Uneven-aged Management of Longleaf Pine Forests Using Selection Silviculture

by

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Abstract

Approximately 38 million hectares were dominated by longleaf pine (*Pinus palustris* Mill.) forests in the Southeastern United States prior to European settlement. Frequent disturbances, especially fire, made this species dominant, and also created an uneven-aged, irregular forest structure in the region. However, with the arrival of Europeans, exploitation of longleaf forests began, large areas were cleared, and as a result, about 97% of longleaf forests were lost to agriculture or conversion to other dominant species such as loblolly pine (*Pinus taeda* L.). Although a concern about the restoration of longleaf ecosystems has increased in recent years, practical methods to accomplish this goal are only beginning to be implemented. Beginning in the 1950s, many of the original restoration studies on regeneration of longleaf pine focused on even-aged (EA) silvicultural techniques because these techniques were considered logical and appropriate for use with shade and competition intolerant species such as longleaf pine. Those methods were successful for regenerating stands, but, the unique longleaf ecosystem has not been fully restored by these approaches. Natural uneven-aged (UEA) longleaf pine ecosystems exhibit a rich biodiversity; however, ecological values such as biodiversity, recreation, aesthetics and wildlife are not fully restored by the regular structure created with EA techniques. At the same time, the UEA mosaic of small EA groups that were present in natural longleaf forests suggests that UEA methods should be successful if we can determine the timing and intensity of disturbance. I believe that residual basal area (RBA) may be an important factor in longleaf pine seedling establishment and sapling recruitment into the canopy. Thus, in this study, the effects of varying levels of RBA (9.2, 13.7, and 18.4 m^2 ha^{-1}) on longleaf pine germination, survival, establishment and growth under selection silviculture using single-tree selection based on the Proportional-Basal Area (Pro-B) method were observed. There was a statistically significant relationship between the number of germinants and RBA during the germination period and the following three growing seasons. Mortality of germinants was not affected by RBA during the first two growing seasons following germination. In addition, RBA did not affect either mortality or growth of planted seedlings during the first and second growing seasons. However, RBA influenced the impact of a growing season fire on the survival of germinants and planted seedlings at year two. In the third growing season, RBA negatively affected the size of both germinants and planted seedlings. Survival rate and number of seedlings at the end of third growing season suggest that UEA methods may be successful for regeneration and restoration of longleaf pine forests, and an alternative to EA methods in longleaf pine forests. Moreover, the comparison of RBA and stocking suggests that stocking may be a better indicator when allocating growing space in longleaf pine forests. Additional measurements are needed to determine the efficacy of UEA methods in these forests. Current data aims to broaden our understanding of how overstory density affects seedling germination, growth, and mortality within longleaf pine forests of southeastern USA.

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Table of Contents

List of Tables

List of Figures

CHAPTER I - GENERAL INTRODUCTION

1. Introduction

The focus of even-aged (EA) management has traditionally been on production. Yet recently, more attention has been given to multiple-use objectives such as restoration, aesthetics, wildlife management, water quality, and recreation (Guldin 2006). It has been suggested that uneven-aged (UEA) management techniques can meet multiple-use objectives including restoration of longleaf pine forests (Guldin 1996).

Due to a dramatic decline (by 97%) in longleaf pine (*Pinus palustris* Mill.) acreage since the arrival of Europeans in North America (Boyer 1990), concern about the restoration of longleaf forests has increased in recent years (Brockway and Outcalt 2000). The small fragments that remain throughout its natural range suggest that longleaf pine can be restored (Brockway *et al.* 2005). However, application of practical methods to accomplish this goal is still needed. Successful regeneration of longleaf pine is essential to restore and sustain this unique ecosystem (Brockway *et al.* 2005). EA methods have been successfully used to regenerate existing longleaf stands (Croker and Boyer 1975); however, complete overstory removal at the end of the rotation is known to negatively impact the ecological functions and values of natural longleaf pine ecosystem such as recreation, wildlife, biodiversity and aesthetics (Brockway *et al.* 2006). Shelterwood method seems to be effective to restore the species, but, ecosystem services are episodic due to the complete overstory removal at the end of the rotation. Thus, there is a need for an approach to ensure continuous ecosystem services while producing high quality timber.

Due to continuous forest cover under UEA systems, UEA methods seem to better address ecosystem services of longleaf pine forests. There have been some trials to demonstrate the use of UEA silviculture in these forests. Stoddard-Neel (S-N) approach is one example of successful application of UEA silviculture in longleaf pine ecosystem (Neel *et al*. 2010). S-N system is a method of UEA management, and it is a modified form of single-tree selection system. Aim of this approach is to preserve all services and values of the ecosystem, then determine the amount of timber available to cut. However, S-N method is not quantitative, and it cannot be tested because there is not a defined target residual structure. The S-N approach can only be applied by professional practitioners, and training someone for this approach is time consuming. S-N approach suggests that UEA system works for longleaf pine restoration, however, it is not clear "how", "at what stand density", and "with how many seedlings". The level of density at which seedling development is considered acceptable under UEA silviculture is still questionable. In this study, it was aimed to eventually answer these questions by observing the influence of stand density on the germination, survival, establishment and growth of longleaf pine.

Another problem with the use UEA methods in longleaf pine forests is the difficulties with the UEA regulation methods. The most common regulation methods, volume guiding diameter limit (V-GDL) and BDq methods (Farrar 1996) are easy to quantify and calculate, but, they require personal skills to apply on the field. In addition, it is difficult to mark the stand in one pass using these approaches. To our knowledge, there have not been extensive criteria suggested for the successful regeneration of longleaf pine forests under VGDL or BDq approaches. In this study, we also present an easy and scientific tree-marking approach, Proportional-Basal Area (Pro-B) to implement UEA system in longleaf pine forests (Brockway *et al*. 2014). Pro-B is based on structural control, allows marking stands in one pass, and does not require any field experience (Brockway *et al*. 2014).

Because regeneration of longleaf pine may be hindered by its intolerance to shade and competition (Croker and Boyer 1975), residual basal area (RBA) seems to be an important factor in longleaf pine germination and establishment. Three levels of RBA (9.2, 13.8, and 18.4 m^2 ha^{-1}) were applied across the Escambia Experimental Forest, located in Brewton, AL to assess the effects of varying levels of stand densities on longleaf pine germination, survival, establishment, and growth as well as the effects of RBA on the growth and survival of planted seedlings under single-tree selection silviculture based on the Pro-B method.

Levels of RBA were selected to contrast this study to previous studies that demonstrate regeneration of longleaf pine under varying stand densities (Croker and Boyer 1975, Boyer 1979, Brockway *et al*. 2014). RBA suggested for shelterwood method ranges from 6.9 to 9.2 m^2 ha^{-1} (from 30 to 40 ft^2 ac^{-1}) because seed production usually peaks within this range of stand density (Croker and Boyer 1975, Boyer 1979), and lower densities may be problematic due to unsufficient amount of needle fall for prescribed fire and inadequate number of seed production under lower densities. For this reason, we selected 9.2 m^2 ha^{-1} (40 ft^2 ac^{-1}) of RBA, the upper limit suggested for shelterwood, as our lowest stand density. In addition, Brockway *et al*. (2014) monitored development of longleaf pine seedlings under 11.5 m^2 ha^{-1} (50 ft^2 ac^{-1}) of RBA, and found that development of longleaf seedlings under this stand density was successful. They stated that they selected this basal area to reflect relative intolerance of longleaf pine. We selected 13.8 m^2 ha^{-1} (60 ft^2 ac^{-1}) of RBA as our mid-level stand density, relatively higher than that observed by Brockway *et al*. (2014). Finally, we chose 18.4 m^2 ha^{-1} (80 ft^2 ac^{-1}) of RBA as our high level stand density in order to see how dense a longleaf stand can be managed to get adequate number of well-developed seedlings under selection silviculture.

In addition to stand density, fire is also important for longleaf pine restoration (Brockway and Outcalt 2000). Longleaf pine is very tolerant of fire (Boyer 1974; Brockway *et al.* 2006). Fire prepares a seedbed for longleaf pine seedlings, facilitates germination by exposing the mineral soil (Boyer and White 1990), decreases the competition of longleaf seedlings with other species (Heyward 1939), reduces the risk of brown-spot needle blight disease (Chapman 1932) and reduces the risk of wildfire. Periodic burning is also necessary to restore groundcover and wildlife communities (Brockway and Outcalt 2000). In this study, it was also intended to observe influence of stand density on the impact of prescribed fire under UEA system.

The goal of the research in this dissertation was to explore the efficacy and applicability of UEA management in longleaf pine ecosystems. The primary objectives of this study were to;

1. Assess the effects of stand density on longleaf pine germination, survival, establishment, and growth,
2. Determine the impacts of stands density on the growth and survival of longleaf pine seedlings planted under canopy,
3. Determine the influence of stand density on the impacts of prescribed fire on the survival of longleaf pine germinants and planted seedlings,
4. Create a Gingrich style stocking chart for longleaf pine forests,
5. Compare two measures of stand density, RBA and stocking, on growing space allocation in longleaf pine forests.

2. General Outline

This dissertation is divided into two chapters (Chapters 3, 4,) that address the natural regeneration of longleaf pine under varying levels of stand densities. The second chapter serves as a literature review covering the topics in chapters 3-4. It reviews the biology, ecology, and management of longleaf pine forests as well as the importance of fire in this ecosystem.

Chapter 3 documents the relationships between RBA and germination of longleaf pine seedlings, and the influence of a growing season prescribed fire on germination success. Survival of germinants following three growing seasons, and following a dormant season prescribed fire are presented in this chapter. Influence of stand density on the size of germinants was also examined. In addition to natural regeneration, this chapter also analyzes the relationships between RBA and survival of planted seedlings, and between RBA and growth of planted seedlings under varying densities. Since cone production of longleaf pine is sporadic, seedlings were planted under varying levels of stand density in the event that natural regeneration was poor or failed during 2011-2012. This chapter also documents the influence of stand density on the impact of prescribed burning on the survival of planted seedlings. Finally, this chapter discusses the efficacy and the applicability of UEA methods in longleaf pine forests.

Chapter 4 presents a Gingrich style stocking chart (Gingrich 1967) created for longleaf pine forests. Given the importance of stand density on the regeneration success and growth of longleaf pine, we believe that a stocking chart would be a useful silvicultural tool for this tree species. The chapter documents the approaches and models used to develop the stocking chart. The chart graphically represents average maximum density (A-line), and minimum density of full site occupancy (B-line). Furthermore, a comparison of RBA and stocking is presented to determine which one is a better descriptor in growing space allocating for regeneration of longleaf pine forests, and stand growth.

Chapter 5 synthesizes the results presented in the two main chapters of the dissertation. Suggestions for the future studies and management implications are discussed in order to better address the efficacy of UEA management methods in longleaf pine forests.

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CHAPTER II - LITERATURE REVIEW

1. Overview

Longleaf pine (*Pinus palustris* Mill.) is one of the most important tree species in the United States because these forests exhibit a rich species diversity (Peet 2006), often containing more than 40 vascular plant species in 1 m^2 (Walker and Peet 1983), provide high quality wood production, and produce wild game and forage grasses (Franklin 1997). Longleaf pine forests also provide high quality wildlife habitat and many animal species depend on the longleaf pine ecosystem exclusively (Brockway *et al.* 2005a). Compared to other southern pines, longleaf pine is more resistant to fire, disease, and insects (Croker and Boyer 1975; Boyer 1999).

Longleaf pine forests occupied 38 million hectares in the southeastern United States prior to European settlement (Frost 1993). Frequent fires caused by lightning strikes made longleaf pine the dominant tree species in the South. In addition, these forests were frequently exposed to fires set by Native Americans to manipulate their environment (Carroll *et al.* 2002). Sometimes fires were not extinguished until they were stopped by streams or rain (Croker 1987). Use of widespread fire by Native Americans also favored longleaf pine forests across the South (Croker 1987). After European settlement, settlers continued to use fire to clear larger areas for homes, maintain habitat for game, and to improve forage quality for cattle grazing (Brockway *et al.* 2005a).

Exploitation of longleaf forests began with naval stores, and continued with widespread lumbering by Europeans (Outcalt 2000), starting in the Atlantic Coast and progressing from the

Carolinas to Texas (Wahlenberg 1946). Longleaf pine was the preferred tree species for naval stores production as well as lumber for home building (Wahlenberg 1946). With the beginning of the railroad era in the late 1800's and early 1900's, vast acreages of longleaf timberland was accessed and old-growth trees were heavily cut, large areas were cleared, and second growth trees were excessively turpentined (Wahlenberg 1946). The heavy cutting in longleaf peaked in 1907 (Wahlenberg 1946). Little thought was given to regenerating longleaf trees; few and only small trees were left on sites (Croker 1987). Since the longleaf forest covered vast areas and appeared to be well-adapted to the southern region, it was assumed that this tree species would replace itself on cutover areas, but this usually did not happen (Outcalt 2000). Irregular seed production, poor seed dispersion due to large and heavy seeds, and seed predation, were reasons for failure in re-establishment on the cutover areas. In addition, hogs brought by the settlers became a serious menace for longleaf pine seedlings (Croker 1987). To make matters worse, exclusion of fire during 1920's resulted in the invasion of hardwoods and other pine species, such as loblolly (*Pinus taeda L.*) and slash pine (*Pinus elliottii* Engelm.) into the ecosystem.

