected in laboratory.

155
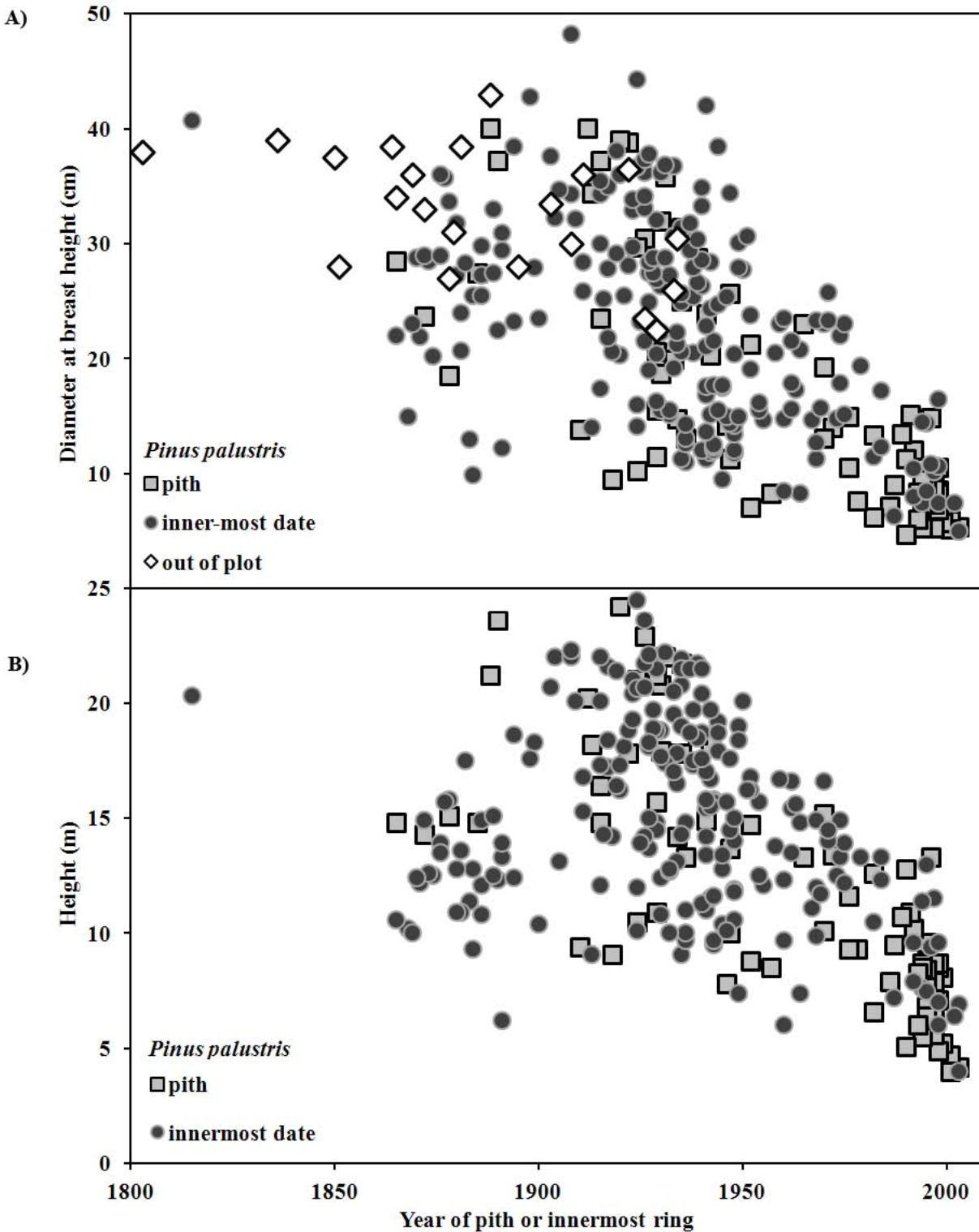
Figure 4.6. Diameter and height relationships between the latest year (innermost ring or pith) for live *Pinus palustris* P. Mill. (longleaf