Conversion to non-forest uses (i.e., urban development, industrial, or agriculture), succession to hardwoods, establishment of plantations, and interruption of natural fire regimes are just some of the reasons for the substantial decline of longleaf pine (Brockway *et al.* 2005b). As a result, across much of its native range, hardwoods and other pines became dominant on longleaf areas (Croker and Boyer 1975; Outcalt 2000). Less than 1.6 million hectares dominated by longleaf pine area remained as of 1985 (Boyer 1990a).

Longleaf pine is now considered an ecosystem at high risk in the USA (Frost 2006). Due to its economic, ecological, and social values, there has been a growing concern about restoration of the remaining longleaf pine ecosystems (Brockway and Outcalt 2000; Guldin 2006). Given that many small segments still exist throughout its natural range, it has been suggested that longleaf pine can be successfully restored (Brockway *et al.* 2005a).

2. Regeneration

Regeneration success can be achieved by understanding the germination and establishment processes of longleaf pine (Brockway *et al.* 2006). Longleaf pine's biology, seed production, seed dispersal, seedling development, competition with other species, grass-stage, initiation of height growth, and interaction with fire must be taken into account. In comparison to other pine species, longleaf pine has larger cones and seeds (Wahlenberg 1946). Good seed crops for longleaf pine occur at irregular 5 to 7 year intervals (Wahlenberg 1946). Cone production decreases with increasing stand basal area (Croker and Boyer 1975); open-grown trees with large and well-formed crowns and with at least 25 cm DBH are better at producing cones (Boyer 1990a). At low stand density (basal area between 6.9-9.2 m^2 ha^{-1}); a higher number of cones are generally obtained (Boyer 1990a).

Dispersion of seeds starts in late October, and due to large and heavy seeds of longleaf pine trees, the dispersal distance is limited and usually not more than 30 meters (Wahlenberg 1946; Croker and Boyer 1975). Unlike other southern pines, germination occurs within a week after the seeds contact the ground and they do not remain viable beyond that time (Croker and Boyer 1975; Boyer 1990a). New germinants spend most of their energy for root growth (Brockway *et al.* 2006). Top killed seedlings may sprout from the root-collar (Brockway *et al.* 2006).

Longleaf pine has a unique and distinctive development phase called the "grass stage". In this stage, a young longleaf pine seedling is stemless, without height growth, and resembles a clump of grass rather than a tree (Brockway *et al.* 2006). During the grass stage, longleaf seedlings cannot compete with hardwoods and other woody plants. In addition, they may be killed and damaged by hogs and heavy grazing, and are more vulnerable to brown-spot needle blight (Croker and Boyer 1975). Grass-stage may last up to 20 years (Croker and Boyer 1975). During this period, seedlings use most of their energy to develop their root system (Brockway *et al*. 2006), and carbohydrate reserved in the root system support the bolting from grass stage when they start height growth (Keeley and Zedler 1998).

During the seedling stage, longleaf pine grows very slowly under an overstory canopy and growth rates decrease with increasing overstory density (Boyer 1993b). The suppressing effect is greater if the overstory trees are hardwoods (Smith 1962). Height growth of seedlings can be further delayed by brown-spot needle blight as well (Brockway *et al.* 2006). Due to the intolerance to competition, increasing distance from adult trees positively influences the growth rate of seedlings (Brockway *et al.* 2006).

Recruitment of longleaf pine seedlings refers to the time they reach their DBH (1.4 m above the ground) because when they reach their DBH, seedlings begin rapid height growth, and recruit into the overstory soon after (Boyer 1990a). When the root-collar diameter (RCD) reaches about 2.5 cm, seedlings usually bolt from grass stage, and attain their breast height and start recruitment (Boyer 1990a). Longleaf pine usually reaches breast height in 4.5-13 years following germination (Wahlenberg 1946). Initiation of height growth of longleaf seedlings is typically associated with disturbances that reduce overstory density.

The degree of tolerance of longleaf pine to shade has been questionable (Samuelson and Stokes 2012). Longleaf pine has been classified as shade intolerant species (Boyer 1990). However, longleaf pine seedlings may survive under shaded conditions for a prolonged time during grass stage (Croker and Boyer 1975). It has been suggested that longleaf pine is moderately tolerant to shade when young, and they become more intolerant of shade with increasing age (Bhuta *et al.* 2008). Samuelson and Stokes (2012) observed longleaf pine's leaf physiological plasticity to light, and found that longleaf pine shows a degree of plasticity when young. For the successful regeneration of longleaf pine, it is important to understand response of longleaf pine seedlings under varying light availability.

3. Ecology of Longleaf Pine

Most of the Atlantic and Gulf Coastal Plains from southeastern Virginia to eastern Texas are included in the extensive natural range of longleaf pine (Croker and Boyer 1975; Boyer 1990a) (Figure 2.1). The reason for this wide distribution is its adaptation to frequent fire (Chapman 1932). Longleaf is found on a variety of sites ranging from wet poorly drained flatwoods to xeric sandhills and mesic uplands (Boyer 1990a). Within its natural range, average annual rainfall is between 115 and 162 cm while the average annual temperature is between 17 and 21 ^{0}C.

Longleaf pine tree can grow on dry and poor soils with low organic matter (Wahlenberg 1946). Sandy, acid and infertile soils are prevalent across the natural range (Croker and Boyer 1975). Wahlenberg (1946) suggests that this is not a preference, but a necessity because more aggressive, invasive, and competitive species outcompete longleaf pine on more fertile and better sites. Ultisols, entisols, and spodosols are three important soil orders within the natural range of longleaf pine (Boyer 1990a). Flat to rolling topography is typical.

Common ground cover in longleaf pine in the Coastal Plain consists of bluestem (*Andropogon* spp.), panicum (*Panicum* spp.), and wiregrass (*Aristida stricta*) (Boyer 1990a). Like longleaf pine, these plants grow on sandy soils (Croker 1987). They are flammable, and facilitate the ignition and spread of fire (Platt *et al.* 1988).

4. Importance of fire

The Southern USA has been subjected to frequent fires ignited by lightning strikes (Komarek 1974). In addition, Native Americans regularly used fire to manage their environment in the region (Van Lear *et al.* 2005). Longleaf pine developed adaptations to survive in this ecosystem (Landers 1991).

Prescribed fire is commonly used to manage longleaf pine (Heyward 1939). Germination of longleaf seed requires exposed mineral soil (Boyer and White 1990), and, frequent fire is a common tool used to remove the litter layer that is detrimental to germination (Bruce 1951; Boyer 1990b; Brockway *et al.* 2006). In addition, recurring fires in longleaf ecosystems keep the hardwoods out, or limit them to an acceptable number (Heyward 1939), consequently increase growth of seedlings by reducing competition.

Since longleaf seedlings do not have stem and cambium above ground while they are in the grass-stage, these are not directly exposed to surface fire (Brockway *et al.* 2005). During this period, the first 5-13 years following germination, they concentrate their growth in the root system. This stored energy in the taproot facilitates recovery after fire (Chapman 1932). Longleaf seedlings become resistant to fire within a year of germination. In addition, the large needles protect the terminal bud from fire (Brockway *et al.* 2006). However, Boyer (1963) suggests that fire may be at least partly responsible for mortality of seedlings in some cases. Fire-caused mortality is higher when seedlings are newly germinated, and during the initial phase of height growth while the terminal bud is in the flaming zone during fire (Brockway *et al.* 2006).

Longleaf pine seedlings may be seriously weakened and consequently killed by brown-spot needle blight disease while they are in grass stage. The disease caused by the fungus *Mycosphaerella dearnessii* (syn. *Scirrhia acicula*) is common within the natural range of longleaf pine. The fungus is known to be of American origin (Phelps *et al*. 1978). The disease emerges where the moisture level is high. Thus, in denser understories, neighboring species and grasses surrounding longleaf seedlings trap more moisture and dew, facilitate infection, and make longleaf seedlings more susceptible to the disease. Prescribed burning reduces the moisture level by removing the surrounding vegetation. In addition, burning is one of the most practical methods to save infected seedlings. Infected needles are destroyed by fire without damaging seedlings (Chapman 1932).

Growing season burning is more effective than dormant season burning to discourage the invasion of hardwoods and other woody plants (Bruce 1951; Brockway *et al.* 2005b). Comparing summer and winter burns, Bruce (1951) stated that winter fires killed less longleaf pine of all sizes than did summer burnings. However, dormant season burning is safer to conduct. In extreme weather conditions, such as high temperature or low relative humidity, fires generate greater heat and cause much more damage to residual stems, especially in the case of where a litter layer has accumulated for several years (Heyward 1939). Woody plants often re-sprout following fire and more sprouting occurs following dormant season burning compared to growing season burning (Drewa *et al.* 2002). Season of fire may influence understory species composition. A growing season fire eliminates more and larger hardwoods and woody plants resulting in an understory dominated by grasses and forbs. But, following a dormant season fire, hardwoods and woody plants usually re-sprout and dominate the understory.

5. Regeneration methods

Longleaf pine exists in an environment that is subject to frequent disturbances such as tropical storms, lightning, insects, and diseases that create canopy gaps (Engstorm *et al.* 2001). Thus, most natural longleaf pine forests are an uneven-aged (UEA) mosaic of even-aged (EA) groups distributed across the landscape (Brockway and Outcalt 1998). Longleaf seedlings occupy growing space created after one or several mature trees are killed by lightning strike, insects, diseases or storms (Wahlenberg 1946).

Regeneration methods have been prescribed to mimic natural disturbance regimes in longleaf pine ecosystems, but these approaches have changed through time. In the early 1900s, the most common and practicable regeneration method was the diameter limit cut. Diameter limits of 35-41 cm (14-16 inches) were usually recommended by the U.S. Forest Service (Schwarz 1907). Older and younger trees were separated, then, all or most of the older trees above a diameter limit were cut, and remaining trees were left until they reached similar sizes (Mohr 1897; Schwarz 1907). By the mid-1900s, Wahlenberg (1946) suggested leaving 8-10 seed trees per hectare and cutting the rest as the best system to regenerate longleaf pine stands. However, he believed that further studies were needed to develop definite recommendations. In addition, Wahlenberg (1946) also indicated that selection, even small clearings, were not satisfactory for longleaf regeneration.

Beginning in the 1950s, many of the original studies on restoration and regeneration of longleaf pine focused on even-aged silvicultural techniques (Croker 1956; Croker and Boyer 1975; Boyer 1979; Boyer 1993a; Boyer 1993b), because these techniques were considered logical and appropriate for use with competition intolerant species such as longleaf pine. Those studies suggested shelterwood methods to successfully regenerate this species (Croker and Boyer 1975) and allow for continued production of high quality timber. However, the unique ecological attributes of the longleaf pine ecosystem including rich animal and plant biodiversity, recreation, wildlife and aesthetics may be better suited to less disruptive silvicultural systems (Brockway and Outcalt 1998). Shelterwood is still the most commonly used regeneration method in longleaf pine forests, but, it has been suggested that uneven-aged may be more appropriate than even-aged methods for the restoration of the rich animal and understory plant diversity in the longleaf pine ecosystem (Engstrom *et al.* 1996; Brockway and Outcalt 1998; McGuire 2001; Brockway *et al.* 2005). For this reason, interest about the use of uneven-aged silvicultural methods in longleaf pine forests has recently increased (Gagnon *et al.* 2003).

5.1. Even-aged management

In EA management, one age class and subsequently a single canopy tier are usually maintained in the vertical canopy profile through time. EA systems are managed based on a rotation (Baker *et al.* 1996); a start and end point in time are defined (Farrar 1996). A normal distribution (bell-shaped curve) of diameters is usually present in mature EA stands (Farrar 1996). Due to its intolerance to competition, infrequent cone crops, poor seed dispersal, and slow seedling growth, longleaf pine forests were commonly managed under EA management techniques including clearcutting, shelterwood, and seed-tree (Farrar 1996).

Clearcutting: In clearcutting, all overstory and midstory trees are removed on the area in one entry. The clearcutting method may be suitable when a stand is damaged by insects, disease, and fire, or when a stand is currently lacking longleaf pine and composed of undesired species (Brockway *et al.* 2006). In such a situation, artificial regeneration (planting of seedlings) is required following the harvest where there is no seed source. This method is not usually suggested to regenerate existing longleaf forests that are in good condition (Brockway *et al.* 2006). Longleaf pine is intolerant of competition, but, regeneration of longleaf pine does not require complete canopy removal (Brockway and Outcalt 1998). Strip or spot clearcuts may be more effective due to the short dispersal distance of large longleaf pine seeds. In addition, invasion of hardwoods and other pines after clearcutting may be problem in longleaf pine ecosystems (Brockway and Lewis 2003). The clearcut area should be within 30 m of a seed source (Boyer 1993b).

Artificial regeneration is another option to regenerate longleaf pine stands following clearcutting. The use of artificial regeneration to reforest longleaf areas was uncommon in the past due to problems such as severe competing vegetation, slow height growth, and poor survival capability of bare root seedlings (Barnett 2002; Larson 2002). Due, in part, to these difficulties, most longleaf stands were converted to other pine species (Hainds 2002). Recently, an increase in the production of containerized longleaf seedlings (Barnett 2001) and the development of planting recommendations that have greatly increased early survival may cause an increase in plantation area of longleaf pine as well. Clearcutting drastically alters forest structure following harvest which may sometimes impair wildlife habitat and aesthetics (Brockway and Lewis 2003). In addition, its economic feasibility may be questionable due to expenses associated with site preparation and tree planting, but this may be mitigated by a substantial decrease in rotation length.

Seed-Tree: With the seed-tree method, a few reproductively mature trees, usually 7-12 per ha (Croker and Boyer 1975), are left across the stand to provide seed for regeneration. These seed trees may be removed from the site after regeneration is established. As a result, an EA structure is created. The biggest advantage of seed-tree is that seed trees can be selected by phenotype, which may improve stand quality (Brockway *et al.* 2006). In this method, failure in distribution of large seeds of longleaf trees is common (Boyer 1963). In addition, seed trees may not produce adequate number of seeds to cover the entire area. Due to unevenly distributed seeds, spaces may be occupied by hardwoods or other pine species. In addition, since residual basal area is reduced to as low as 2.3 to 3.5 m^2 ha^{-1} in the seed-tree method, hardwood competition is often increased, and prescribed fire is made difficult to apply due to reduced needle fall (Brockway *et al.* 2006). Due to the many disadvantages of low overstory density using the seed-tree method (Kirkman *et al.* 2007), by the 1960s, the shelterwood method became the favored approach for regenerating longleaf pine (Boyer 1993b).

Shelterwood: In the shelterwood method, more residual trees than the seed-tree method are left to produce seed and a minimum of 4.6 m^2/ha basal area is suggested to regenerate longleaf pine (Croker and Boyer 1975). Shelterwood method employs either three cuts (preparatory cut, seed cut, and final removal), or two cuts in which the preparatory cut is eliminated (Croker and Boyer 1975). In longleaf pine stands, the preparatory cut is done about 10 years before the final cut by reducing basal area to 13.7-16 m^2 ha^{-1}. Then, about 5 years before the final harvest, basal area is reduced to about 7 m^2 ha^{-1} for the seed cut. The shelterwood method can provide better distribution of seed than the seed-tree method because it leaves more mature trees behind. More frequent good seed crops are also obtained by this method (Croker and Boyer 1975). Higher establishment and survival of longleaf pine have been observed under shelterwood method (McGuire *et al.* 2001). In addition, residual trees produce enough needlefall to apply prescribed fire which may better to restrict brown-spot blight disease (Croker and Boyer 1975). Shelterwood may also be more aesthetically pleasing than the seed-tree method and provide better wildlife habitat.

Because longleaf pine is known to be competition intolerant, few people considered shelterwood to be a practical method to regenerate the species, at least not until controlled silvicultural studies were conducted (Croker and Boyer 1975; Boyer 1979; Boyer 1993a). After monitoring 27 regeneration areas, Boyer (1993a) found that longleaf pine stands were successfully naturally regenerated using shelterwood method. However, like seed-tree method, residual overstory trees are removed after regeneration is established, and an even-aged structure results. This removal disrupts vertical diversity and may interrupt flow of ecosystem's services. UEA methods never completely remove the mature overstory and, thus, may be more appropriate than EA methods for restoration of the rich animal and understory plant diversity in longleaf pine ecosystems (Brockway and Outcalt 1998; Brockway *et al.* 2005b).

5.2. Uneven-aged management

An UEA stand contains three or more distinct diameter classes. Forest managers are not usually interested in tree ages in UEA systems. Instead, diameter class distribution is the variable of interest (Farrar 1996). Canopy structure is usually irregular; the DBH distribution exhibits a reverse-J shape rather than the normal distribution typical of EA stands (Farrar 1996). Unlike EA silviculture, UEA management is based on a cutting cycle rather than a rotation (Baker *et al.* 1996). Regeneration, recruitment and harvest are episodic (Farrar 1996). Because of the continuous canopy cover through time, UEA systems may better serve the needs of multiple use management, fulfilling objectives such as wildlife, recreation, water quality and aesthetics (Guldin 1996). In addition, because of the presence of several diameter classes, UEA stands have greater resistance and resilience to disturbances (O'Hara and Ramage 2013).

Some scientists have stated that selection systems may not be a practical management approach for intolerant species (Wahlenberg 1946). However, others disagree (Farrar and Boyer 1991; Boyer 1993a; Guldin 2006). Brockway *et al.* (2005a) state that selection methods can be used to manage even the most intolerant species as long as the harvest is of appropriate density and timely. In addition, the UEA mosaic of small EA groups that were present in natural longleaf forests suggests that UEA methods should be successful if we can mimic the timing and intensity of natural disturbance (Brockway and Outcalt 1998).

Group selection: In the group selection method, a cluster of adjacent mature trees are removed to create 0.1 to 0.8 hectare canopy gaps. This method is generally practiced as an UEA silvicultural system for intolerant trees (Guldin 2006). It encourages seedling growth in gaps and eventual recruitment into the canopy (Brockway and Outcalt 1998). As stated before, regeneration of longleaf pine is associated with canopy openings. The natural gap-phase regeneration pattern can be closely achieved using group selection (Brockway and Outcalt 1998; McGuire *et al.* 2001). Gagnon *et al.* (2003) observed the effects of canopy gap position on survival and growth of planted containerized longleaf seedlings using the group selection method and concluded that this method may be appropriate for successful regeneration of longleaf pine forests. Farrar and Boyer (1990) also found that longleaf pine stands can be managed and sustained using group selection, but Boyer (1963a) suggested that distribution of seed may be problem in larger groups since longleaf pine may not disperse farther than 30 m from forest edges. At the other end of the gap size spectrum, small gaps can become closed before regeneration is established (Guldin 2006). Availability of water, nutrients, and light may vary depending on size of gaps (Gagnon *et al.* 2003). An additional consideration is that the control of many small groups may be difficult, and operations may be expensive (Roach 1974).

Understanding the regeneration dynamics within canopy gaps is essential for the success of group selection within longleaf pine forests (Gagnon *et al.* 2003). Some scientists have suggested larger gaps (Palik *et al.* 2002; Brockway *et al.* 2006) while others recommend that smaller gaps such as those created by single-tree selection may be sufficient for securing adequate reproduction (McGuire *et al.* 2001; Jack *et al.* 2006).

Single-tree selection: Single-tree selection consists of removing individual trees across all diameter classes within a stand. The smallest scale of disturbance such as by insects, diseases, or lightning is imitated, and small canopy gaps are created by single-tree selection (Guldin 2006). The growing space left vacant after a tree is dead or removed becomes available for mature overstory trees, smaller midstory trees, and understory regeneration (Guldin 2006). Slow seedling growth and recruitment is typical under single-tree selection.

Lightning is one of the most frequent disturbance agents in longleaf pine forests in the southern US (Palik and Pederson 1996; Outcalt 2008), and creates gaps suitable for longleaf pine establishment and recruitment (Outcalt 2008). Since single-tree selection methods closely mimic small scale disturbances such as lightning, this method may create a favorable environment for longleaf recruitment as well (McGuire *et al.* 2001; Jack *et al.* 2006). McGuire *et al.* (2001) suggest that the minimum gap size for longleaf regeneration may be achieved by removal of only one or just a few overstory trees in longleaf pine stands. Rodriguez-Trejo *et al.* (2003) found that survival of planted seedlings was higher in small canopy gaps than in large gaps suggesting that the shade of overstory trees decreased mortality. Similarly, Jack *et al.* (2006) stated that higher survival of longleaf pine seedlings was observed under greater overstory canopy density than within larger groups. However, single tree selection has not yet been clearly demonstrated as an effective method to regenerate longleaf pine forests (Brockway *et al.* 2005b).

6. Research Needs

In comparison to EA systems, the application of an UEA system may seem to be both more complicated and more difficult (Farrar 1996). However, since UEA silviculture provides concurrent and continuous multiple-use objectives such as timber, aesthetics, recreation, wildlife, and water quality, interest on the use of UEA silviculture has increased during the past 25 years (as of 2006) (Guldin 2006). In order to increase the success of natural regeneration with longleaf pine, the proper timing of seedling release is essential (Brockway *et al.* 2006). With EA systems, after seedlings are established, they are released by removing the overstory, and all seedlings have the opportunity to grow into the overstory. But, in UEA systems, the release is always only partial, because there is never a complete canopy removal. Thus, we do not know how much removal is needed in UEA systems to secure enough release to sustain the stand through time. Although limited research has shown that UEA silviculture closely mimics natural disturbances of longleaf pine forests (Outcalt 2008), there has not yet been enough long-term research in the use of UEA management to verify that selection silviculture can sustain these forests (Brockway *et al.* 2005a).

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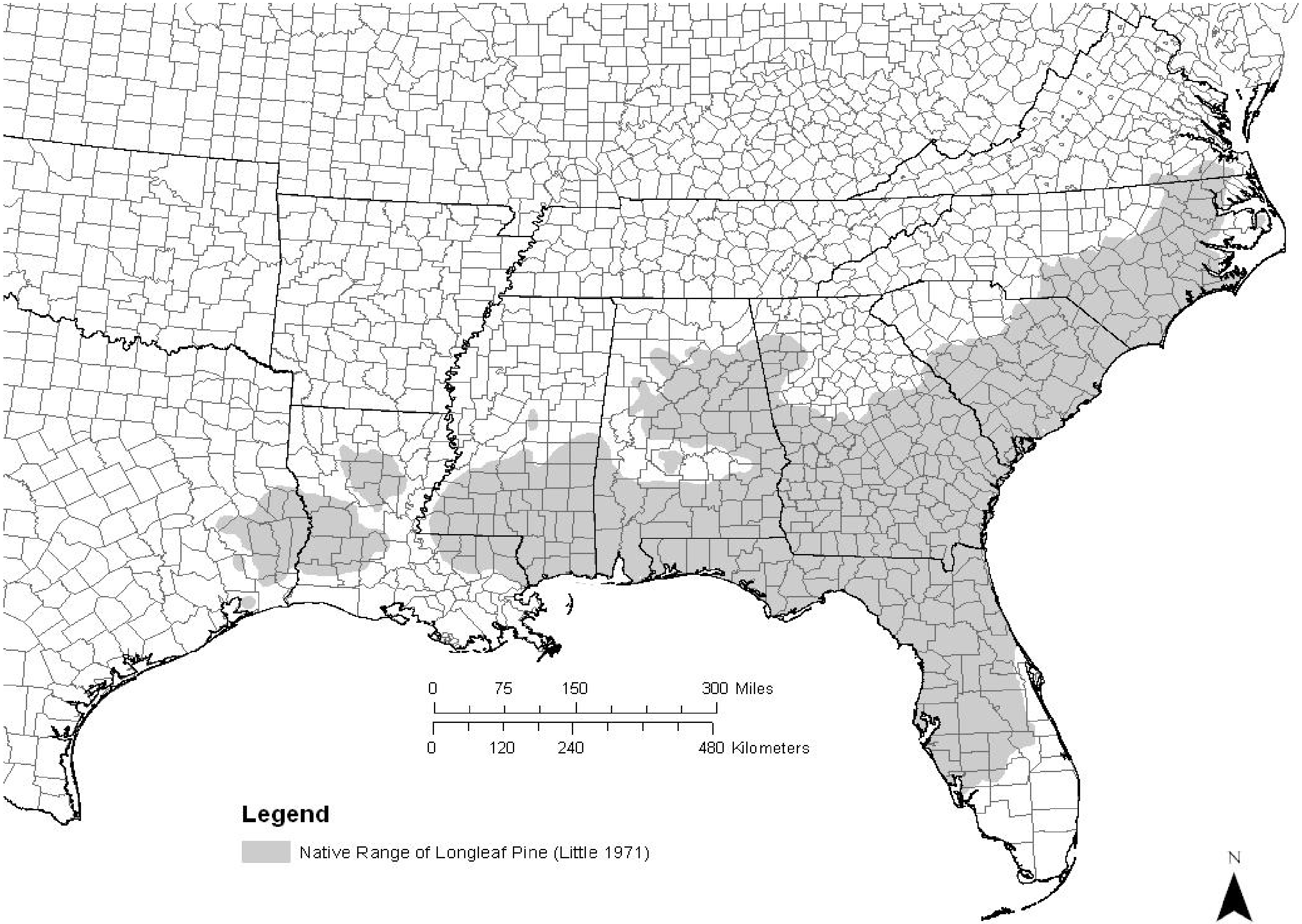

Figure 2.1: Location of the Escambia Experimental Forest within the longleaf pine natural range (Little 1971).