pine), n = 303, derived from cores taken at Big Smith Mountain, southern-inner Piedmont, Alabama.
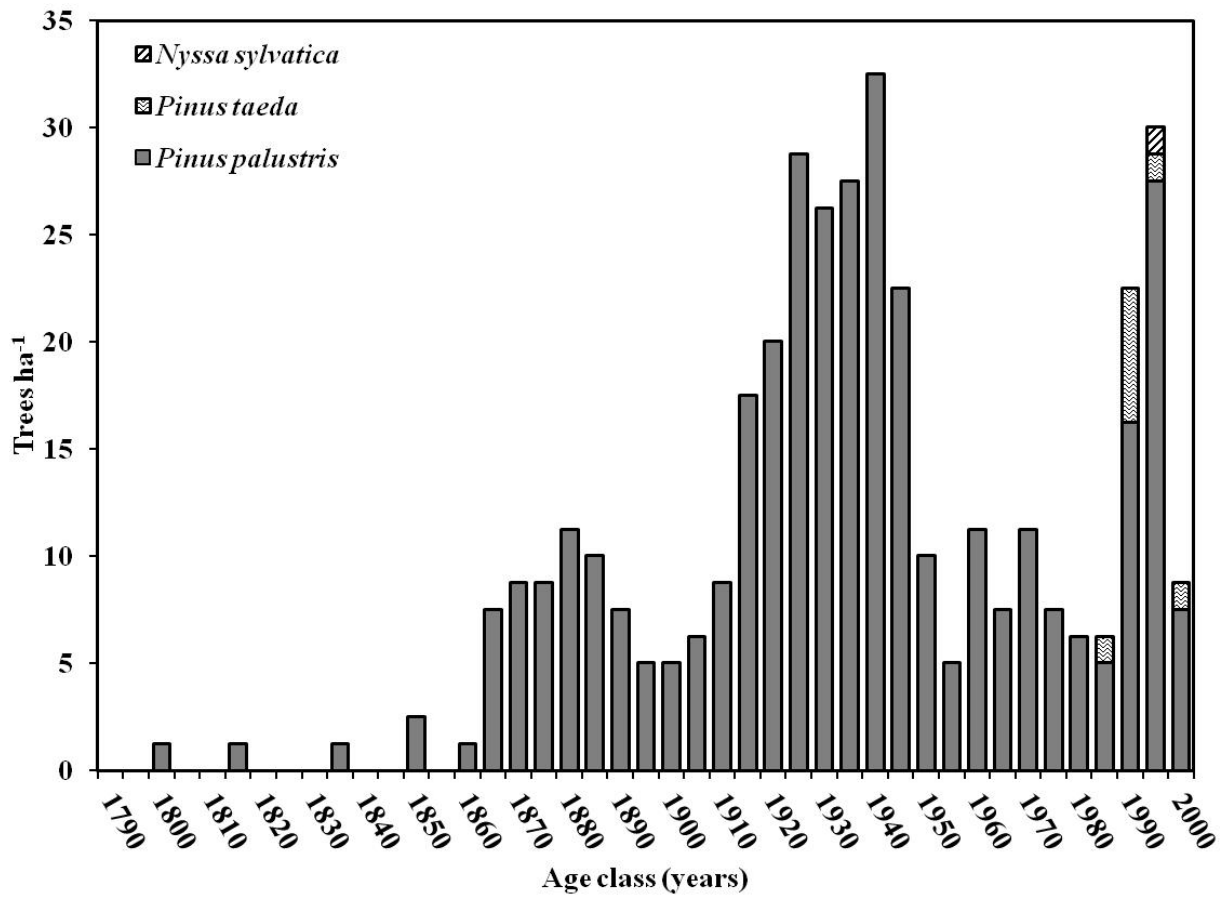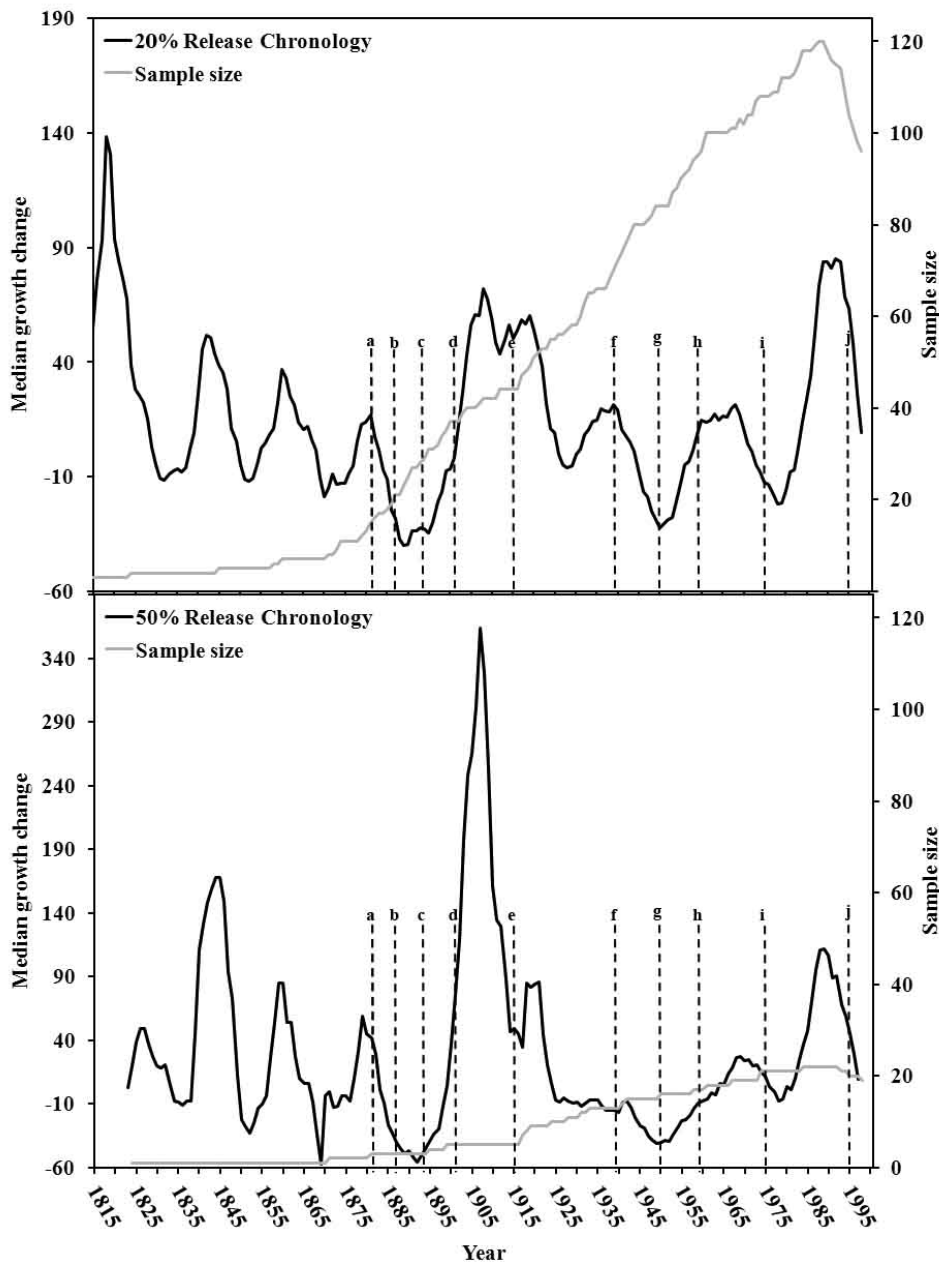