CHAPTER III - INFLUENCE of RESIDUAL BASAL AREA on LONGLEAF PINE (P*inus palustris* Mill.) GERMINATION, SURVIVAL, ESTABLISHMENT and GROWTH under SELECTION SILVICULTURE

Abstract: Even-aged (EA) silvicultural methods have been successfully used to manage longleaf pine (*Pinus palustris* Mill.) forests for wood production; however, our ability to use uneven-aged (UEA) methods to manage this ecosystem is still open to question due to longleaf pine's intolerance of competition. In this study, the effects of varying levels of residual basal area (RBA) (9.2, 13.7, and 18.4 m^2 ha^{-1}) on longleaf pine germination, survival, growth and establishment under selection silviculture, implemented with the Proportional-Basal Area (Pro-B) method were observed. In addition to natural regeneration of longleaf pine, influence of stand density on the survival and growth of planted longleaf pine seedlings was also monitored. Photosynthetically active radiation (PAR) was measured, and the relationships between light penetration, germination, survival and growth were examined. The study found an inverse relationship between RBA and number of germinants, but the mortality of germinants was not influenced by RBA. PAR had a significant positive effect on germination but did not affect mortality of germinants. RBA influenced the impact of burning on the survival of germinants at age two showing that higher survival occurred under lower RBA plots. At the end of third growing season, an inverse significant relationship was observed between RBA and RCD (root collar diameter) growth of germinants. All study plots, even those with higher RBA, had more than the projected number of seedlings needed to sustain the target diameter structure (reverse-J shape) that was obtained using

Pro-B method. There was no significant relationship between RCD growth of planted seedlings and RBA/PAR three growing seasons following planting. In addition, RBA influenced the impact of burning on the survival of planted seedlings in the second year of planting, with higher survival observed under lower RBA plots. Long-term continuous monitoring of seedling development and recruitment into the canopy will be required to determine the efficacy of UEA management in this system. However, nothing in the current data suggests that this approach will not be successful in regenerating a new cohort within UEA stand. Current data suggests that UEA methods may be a viable alternative to exclusive use of EA regeneration methods in longleaf pine ecosystems. In addition, three year data suggest that under planting may be an option to speed conversion from an EA to UEA structure in longleaf pine forests, and also change species composition.

Keywords: Even-aged, germination, growth, prescribed burning, survival, recruitment, uneven-aged.

1. INTRODUCTION

The longleaf pine (*Pinus palustris* Mill.) ecosystem has historically been very important in the southeastern USA due to its extensive area and high biodiversity. These forests produce high quality timber (Boyer 1979) and usually provide important habitat for many animal species (Brockway *et al.* 2005). Longleaf pine is resistant to fire, disease, and insects (Boyer 1999; Croker and Boyer 1975). It is thought to have occupied up to 38 million hectares in the southeastern USA prior to European settlement (Frost 1993). Frequent disturbance across this region, especially fire, contributed this species' dominance (Chapman 1932), and also created an irregular, uneven-aged (UEA) structure across the landscape. However, with the arrival of European settlers, exploitation of longleaf pine forests began in the early 1700's (Outcalt 2000), and large areas of longleaf pine were cleared without concern for regeneration. As a result, approximately 97% of these forests were lost to agriculture or to dominance by other species such as loblolly pine (*Pinus taeda* L.). Only 1.2 million hectares of longleaf pine forests remained by 1995 (Brockway *et al.* 2005). The longleaf pine forest type is now considered an ecosystem at high risk in the USA (Frost 2006).

With an increasing awareness of the economic, ecological, and social values provided by the longleaf pine ecosystem, there has been a growing interest in the restoration and management of longleaf pine forests that remain (Brockway and Outcalt 2000; Guldin 2006). Beginning in the 1950's, silvicultural studies focused on restoration and regeneration of longleaf pine using even-aged (EA) silvicultural methods including clearcutting, seed-tree and shelterwood (Gagnon *et al.* 2003). These techniques were considered to be the logical and appropriate approach to the regeneration problem, given that longleaf pine is a shade and competition intolerant species (Boyer 1990). Of those early studies, the shelterwood trials were particularly successful, and have been used since that time to regenerate the species (Croker and Boyer 1975). The shelterwood system allows for continued production of high quality timber; unfortunately, overstory removal at the end of the rotation has been shown to have a negative impact on the ecological functions and values of the longleaf pine forest (Brockway *et al.* 2006). The recurring and complete overstory removal may impact the rich animal and plant diversity typical of the natural longleaf ecosystem and this diversity does not recover during the length of a typical EA rotation of 50 years (Texas Forest Service 2010). As a result, some animal (red cockaded woodpecker, gopher tortoise) and plant (wiregrass) species associated with the natural ecosystem have become threatened or endangered species (Van Lear *et al.* 2005).

Given their perpetual maintenance of a mature canopy cover, UEA techniques seem to be a more suitable alternative to EA methods for the restoration and management of the rich animal and understory plant diversity in the longleaf pine ecosystem (Brockway and Outcalt 1998;

Brockway *et al.* 2005). However, some scientists and forest managers have suggested that selection systems are impractical in these forests, because regeneration of the species will be hindered by its intolerance to shade and competition (Croker and Boyer 1975). On the other hand, the UEA mosaic of small EA groups that were present in natural longleaf forests (Brockway and Outcalt 1998) suggests that selection methods should be successful, if we can determine the appropriate type, timing and intensity of disturbance needed to mimic that which historically occurred in these forests. But, there has not been sufficient research on, or demonstration of, selection methods as an effective method for sustaining longleaf pine forests (Brockway 2005b).

Successful natural regeneration of longleaf pine may be difficult where there is insufficient number of seed trees in the stand (Brockway *et al.* 2006) and poor seed production by those trees (Boyer 1979). Although natural regeneration can be cost-effective, due to periodic problems with obtaining sufficient natural regeneration of longleaf pine, seedling planting may be an alternative method to restore stands where longleaf originally grew (Barnett 2001). In addition, planting is an essential component of restoring longleaf ecosystem because of the currently limited acreage of these forests (Barnett 2001).

We believe that canopy openness as measured by residual basal area (RBA) may be one important factor in longleaf pine germination and establishment. Croker and Boyer (1975) documented that shelterwood regeneration requires a minimum of 4.6 m^2 ha^{-1} of BA to obtain an adequate number of established seedlings. In addition, Boyer (1979) stated that seed production is maximized with a BA of 6.9 m^2 ha^{-1} and it declines sharply above a BA of 9.2 m^2 ha^{-1} with the shelterwood method. Moreover, Boyer (1993) recommended that RBA of shelterwood should not exceed BA of 6.9 m^2 ha^{-1} for successful regeneration. However, similar studies for UEA silviculture have not been undertaken. It is unlikely that the RBA limits determined for EA stands are also applicable for UEA management of longleaf pine, given that the overstory is never completely removed and recruitment requirements are substantially lower because the stand is not being replaced by a single cohort of reproduction. We further believe that planting may be the appropriate option if the objective is to convert a stand with other pine species to a longleaf pine stand (Franklin 2008), or to alter stand structure from EA to UEA.

Thus, in this study, we examine the effects of varying levels of RBA (9.2, 13.8, and 18.4 m^2 ha^{-1}) on longleaf pine germination, establishment and recruitment under single-tree selection silviculture implemented with the Proportional-Basal Area (Pro-B) method (Loewenstein 2005; Brockway *et al*. 2014). Our hypothesis are 1) establishment of longleaf pine seedlings increases with decreasing overstory density, 2) adequate numbers of seedlings can be established under higher levels of RBA than the upper limit suggested for shelterwood, 3) survival of longleaf germinants and planted seedlings during prescribed burning is negatively influenced by overstory density.

2. METHODOLOGY

2.1. Study Site

The study was conducted on the Escambia Experimental Forest which is located 11 km south of Brewton, Alabama, in the southeastern USA (Little 1971) (Figure 2.1 in Chapter II). This 1,214 hectare forest was established in 1947 to study the ecology and management of longleaf pine forests. About 80% of the forest is dominated by longleaf pine, and the remainder consists of slash pine (*Pinus elliottii* Engelm.) and mixed hardwoods. Bluestem grasses (*Andropogon* spp.) are the predominant ground cover. Average site index for longleaf pine is about 21-23 m (base age 50). Soils are coarse to fine, loamy, siliceous thermic Paleudults (Adams *et al.* 2003). Troup fine sand is the predominant soil type on the forest (Boyer 1987). The climate is subtropical with mild winter temperatures and high summer humidity. Annual precipitation is about 1520 mm, and average range of temperature is 5 to 33°C (Estes 2006). Elevation ranges from about 30 to 87 m above sea level. Topography is flat to rolling, and most slopes are in the range of 3 to 10%.

2.2. Experimental Design

The study was laid out as a completely randomized design. In the winter of 2010, nine 2-hectare square plots were established, and randomly assigned to one of three levels of BA, 9.2, 13.8, 18.4 m^2 ha^{-1} (40, 60, 80 ft^2 ac^{-1} respectively). Plots were named as H_1, H_2, and H_3 for high-RBA; M_1, M_2, and M_3 for mid-RBA; and L_1, L_2, and L_3 for low-RBA treatments. Each treatment was replicated three times. Assigned treatments were applied to the entire plot (the experimental unit). Treatment response was estimated by measurements conducted on subplots. Each study plot includes six (100 m^2) square overstory measurement subplots, and eighteen (10 m^2) circular understory subplots. Overstory and understory subplots were systematically located within each plot.

2.3. Harvesting

Harvest operations were completed during the first week of May, 2011. Stands were marked to the defined treatment RBA using single tree-selection implemented with the Pro-B method (Brockway *et al*. 2014). Pro-B is an UEA marking method that is based on structural control and allows one-pass marking of a stand. We used a standard ‘target structure’ defined by a q-value of 1.3 (for 5 cm diameter class) and a largest diameter tree (LDT of 45 cm). This structure apportions its BA among three product classes (<15 cm; 15-30 cm; >30 cm) in a ratio of approximately 1:2:3 (Loewenstein 2005; Brockway *et al*. 2014). Maintaining this distribution ensures a continuous canopy cover, maintains full site utilization with approximately 80% of stand BA allocated to the sawtimber diameter classes. In addition, it has been shown that the distribution allows sufficient growing space for the recruitment of new cohorts in studies with longleaf pine (Dyson *et al.* 2009) and with different species (Loewenstein 2005).

Loewenstein (2009) outlines the following steps to create a marking guide using the Pro-B method (Table 3.1).

- Conduct current inventory and sum BA by diameter class
- Decide on a RBA. Target is based on proportions
- Subtract target BA from current inventory
- Calculate proportion to cut (1 – Target BA/ Current Inventory)
- Record 'simplified' marking guide, as a rate of removal fraction.

The marking guide gives the proportion of trees to be cut in each of the three product classes. Tree markers then walk through the stand and trees are marked based on the concept of "Take the worst and leave the best" (Baker *et al.* 1996). For example, according to the guide above, five trees larger than 30 cm are counted. After that, the two most undesirable, poor form or damaged of these five trees are marked. Then, next five trees are selected and the same action is repeated. The same process is conducted for each product class throughout the marking. The marking guide for each study plot was created based on pre-harvest measurements (Appendix A).

2.4. Prescribed Fire

A growing season burn was conducted in the first week of September, 2011, following the harvest and prior to seed dispersal in order to reduce competition and expose the mineral soil. We aimed to eliminate hardwood sprouts and other woody plants, and prepare the seedbed before the seed dispersal of longleaf pine, which occurs in late October. During burning, average air temperature was 24-26 ^{0}C, and relative humidity ranged from 42 to 64 percent, decreasing in the afternoon.

A dormant season fire was conducted in 2014 (January-February). The aim of this burning was to reduce competition of longleaf pine seedlings with hardwoods and observe the influence of stand density on the impact of burning 2-year old seedlings. During the burning (January- February 2014), temperature ranged from 11 to 23 ^{0}C while relative humidity ranged from 23 to 47 percent.

Plots were burned in strips or spots depending on presence of advance longleaf pine reproduction. A backfire was used along the inner edge of fire-lines in the opposite direction of the prevailing wind using drip torches and an ATV torch. Ignition was followed using strips or spots until the entire plot was burned. Most of the understory vegetation was consumed and full reduction with high percent topkill of hardwoods within the study plots was accomplished. No damage to the overstory trees was evident following the burning.

2.5. Planting

The main focus of this study is on natural regeneration. However, since longleaf pine exhibit a high degree of annual variation in seed production, producing only sporadic and irregular cone crops, we decided to plant seedlings in the event that seed production was poor or failed during 2011-2012. Seedlings were obtained from Meeks' Farms and Nursery, Inc., Georgia, and kept in a cold storage until they were planted. Three longleaf seedlings were planted in each regeneration subplot (486 in total) following the previously described prescribed fires. Seedlings were 15-cm deep-plug containerized seedlings with a rooting volume of 100 cm^3. Seedlings with dark green foliage and larger root-collar diameters were selected, plugs were created using a container seedling dibble with 15-cm hollow tip, and seedlings were hand-planted on the same day, in early

December, 2011. Planting was completed following a rainy period. They were planted approximately 1-m away from plot center and equidistant from each other to minimize the competition with each other. Seedlings were tagged and numbered after planting in order to monitor their growth and survival.

2.6. Measurements

Overstory trees (>10 cm in diameter) were tagged in the 100 m^2 overstory subplots, diameter at breast height (DBH) measured at 1.4 m above the ground, was measured in December 2010 before the treatments were imposed and again in July 2012, 2013, and 2014 during the first, second and third growing seasons, respectively. The diameter increment of overstory trees was calculated as the difference between the December 2010 and July 2012, 2013, and 2014 measurements.

New germinants were counted on the regeneration subplots and individually flagged soon after the germination period (January 2012). Unlike other southern pines, longleaf pine seeds germinate soon after they are dispersed (Boyer 1990). Seeds germinate in less than a week after dispersal and they do not remain viable beyond that time (Boyer 1990). Seed dispersion of longleaf pine occurs in late October; no additional germination was observed between January 2012 and July 2012. Germinants flagged in January 2012 were tallied again in July 2012, 2013 and 2014 to monitor survival. In addition, three germinants in each regeneration subplot were randomly selected and tagged before the dormant season burning in order to observe their survival following the burning. After the dormant season burning, three germinants among those that survived the burning were randomly selected in each regeneration subplot, and their root-collar diameters (RCD) were recorded to observe growth.

RCD of the seedlings planted in the regeneration subplots was recorded soon after the planting (January 2012). RCD, which is the diameter of the seedling at the base of the main stem, was measured to the nearest millimeter using a digital caliber. RCD measurements were repeated in the first (July 2012), the second (2013), and the third growing seasons (June 2014) to calculate growth of planted seedlings. Mortality of planted seedlings was also recorded at each growing season, and following the growing season burning.

Photosynthetically active radiation (IPAR) was measured under the canopy, on nearly cloudless days between 11:00 am and 2:00 pm, during each measurement period. Readings were taken 1.25 m above the ground at the center of each regeneration subplot using an AccuPar Linear PAR/LAI Model PAR-80 ceptometer (Decagon Devices, Inc., Pullman, WA). The ceptometer was leveled during measurement, and special care was taken to prevent the operator's shadow from falling across the sensors. The ceptometer averages readings of 80 individual sensors along a 0.8 meter long array. A total of 5 readings were taken at the center of each regeneration subplot (90 readings on each 2-ha plot). In addition, a HOBO weather station PAR sensor (Onset Computer Corporation 2009) was installed in a treeless area (about 8 ha). Intercepted PAR (IPAR) was calculated using the following formula;

$$IPAR = 1 - (PAR\ under\ canopy\ /\ PAR\ in\ open) * 100$$

PAR in the treeless area ranged from 2446 to 2553 µmol m^{-2} s^{-1} while PAR under canopy ranged from 120 to 1360 µmol m^{-2} s^{-1} across all subplots.

PAR measurement is affected by some factors such as topography, elevation and solar zenith angle. Liang *et al*. (2012) suggested that PAR can be corrected for varying zenith angles and topography elevations using the following formula;

$$f = 1 + 1 / (18.56+121.55 * \cos (\cos (\theta))) * z - 0.00035 * z^2$$

where f is the PAR correction factor, θ is solar zenith angle, and z is elevation (in kilometers). Solar zenith angle of the measurement periods for the study area was calculated using NOAA Solar Calculator (NOAA 2014). Then, PAR measurements were corrected using the correction formula (Liang *et al*. 2012). Change in PAR following the correction was negligible. We believe that this may be because our PAR measurements were taken during same period of the year (early August), and during same time period of the day (between 11:00 am and 2:00 pm).

2.7. Statistical Analysis

Deviations of final RBA from the target RBA was calculated for each study plots. Due to deviations from the target RBA levels, instead of ANOVA, simple linear regression (α-level=0.05) was used to test the relationships between RBA and 1) diameter increment of overstory trees, 2) survival of germinants, 3) influence of stand density on the survival of germinants following fire, 4) growth of germinants, 5) the survival of planted seedlings, 6) the growth of planted seedlings, and 7) the influence of RBA on the survival of the planted seedlings following fire. Relationships between IPAR and the same variable were also determined using simple linear regression (α-level=0.05). To check the effect of initial BA and its interaction with RBA on germination, a multiple regression model was used.

In order to more appropriately model the relationship between stand density and number of germinants, Poisson regression was used. For count data such as number of germinants, Poisson regression model is usually recommended (Rodriguez 2007). Seedling survival percentages were averaged on each plot, and the percentages were arcsine transformed before regression analysis. Arcsine transformation of data is appropriate for the data expressed as percentages such as survival

(Davis *et al.* 1999), because distribution of percentage data is usually binomial and arcsine transformation makes the distribution normal. Growth data was log-transformed to improve residual homogeneity and normality (McDonald 2014). The models used plot level data defined by the mean value of all subplots within a given 2-ha experimental unit. R-Statistical software (R-Project 2008) was used for the analyses. See Appendix C for a full description of the errors and for additional statistical results.

A wildfire occurred on one of the mid-level BA plots, M_2, (13.8 m^2 ha^{-1}) before the first growing season (May 21st, 2012). All of the new germinants were consumed; therefore, data from this plot was not included in the analysis of subsequent measurement periods.

3. RESULTS

3.1. Harvesting

Following harvest using the Pro-B method, measured RBA was fairly close to our target RBA on most plots ($p<0.05$) (Table 3.2). The greatest deviation from the target BA was +1.8 m^2ha^{-1} and -1.2 m^2ha^{-1} on two of the low-BA plots (-12.9 and +17.1% respectively). One additional plot was off target by 0.9 m^2ha^{-1} (+6.2%), the remainder of the plots were within 5% of the target. The large deviations in the two low-BA plots were probably due to the presence of large diameter trees. Missing even one large marked tree, or cutting one large unmarked tree during harvesting results in substantial deviation from the target.

3.2. Overstory

IPAR ranged from 57 to 78% across all plots in the first growing season. There was a statistically significant, inverse relationship between RBA and IPAR ($p=0.0003$) (Figure 3.1a). There was also a significant negative relationship between RBA and cumulative diameter increment of overstory trees during three-year period (p=0.002) (Figure 3.1b) as well as a significant positive relationship between diameter increment and IPAR (p=0.011). Average cumulative diameter growth ranged from 0.62 to 1.35 cm across all plots during three-year period, with higher diameter growth on low RBA plots. In the second growing season, there was still a significant inverse relationship between IPAR and RBA (p<0.0001) (Figure 3.1c). However, intercepted light in the second year was relatively low across all plots in comparison to intercepted light in the first growing season.

3.3. Germination

There was a statistically significant inverse relationship between the number of germinants and RBA (p<0.0001) during the germination period following harvest operations (Figure 3.2a). Higher numbers of germinants were observed in low RBA plots. The average number of germinants ranged from 11,000 to 88,000 per hectare across all plots. As can be seen in Figure 3.7a, one of the mid-level RBA plots, M_1, (13.8 $m^2 ha^{-1}$) had a large number of germinants. Despite our efforts to install the plots in a block and away from roads, this specific plot was located at an intersection of two forest roads. As previously stated, cone production of longleaf pine decreases with increasing overstory density (Croker and Boyer 1975). We believe that the trees along the roads had relatively greater amounts of growing space, developed larger crowns, produced more cone and seeds, and this consequently increased number of germinants in this specific plot. The roads were also likely responsible for the relatively greater light penetration in this stand. Regression equations both with and without the M_1 were fit, and their slopes were compared. The slopes were not statistically different for the first year germinant-RBA relationship (p=0.89), for the germinant survival-RBA relationship (p=0.99), or for the second year germinant-RBA relationship (p=0.88). Although removal of M_1 did not significantly change the regression slopes, its removal substantially increased R-square values and decreased p-values. However, it is also possible that this plot may simply be within the inherent range of variability in these stands because M_1 seems to be within the range of the data across all plots. In addition, removal of M_1 would flatten the regression lines and decrease the strength of the relationship. For all of these reasons, it was retained in the analysis.

Our harvest operations were conducted in May and were designed and timed to influence germination. This treatment would not have affected cone production in that year because it was initiated after the emergence of conelet buds which occurs in January or February (Boyer 1990). However, because stand density is known to impact cone production in longleaf pine (Croker and Boyer 1975) and consequently may influence the number of germinants, and because pre-harvest BA on the study plots ranged from 11.5 to 30 m^2ha^{-1} (Table 1), we used multiple regression to determine whether initial BA may have confounded our results. There were no statistically significant effects of initial BA on the number of germinants ($p=0.94$) nor was there an effect from the interaction of initial BA with RBA on the number of germinants ($p=0.93$).

Mortality of germinants was not affected by either RBA ($p=0.23$) or IPAR ($p=0.22$) during the first growing season (Figure 3.3). Average survival was approximately 55% across all plots with a single exception; one plot (H_2) had 75% survival. There was a statistically significant inverse relationship between the number of germinants and RBA in the first growing season (July 2012) ($p<0.0001$) (Figure 3.2b). In addition, a significant positive relationship between IPAR and germinant number was observed ($p<0.0001$). Despite the approximate 45% mortality that occurred during the first year, there are still large numbers of germinants, even under the high RBA plots. The number of seedlings in the first growing season ranged from 8,000 to 46,000 seedlings per hectare.

In the second growing season (July 2013), there was no significant relationship between RBA and mortality of germinants again (p=0.85) (Figure 3.3). Nor did IPAR affect survival of germinants (p=0.79). Survival rate of established germinants was high across all plots ranging from 95 to 98%. A statistically significant inverse relationship between RBA and number of germinants was observed in the second growing season as well (p<0.0001) (Figure 3.2c) as well as a significant positive relationship between IPAR and number of germinants (p<0.0001).

3.4. Survival of germinants following the dormant season fire

Although high numbers of germinants were observed in all plots, for successful regeneration it is important to know how many of those germinants would survive burning and whether there will be an adequate number of established seedlings following the fire. We also wondered how stand density would influence the impact of burning on those germinants. Thus, survival of those germinants was monitored following burning at age two. There was a statistically significant inverse relationship between RBA and survival of germinants following the dormant season fire (p=0.003) (Figure 3.3). Survival rate ranged from 26 to 87% across all plots, and increased with decreasing stand density. Following the dormant season fire, there was a significant relationship between RCD growth of germinants and RBA observed in the third growing season (p=0.006) (Figure 3.4). It should be noted that RCD growth of the germinants was measured only in the third growing season, thus, growth of germinants was the cumulative growth during the three-year period.

In the third growing season (June 2014), following the dormant season prescribed fire, the number of germinants ranged from 2,270 to 37,870 per hectare across all plots. There was still a significant inverse relationship between RBA and number of germinants (p<0.0001) (Figure 3.5).

3.5. Survival of underplanted seedlings

In the first year following planting, there was no significant relationship between RBA or IPAR and survival (p=0.56 and p=0.45, respectively) (Figure 3.6). Survival ranged from 93 to 100% across all plots. As observed in the first year, mortality of planted seedlings was not affected by RBA or IPAR during the second year following planting (p=0.87 and p=0.76, respectively) (Figure 3.6). Most of the planted seedlings survived second growing season. Survival ranged from 96 to 100 % across all plots.

Survival of planted seedlings was very high during the first two growing seasons. The question was whether those seedlings were well-established in two years to survive the first fire. We found that there was a statistically significant negative relationship between RBA and survival of planted seedlings following the prescribed fire (p=0.04) (Figure 3.6). Survival rate ranged from 39 to 85% across all plots, and increased with decreasing stand density.

3.6. Growth of underplanted seedlings

It should be noted that the growth in the first growing season was the initial growth following planting, growth in the second growing season was the cumulative growth during two-year period following planting, and the growth in the third growing season was the cumulative growth during three-year period following planting. RBA did not significantly affect RCD growth of planted seedlings in the first growing season (p=0.85) (Figure 3.7a). Average RCD growth of seedlings ranged from 1.04 to 2.06 mm across all plots. IPAR also did not have a significant influence on RCD growth of planted seedlings (p=0.98). In addition, as we observed in the first growing season (July 2012), there was no statistically significant relationship between RBA and RCD growth of the planted seedlings in the second growing season (July 2013) (p=0.41) (Figure 3.7b), nor did we observe any significant relationship between IPAR and RCD growth (p=0.54). Average RCD growth during two-year period ranged from 2.48 to 4.37 mm across all plots. Even though RBA did not significantly affect RCD growth of planted seedlings in the third growing seasons either ($p=0.13$) (Figure 3.7c), the relationship during the third year itself was significant ($p=0.0009$). Average RCD growth ranged from 3.47 to 5.27 mm across all plots during three-year period.

4. DISCUSSION

4.1. Overstory

Growth in basal area is associated with stand density (Kush *et al*. 2006). Average tree growth during three-year period ranged from 0.62 to 1.35 cm across all plots. Average annual growth in basal area ranged from 0.2 to 0.38 m^2 ha^{-1} across all plots. It is considered more difficult to model growth and yield of uneven-aged stands than even-aged stands (Kush *et al*. 2006). Average annual growth of uneven-aged loblolly and shortleaf pine stands is expected to be around 0.3 m^2 ha^{-1} in basal area (Farrar *et al*. 1984, Murphy and Farrar 1985). The model created by Farrar (1979) is known to be one of best growth and yield estimate of longleaf pine (Kush *et al*. 2006). Farrar (1979) predicted basal area using the following formula;

$$BA = e\ [(A_i / A_e)\ ln\ (B_i) + 6.0594\ (1 - A_i / A_e)] * 0.2296$$

where BA is the projected basal area at the end of the period (m^2 ha^{-1}), e is exponential function, A_i is initial stand age, A_e is stand age at the end of the period, ln is natural logarithm, and B_i is the initial basal area in square feet per acre. When we predict BA for each plot using the model (Farrar 1979), average annual growth in BA ranged from 0.19 to 0.31 m^2 ha^{-1} which seems to be consistent with our measurements.