Figure 4.7. Age-class distribution in five-year increments for all living canopy trees observed at eight random plots in Big Smith Mountain, southern-inner Piedmont, Alabama.
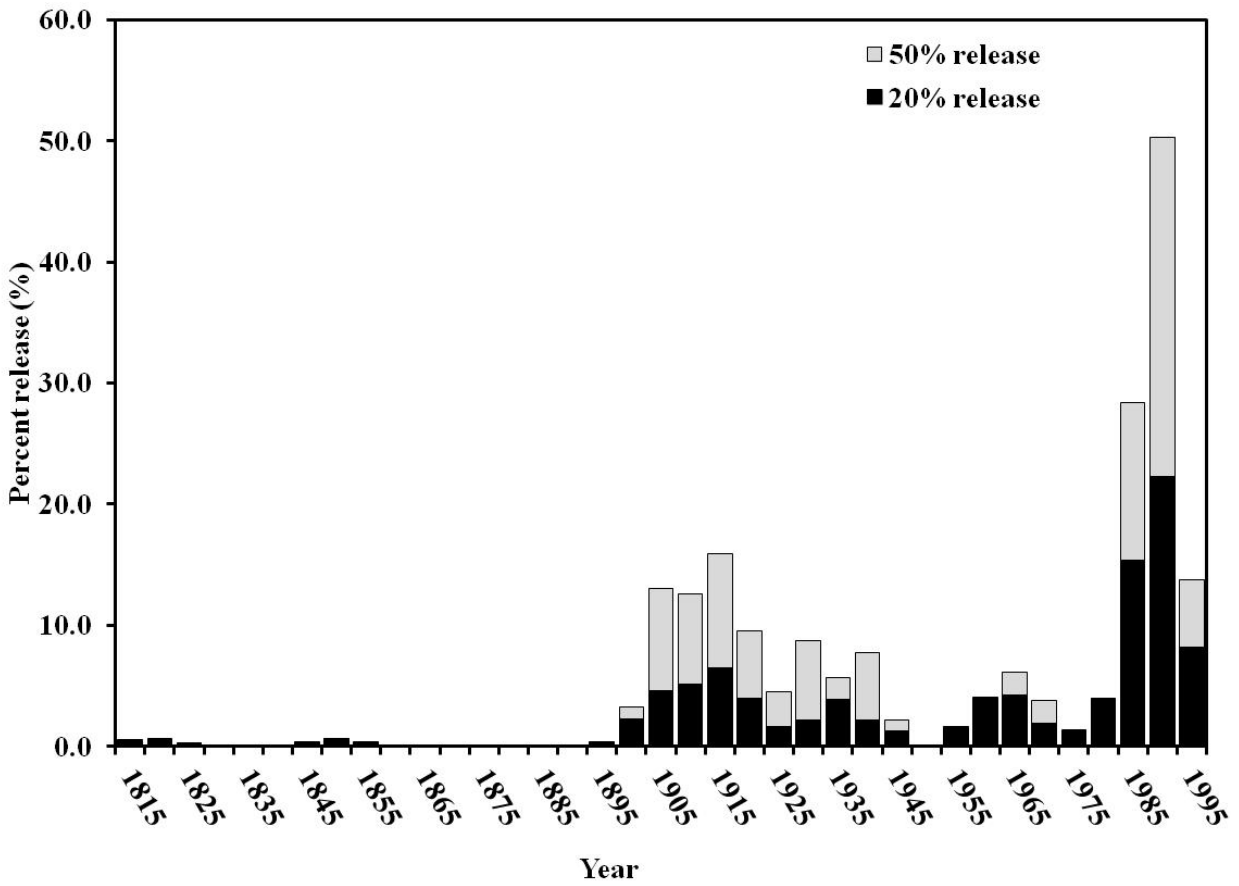
Figure 4.8. Release events (20 % and 50 %) derived from 18,174 *P. palustris* annual rings using boundary-line criteria (Black & Abrams 2003) for Big Smith Mountain, southern-inner Piedmont, Alabama.