Compared to second growing season, relatively lower IPAR was observed across all plots in the first year (Figures 3.1a and 3.1c). Although we did not take any measurements of needle fall following the growing season burning, this difference may be associated with reduced foliage following the burning in the first year. Reduced foliage may have resulted in increased light transmittance on the ground. Waldrop and Van Lear (1984) observed effects of crown scorch on the growth of loblolly pine, and found that needle drop was significantly higher on burned stand than control stand. They also stated that fire intensity significantly affect needle fall. Johansen and Wade (1987) suggested that growth of southern pines is reduced in the event of scorch and needle fall following high intensity burnings. Another consideration for the decreasing light transmittance in the second year may be expanding tree crowns.

Battaglia *et al*. (2003) estimated light transmittance in longleaf pine forests of varying densities and found higher amount of light transmitted (ranging from 38-80%) to the understory than that we observed. However, it should be noted that their measurements were taken under lower stand densities, and in canopy gaps ranging from 0.1 to 0.2 ha. Brockway and Outcalt (1998) investigated gap-phase regeneration in an uneven-aged longleaf pine forest, measured relatively lower amount of light transmittance, and found that PAR levels ranged from 290 to 520 μmol m^{-2} s^{-1} along canopy gap edges, and ~900 μmol m^{-2} s^{-1} in the center of the gap during midday. This inconsistency may be explained by highly variable light availability temporally and spatially in longleaf pine ecosystems (McGuire *et al*. 2001). Palik *et al*. (1997) stated that the relationship between stand density and light availability was curvilinear while Brockway and Outcalt (1998) suggested that the distribution of solar radiation was uniform across canopy gaps. Our PAR measurements ranged from 90 to 1400 μmol m^{-2} s^{-1} under varying levels of stand densities during midday, and seemed to be more consistent with that measured by Brockway and Outcalt (1998). McGuire *et al*. (2001) suggested that building a relationship among canopy structure, light availability and seedling response is crucial due to the temporal and spatial variability in light environment of longleaf pine forests.

4.2. Germination

Number of germinants was higher in low stand densities. We speculate that this relationship is primarily due to higher levels of light penetration to the ground with decreasing RBA across the plots, rather than the amount of tree removal or soil disturbance caused by logging and skidding operations in the plots. Note that, in the two most heavily harvested plots where BA was reduced by around 40%, the number of germinant was still lowest. These were high BA plots where the light penetration was still relatively less in spite of the higher intensity of tree removal. Also recall that a prescribed fire was applied in advance of seed-fall to prepare an exposed mineral soil seedbed. It is unlikely that the additional disturbance caused by harvesting operations was necessary to further improve conditions for germination.

Most of the plots had a great number of seedlings become established during the first germination period, January 2012. This was probably a result of the timing of harvest and prescribed fire. Longleaf pine is a sporadic and typically poor seed producer. Good seed crops are irregular and occur at 5 to 7 year intervals (Boyer 1990). Based on the 2011 cone crop report for longleaf pine (Brockway and Boyer 2012) (Appendix B), we were fortunate to have initiated this study during a good seed year. Our cultural operations were designed to maximize seedling establishment regardless of the cone crop. Harvest operations were performed prior to seed dispersal in order to increase success. As longleaf pine germinates immediately following seed dispersal, even a short delay in the harvest would have had an adverse effect on initial establishment due to mechanical disturbance of the new germinants and a poor light environment at the time of germination. Under lower stand densities, our number of germinants were more than

80000 per ha following germination in a good seed crop year. Similarly, Kush *et al*. (2004) monitored the number of germinants in an old-growth stand following a large cone crop in 1997, and reported 103000 germinants per ha.

In addition, as previously stated, germination of longleaf pine seed requires exposed mineral soil. This is often accomplished using prescribed fire and in its absence, the large seed and wing may not reach the soil because of dense grass or accumulated litter (Brockway *et al.* 2006). By using a growing season fire, our primary objectives were to expose mineral soil, control other woody species, and prepare the seed bed shortly before seed dispersal. Our germination results suggest both good planning and good fortune. Even so, it is important to understand that we were able to apply a growing season fire only because these study plots have been regularly burned in the past. None of them had more than 3.5 years of fuel accumulation at the time of the burn. For stands that have not been burned for a prolonged period, growing season prescribed fire is not commonly used because of the increased risk of mortality to the overstory trees. We observed no fire induced mortality of overstory trees on our study plots.

4.3. Survival of germinants

Survival of longleaf germinants is lowest during first year (Brockway *et al.* 2006) with mortality attributed to factors including: disease, grazing, drought, flooding, and frost (Croker and Boyer 1975; Boyer 1993). Brockway and others (2006) stated that first year mortality of 50% is common during the spring drought period. Grace and Platt (1995) reported 78% survival in the first year following germination. In addition, it is known that new longleaf seedlings may stay and survive in its well-known grass stage for up to 15 years, even under overstories ranging up to 21 m^2 ha^{-1} (Coker and Boyer 1975; Boyer 1993; Brockway *et al.* 2006). Our first year mortality data seem to substantiate the previous studies.

Although mortality is highest during the first year following germination (Brockway *et al.* 2006), and it decreases in following years (Boyer 1963). Our observations on mortality were consistent with previous studies; mortality of longleaf seedlings is not related to overstory density in the absence of fire (Boyer 1963; Palik *et al.* 1997). In addition, it has been suggested that although overstory density greatly affects height growth of seedlings, it does not influence mortality (Croker and Boyer 1975).

Even though survival is lowest during the first year following germination (Brockway *et al.* 2006), Boyer (1963) states that subsequent survival of one-year old seedlings ranged from 65 to 80 percent through age 7. If the mortality of our germinants follows a similar trend, then we should have at least 7,000 seedlings per hectare in any plot by age 7, and this conservatively assumes that no additional germinants would become established during this time period. Further, if we project seedling establishment only during a good seed crop and use the high end of the published interval of 5-7 years between good crops (Wahlenberg 1946; Boyer 1990); in addition, if we assume that all grass stage seedlings die by age 15 (Brockway *et al.* 2006), another conservative assumption, there should still always be at least two cohorts of seedlings on site. This would continuously maintain an adequate seedling bank available for recruitment into the canopy whenever conditions were conducive for release. However, a dormant season fire conducted at age 2 decreased survival of our seedlings.

4.4. Survival of germinants following the dormant season fire

In denser plots, it is likely that a higher amount of pine needles accumulated. Although needle accumulation was not measured before the burning, a statistically significant relationship between stand density and needle accumulation prior to the growing season burning (p= 0.033) may suggest the existence of this relationship prior to second burning as well. As a result, a greater volume of needles may have resulted in a hotter and higher intensity fire, and thus, higher mortality rates among understory seedlings. Similarly, several studies concluded that mortality of longleaf seedlings increases with increasing litter accumulation (Boyer 1963; Croker and Boyer 1975; Platt *et al.* 1988; Grace and Platt 1995). Grace and Platt (1995) observed the influence of stand density and fire on the survival of juvenile longleaf pine seedlings, and found higher survival under lower stand densities due to lower needle litter accumulations in areas of low overstory densities.

Another consideration for explaining fire induced mortality is the significant relationship between RCD growth of germinants and RBA observed in the third growing season (p=0.0064) (Figure 3.10). It is suggested that seedling size is negatively affected by stand density (Grace and Platt 1995; Brockway *et al.* 2006), and that seedling size positively affects the survival rate of longleaf seedlings following burning (Croker and Boyer 1975). Grace and Platt (1995) investigated the effects of seedling size on the survival during burning, and reported that larger size of seedlings under lower stand densities increased the survival rate of the seedlings during fire. When longleaf seedlings reach a RCD of 1.3 cm, they usually have thicker bark to protect them from fire (Boyer 1974). We believe that germinants under lower stand densities reached larger size and had better root development, and thus, became more resistant to fire.

Grace and Platt (1995) found that seedling RCD ranged from 5.5 to 6.8 mm in the second year following germination. As stated before, we measured RCD of the germinants in the third growing season only, and RCD ranged from 4.11 to 5.9 mm that seems to be relatively lower than that measured by Grace and Platt (1995). However, it should be noted that their overstory stand density levels were lower than our target stand densities.

Stand density also affects wind speed through the stand with wind speed decreasing with increasing stand density (Weir 2009). Although no wind speed measurements were taken, it may be possible that fire was carried more slowly in denser stands due to slower wind speeds. As a result, in denser stands, residual flame time might have been longer, and seedlings might have exposed to higher temperatures for a longer duration. Another consideration is that the canopy can slow down dispersion of heat into the atmosphere and thus keep more heat under the canopy for a longer duration in denser stands. This too may have also resulted in longer exposure of seedlings to higher temperatures during the burning.

4.5. Sustainable Recruitment

Given the substantial seedling bank that was created onsite across the range of RBA examined in this study, the next logical question is whether these stand conditions are suitable to provide sustained recruitment into the overstory. Existing research provide some evidence as to whether the current seedling bank is adequate to regenerate the stand using the commonly successful shelterwood method. Croker and Boyer (1975) suggest that 1250 longleaf seedlings per hectare, within 6 years of release following shelterwood removal, are the criteria for successful regeneration. In order to obtain these numbers, they recommend between 10,500 and 17,250 well established seedlings per hectare at the time of release. Since all overstory trees are removed at the time of release (the removal cut under a shelterwood system), the seed source is gone which precludes additional germination. Thus, an excessive number of seedlings are needed under even-aged methods because no replacement is likely in the event of seedling mortality. It is noteworthy that even under these conservative even-aged criteria, half of our research plots already contain sufficient well established seedlings to succeed following complete release.

However, such conservative criteria should not necessarily be required under an uneven-aged scenario. Our target stand structures that were created based on the Pro-B method show that a much smaller number of seedlings are required in the smallest diameter class (0-5 cm in DBH) ranging from only 71 to 145 seedlings per hectare depending on RBA (Figure 3.8). Assuming 65% survival to year 7 (Boyer 1963), we project more than 1475 seedlings per hectare at that time across all plots. Thus, only a small fraction of these seedlings must be recruited into the canopy to maintain a stable diameter structure. Again, the question becomes, at what rate must seedlings be recruited into the 0-5 cm diameter class to replace those lost to mortality and upgrowth into the next larger size class? We cannot yet predict the rate of seedling development under our range of RBAs, when any of these seedlings will begin height growth, or if they do, how many will be recruited into the canopy. We do expect that due to the gappy and patchy nature of a longleaf pine stand, further exacerbated by the periodic removal of trees under a selection system, that if and when height growth of seedlings is initiated, it will occur only where these seedlings obtain adequate light while those under a more dense portion of the stand will not recruit. Our current study is well designed to eventually answer these questions. Through continued monitoring of survival and growth of seedlings as well as the episodic recruitment of new germinants, we should be able to identify a range of stand density, disturbance frequency and intensity that will recruit sufficient seedlings into the stand to ensure sustainability.

4.6. Survival of underplanted seedlings

Survival rates in this study were consistent with reports from previous studies. South *et al.* (2005) observed 87% survival two years after planting on a cutover site nearby Escambia County, Alabama. Palik *et al*. (1997) monitored the effects of canopy structure on longleaf pine seedling survival, and found a 100% survival soon after planting, and an average of 97% survival 12 months after planting. Timing of planting is considered an important factor for higher seedling survival (Dyson 2010). Franklin (2008) suggests that early planting (as early as October) with adequate soil moisture usually result in better developed root system, more drought tolerance, and better competition with other vegetation in spring and summer. Our planting following a rainy period in early December probably favored seedling survival during first two years after planting.

It has been suggested that longleaf pine seedlings may survive under parent trees for up to 8 years or longer (Croker and Boyer 1975: Boyer 1990). Whether survival is affected by overstory density is a matter of debate. Some studies have found that survival decreases with increasing overstory density (Wahlenberg 1946; Platt *et al.* 1988; Grace and Platt 1995), while other studies support our observations that seedling survival is not influenced by overstory density (Boyer 1993; Palik *et al.* 1997; McGuire *et al.* 2001; Gagnon *et al.* 2003). Rodriguez-Trejo *et al.* (2003) even concluded that shade from overstory trees increased the survival of planted seedlings after examining artificial regeneration of longleaf pine in canopy gaps.

One possible reason for these inconsistent results on the influence of overstory density on survival may be the climate. Rodriguez- Trejo *et al.* (2003) states that they conducted their study during a very hot and dry year, thus, nurse effects of trees and shrubs increased the survival of seedlings under the canopy. The other reason for the higher survival may be the fact that containerized longleaf seedlings have much lower mortality rate in comparison to bare-root seedlings (Barnett *et al*. 1996; Rodriguez- Trejo *et al.* 2003). Although longleaf pine is classified as an intolerant species (Wahlenberg 1946; Boyer 1963; Boyer 1993; Barnett 1999; Boyer 1999; McGuire *et al.* 2001), research has shown that seedlings may be very tolerant to shade beneath parent trees when young (Croker and Boyer 1975; Boyer 1990).

4.7. Growth of underplanted seedlings

Initial average RCD at the time of planting was 8 mm. Dumroese *et al*. (2009) suggest that RCD of the seedlings should be larger than 6.35 mm or more. During the first two years following planting, average RCD growth ranged from 2.48 to 4.37 mm across all plots. Similarly, Dyson (2010) observed influence of overstory and understory competition on seedling growth in both subxeric and mesic sites, and found that two-year average RCD growth ranged from 2.5 to 4.5 mm. In another study, Gagnon *et al*. (2003) monitored the growth of longleaf pine seedlings planted within canopy gaps, and reported that average RCD growth ranged from 1.4 to 3.6 mm per year depending on the position of seedlings within the canopy gaps; larger RCD was measured near the gap centers while smaller RCD was measured along the gap edges.

Although it has been shown that early growth of longleaf seedlings is quite slow, even under low levels of overstory RBA (Boyer 1993), it is usually expected that higher RCD growth would be observed under low RBA (Palik *et al.* 1997). McGuire *et al.* (2001) observed larger average RCD within gap openings in comparison to uncut longleaf pine forest; however, they did not see any difference among three canopy gap sizes (0.11, 0.41 and 1.63 ha). Similarly, Gagnon *et al.* (2003) found that longleaf seedling growth was positively correlated with light transmittance.

We believe that lack of the significance between RBA and RCD growth in this study may have occurred because of transplant shock in the first and second year following planting. Another reason might be weather conditions during the measurement years. As stated before, the average annual precipitation in the study area is 1521 mm, while during measurement years (2011 and 2012) precipitation was relatively low (1100 and 1350 mm, respectively) (NOAA 2013). Low precipitation during the measurement years may have impacted RCD growth. It should be noted that average temperatures (20 and 20.6 °C, respectively) were not significantly above the average of the region (19 °C) (NOAA 2013).

Although the relationship between RBA and RCD growth of planted seedlings during three-year period was insignificant, this relationship during third year only was statistically significant (0.0009). It is likely that planted seedlings recovered from transplant shock after two years, and that the relationship between RBA and RCD growth of planted seedlings would be significant following growing seasons.

4.8. Survival of planted seedlings following the dormant season fire

Survival of planted seedlings across all levels of stand density was high, as expected. However, a more important question was how many of those seedlings would survive the first prescribed fire: were these seedlings sufficiently established by age two to survive a dormant season fire? It is known that pine needle accumulation is positively related to stand density (Boyer 1963). As stated above, the greater volume of needles in high RBA plots resulted in hotter and higher intensity burns, and thus, higher mortality rates among understory seedlings. These results were similar to several other studies that concluded that mortality of longleaf seedlings increases with increasing litter accumulation (Boyer 1963; Croker and Boyer 1975; Platt *et al.* 1988; Grace and Platt 1995; Jack *et al.* 2010).

Larger RCD growth was observed under lower density plots in the third growing season. It is suggested that seedling size positively affects survival rate of longleaf seedlings (Croker and Boyer 1975). When longleaf seedlings reach a root-collar diameter (RCD) of 1.3 cm, they usually have thicker bark to protect them from fire (Boyer 1974). We believe that seedlings under lower stand densities reached larger size and root development by the third growing season, and became more resistant to fire. Although we will continue to monitor seedling development, given the current data, we believe that under-planting of longleaf pine seedlings appears to be an option where species conversion is an objective, or where enrichment planting is needed.

5. CONCLUSIONS

EA methods, especially the uniform shelterwood, have proven to be very successful for longleaf pine regeneration and timber production, but, their effectiveness in restoring historic stand structure of the longleaf pine ecosystem may be questionable. Dynamics of EA methods have been well-understood, but, less is known about the use of UEA methods in longleaf pine forests. In addition, multiple-use objectives and continuous cover forestry are becoming more popular, and selection silviculture may be an alternative to shelterwood to meet these demands. We believe that if sufficient research demonstrates the success of uneven-aged methods in longleaf pine forests, these methods may become an alternative to the use of even-aged methods in situations where they might better fulfill a landowner's objectives. As Farrar (1996) stated, there is no single best method in forest management, there are alternatives, and the best depends on the objectives.

This study presents the preliminary effects of UEA methods on longleaf pine regeneration based on three years of measurements. We observed that number of germinants was inversely related to RBA, but, RBA did not affect mortality of new germinants. High numbers of germinants were obtained across all plots. However, RBA did influence the impact of prescribed burning on the survival of germinants. Based on our target structure created using Pro-B method, there was still a higher number of germinants following burning than required for sustainability.

The study also showed that RBA did not influence mortality and growth of planted seedlings in the first two years, but, did affect diameter growth by the third year only. In addition, with the prescribed burning conducted in the second year following planting, we observed that RBA influenced the impact of the burning on the survival of seedlings showing that higher survival was observed under lower stand density. Among those that survived burning, we cannot yet predict the number of seedlings that will be recruited into the canopy or how much recruitment will be affected by RBA. However, given the mortality rates reported in the literature (Boyer 1963), we may already have more than an adequate number of germinants in most of the study plots.

Future measurements are required to improve our understanding of the applicability of the single-tree selection method in longleaf pine forests. Measurements will continue until the recruitment of the new seedlings into the overstory is documented, to determine the efficacy of single-tree selection in these forests. Present data are not yet sufficient to address recruitment into the overstory. However, nothing in the current data suggests that this approach cannot be successful in establishing a new tree cohort in an UEA longleaf pine stand. Three-year results show that this approach may be a viable alternative to traditional EA methods in longleaf pine forests, if appropriate density, disturbance frequency and intensity are determined. In addition, current data suggest that understory planting of longleaf pine may be an option to convert from EA to UEA structure in longleaf pine forests. Moreover, the data also suggest that under-planting of longleaf pine seedlings may be an option where species conversion is an objective. Three-year results also showed that Pro-B method is an easy and effective marking method in UEA management of longleaf pine forests, and it can be an alternative to other traditional marking approaches

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Table 3.1: An example of a marking guide.

Diameter (DBH)	Inventory	Target	Harvest	Proportion	Guide
< 15 cm	11 m^2h^{-1}	10	1	0.09	None
15-30 cm	45 m^2h^{-1}	20	25	0.56	3 of 5
>30 cm	50 m^2h^{-1}	30	20	0.4	2 of 5

Table 3.2: Summary of the harvesting in each plot.

Plot	Target BA (m^2/ha)	Final BA (m^2/ha)	Deviation from the target BA (%)
H_1	18.4	17.6	-4.1
H_2	18.4	18.2	-0.9
H_3	18.4	18.0	-2.2
M_1	13.8	14.7	+6.2
M_2	13.8	14.5	+4.9
M_3	13.8	13.8	0.0
L_1	9.2	8.0	-12.9
L_2	9.2	9.3	+1.0
L_3	9.2	10.8	+17.1

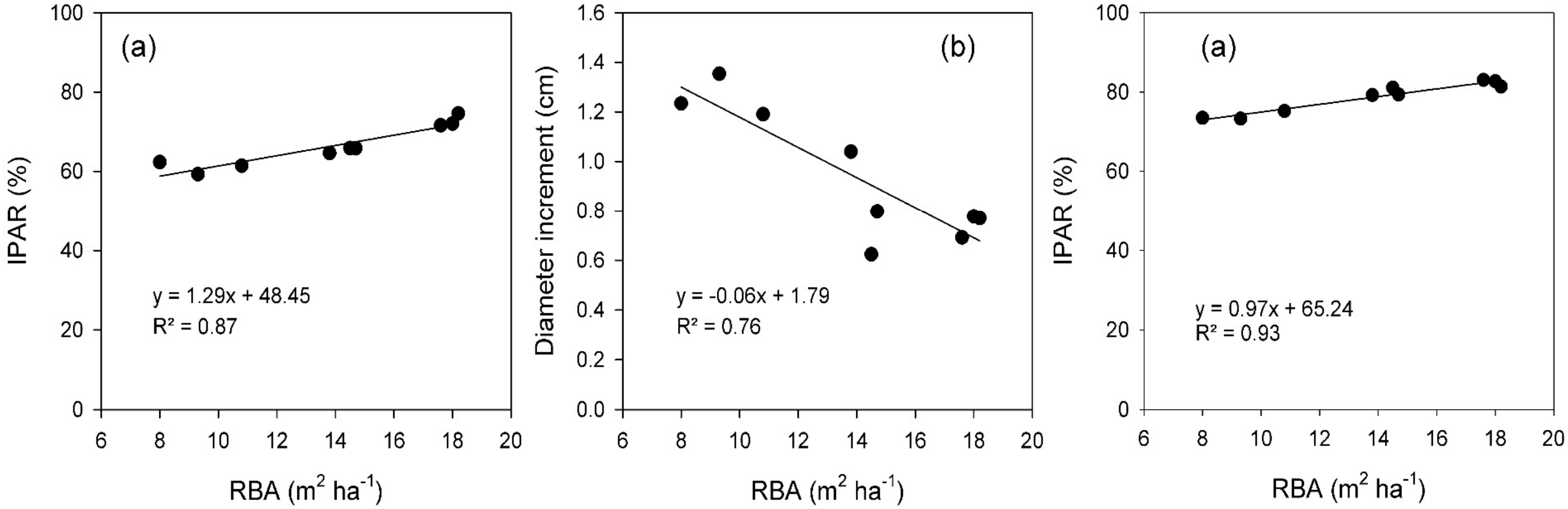

Figure 3.1: Relationships between RBA and (a) IPAR in the first growing season; (b) cumulative diameter increment during three-year period; (c) IPAR in the second growing season.

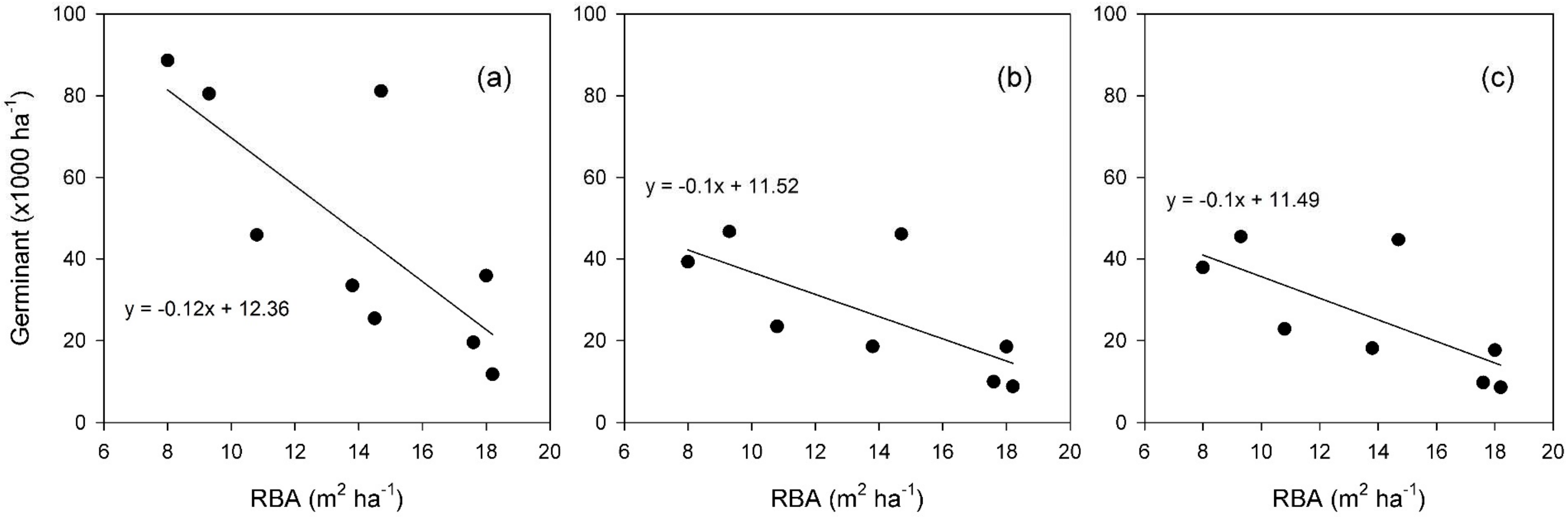

Figure 3.2: Relationships between RBA and number of germinants (a) during the germination period; (b) in the first growing season; (c) in the second growing season.