Figure 4.9. Release event chronologies (20 % and 50%) derived for Big Smith Mountain, southern-inner Piedmont, Alabama. First vertical y-axis represents the median growth change and the second vertical axis is the sample size. Dashed lines are event years that were used in the superposed epoch analysis and letters above lines refer to the following events: a) 1881 unnamed hurricane category 2; b) 1887 unnamed hurricane, category 2; c) 1893unnamed hurricane, category 4; d) 1902 unnamed hurricane, category 2; e) 1915 unnamed hurricane category 2; f)1939 construction of fire tower; g) 1950 Hurricane Easy, category 3; h) 1959 timber harvest; i)1975 Hurricane Eloise, category 3; j) 1995 Hurricane Opal, category 4.

159
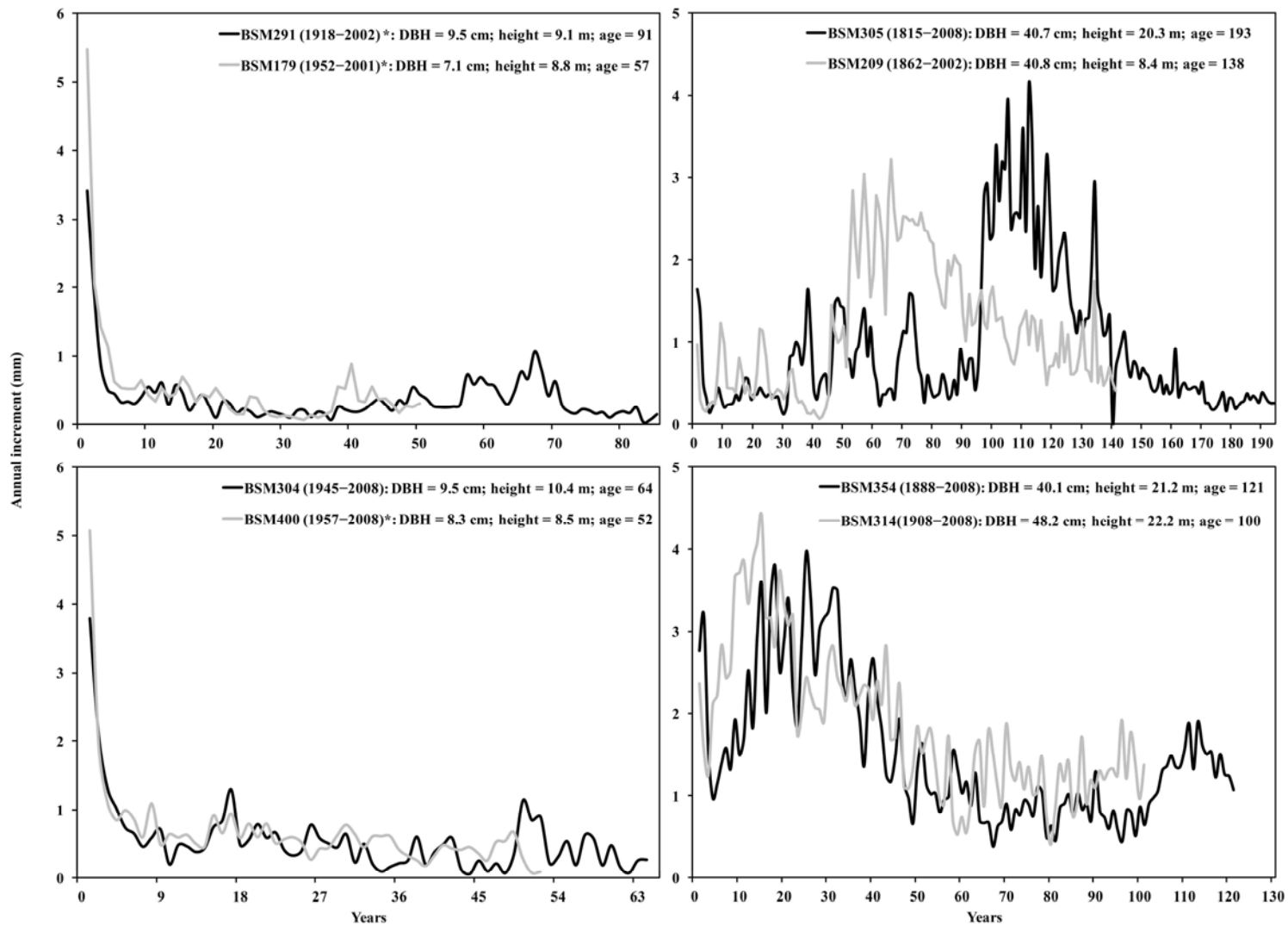
Figure 4.10. Annual increment patterns for eight *P. palustris* at Big Smith Mountain southern-inner Piedmont, Alabama. The left column shows suppressed individuals < 10 cm DBH and the right column shows individuals in the canopy > 40cm DBH, with the exception of BSM 209 which was a broken snag. * indicates that individual was dated back to the pith.

Chapter 5: Conclusions

Many studies focus on longleaf pine (*Pinus palustris* P. Mill.) communities in the Southeastern Plains and Coastal Plain, where it is more abundant at present and serves as a foundation species for many plants and animals. Many fragmented longleaf pine communities exist in second-growth and old-growth forests located in Piedmont and Montane Uplands outside of the Southeastern Plains and Coastal Plain; these have received much less study. This dissertation explored the geographical variation at multiples spatial and temporal scales of longleaf pine communities in the Piedmont and Ridge and Valley. I used a variety of techniques, approaches, and analyses in ecology, dendrochronology, and GIScience to examine the changes in longleaf pine communities across space and time. The objectives for this research were to examine 1) the variation in the tree community along longleaf pine's northern range margin, 2) the relationship between longleaf pine radial growth and climate across two gradients, one from south to north in Alabama and Georgia and then second along the northern range margin of longleaf pine, and 3) the structure, composition, and disturbance dynamics for a Piedmont longleaf pine community in Alabama.

I found a number of differences between longleaf pine communities in the Piedmont and Ridge and Valley compared with their Coastal Plain counterparts. For example at my study sites, Piedmont and Ridge and Valley longleaf pine communities exhibit large variation in tree diversity, are found on less deep soils, and are also mostly relegated to ridges and hills. A few other researchers (Shankman & Wills 1995; Maceina et al. 2000; Varner et al. 2003a; Varner et al. 2003b; Stokes et al. 2010; Womack & Carter 2011) have published similar findings in these ecoregions. One finding that was contrary to prior research is that longleaf pine in my study sites were not restricted to just south-facing slopes and aspects, but occurred on multiple slopes and

aspects (Chapter 2). One possible explanation relates to historical land-use practices. Perhaps, longleaf pine historically occurred on other slope aspects in the Piedmont and Ridge and Valley, but due to impacts from the naval stores and timber industry coupled with agriculture over the last 250 years, the majority of the fragmented longleaf pine communities recently observed are relegated to mostly south facing slopes. Other pines and hardwood species are able to recruit faster than longleaf pine along slopes other than southern facing ones, probably due to the cessation of natural and human-caused fires that occurred more frequently prior to European settlement of these areas.

In terms of the effects of climate on radial growth, I found that drought and precipitation are statistically related to longleaf pine radial growth across all sites, but in the interior portions of its range along its northern range margin, minimum winter temperatures influence the radial growth of longleaf pine. At all elevational, latitudinal, and longitudinal extremes, longleaf pine is influenced almost solely by minimum winter temperatures. Elsewhere throughout my study area, from Alabama to Virginia radial growth is influenced mainly by precipitation and drought (excluding Florida; Chapter 3). Future studies could look for this pattern in other tree species that dominate the southeastern United States. My research is the first to investigate the influence of climate on longleaf pine radial growth across multiple sites at broad scales. Future studies incorporating longleaf pine west of Alabama and to the south in Florida would add to an understanding of the influence of climate throughout longleaf pine's entire range.

In my study of a longleaf pine Piedmont community in Alabama (Chapter 4), I found an old-growth Piedmont longleaf pine community at Big Smith Mountain, Alabama. The longleaf pine community displayed the typical reverse j-shaped diameter distribution for old-growth forests, with few small stems and many large ones. This contrasted greatly from the age-diameter

distribution of the same site, which displayed a trimodal distribution. The differences between these two distributions violate the general assumption that the reverse j-shaped distribution is the same across age classes as it would be across diameter classes. This is evident in some of the longleaf pines that were over 50 years old, but were still less than 10 cm diameter at breast height. Additional studies could determine whether similar patterns are found at other sites. The vicinity of Big Smith Mountain should also be searched thoroughly to determine whether there are other pockets of old-growth trees.

The longleaf pine communities studied for this dissertation, with the exception of one site, were either in the Piedmont and Ridge and Valley. This research provided several insights on the similarities and difference in longleaf pine in Piedmont and Montane Uplands sites versus the more well-studied southern Southeastern Plains and Coastal Plain sites. The output from this research provided substantial data (over 4,000 trees across 56 permanent plots at 10 sites in 5 states) including tree rings, tree morphometrics, and community composition and structure, that can be used in future studies at plot or site level to landscape level. My permanent plots could be resampled in the future to determine changes in recruitment patterns or composition that might reflect climatic or land use changes. This dissertation documented biogeographical patterns within the lesser-known upland longleaf pine systems and provided comparisons between those and systems and communities in the Southeastern Plains and Coastal Plain where longleaf pine ecology is well understood. This work will support decisions of land managers of longleaf pine communities and ecosystems that are part of private and public landholdings in the Piedmont and Montane Uplands by providing them with baseline information on biogeographical patterns and ecological variation in these communities. This knowledge will be important as climates and land use continues to change in landscapes of the southeastern U.S.

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