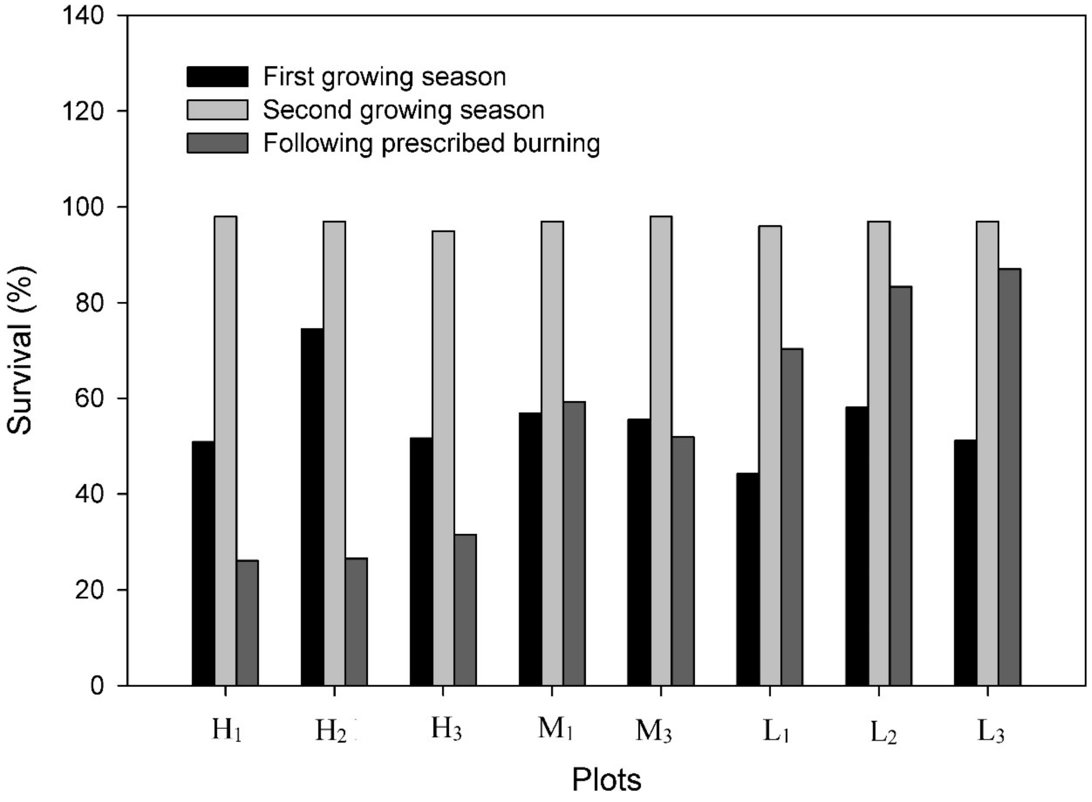

Figure 3.3: Relationships between RBA and survival of germinants in the first and second growing season, and following prescribed burning.

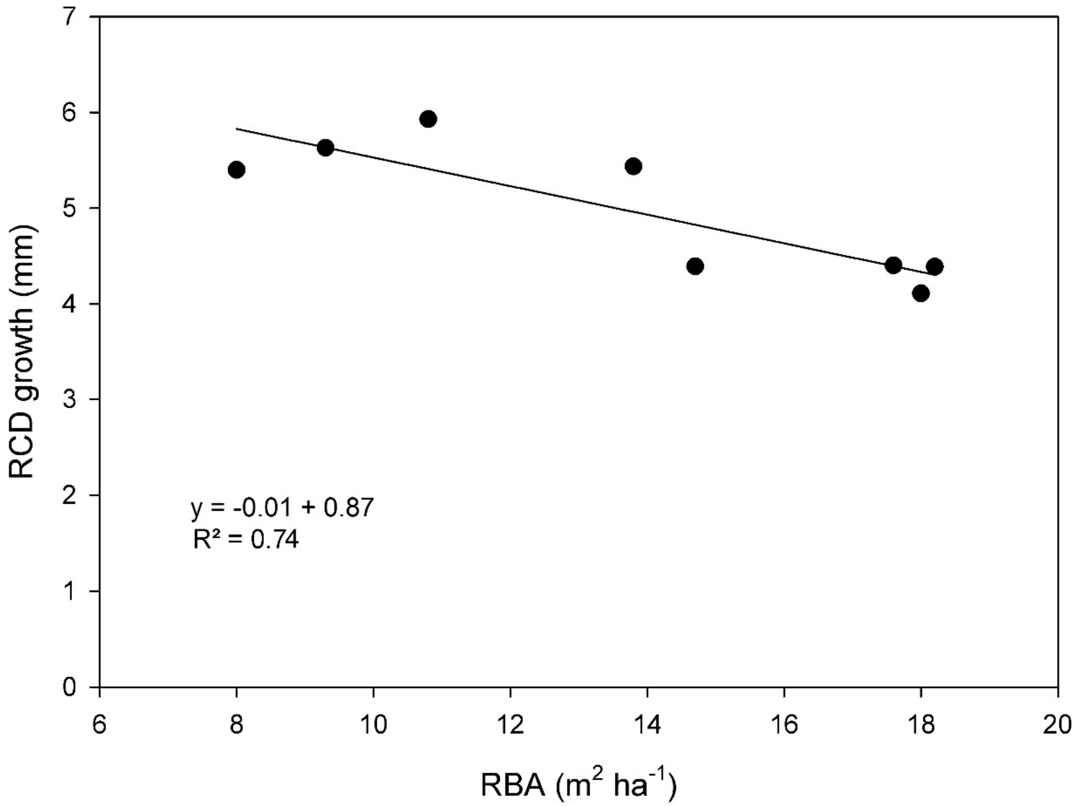

Figure 3.4: Relationships between RBA and RCD growth of germinants by June 2014.

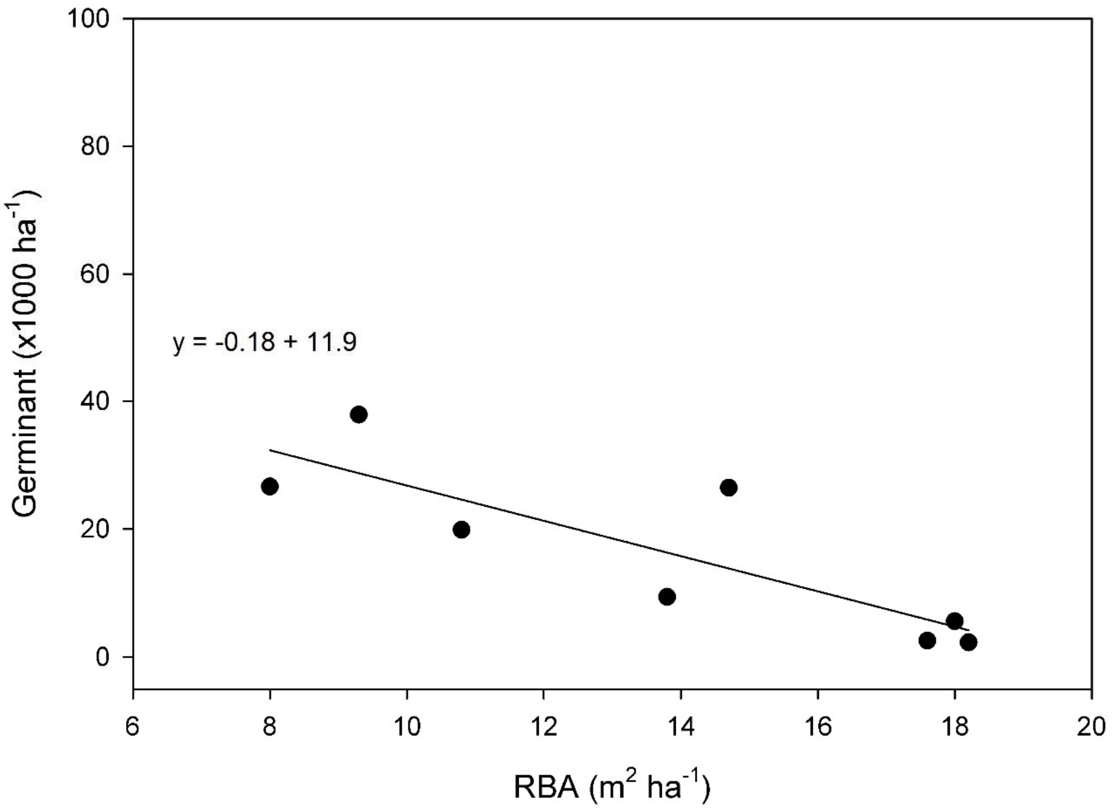

Figure 3.5: Relationships between RBA and number of germinants in the third growing season.

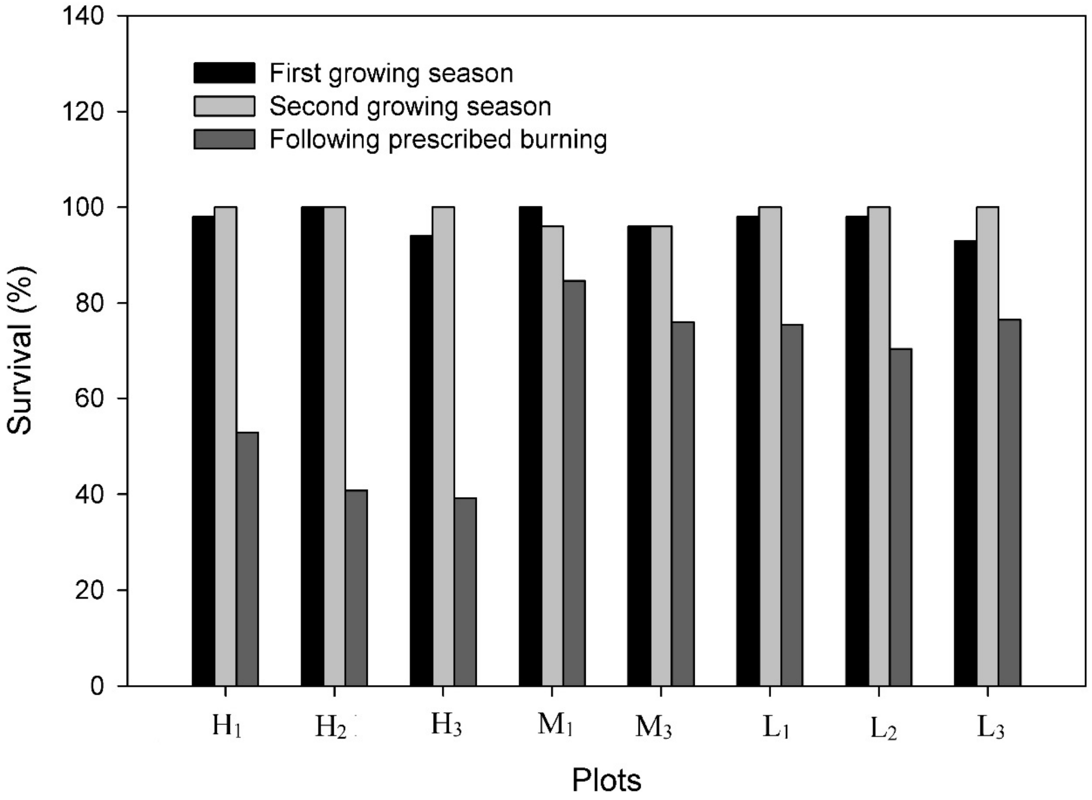

Figure 3.6: Relationships between RBA and survival of planted seedlings in the first and second growing season, and following prescribed burning.

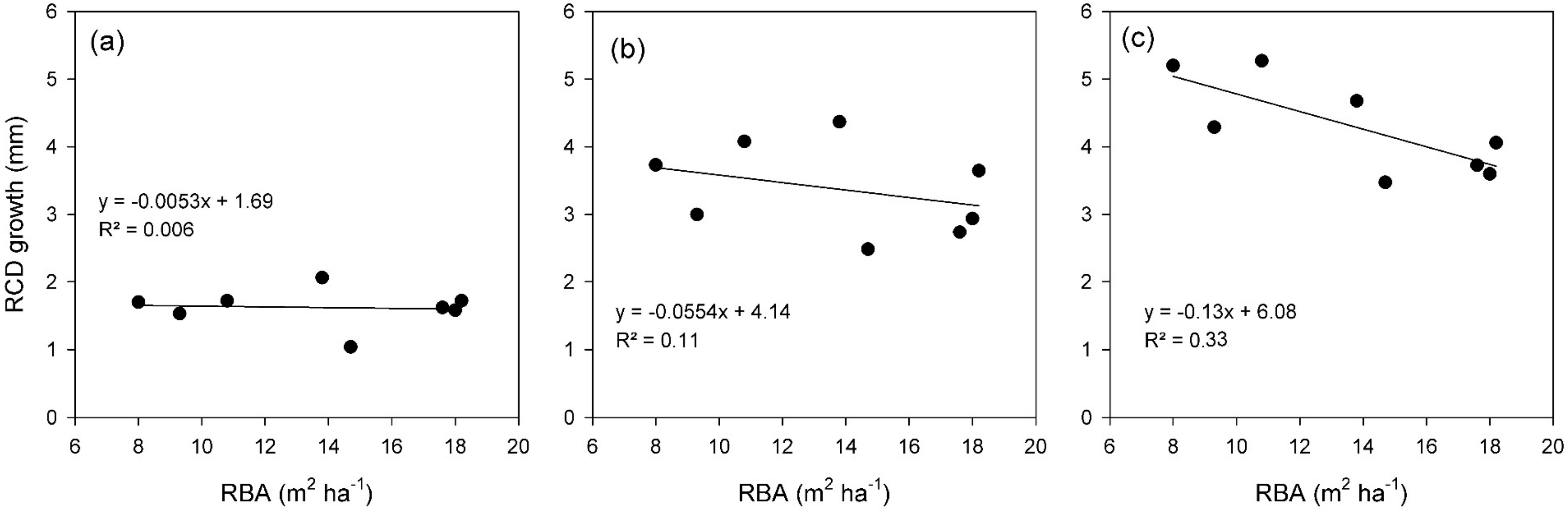

Figure 3.7: Relationships between RBA and RCD growth of planted seedlings (a) in the first growing season; (b) in the second growing season; (c) in the third growing season.

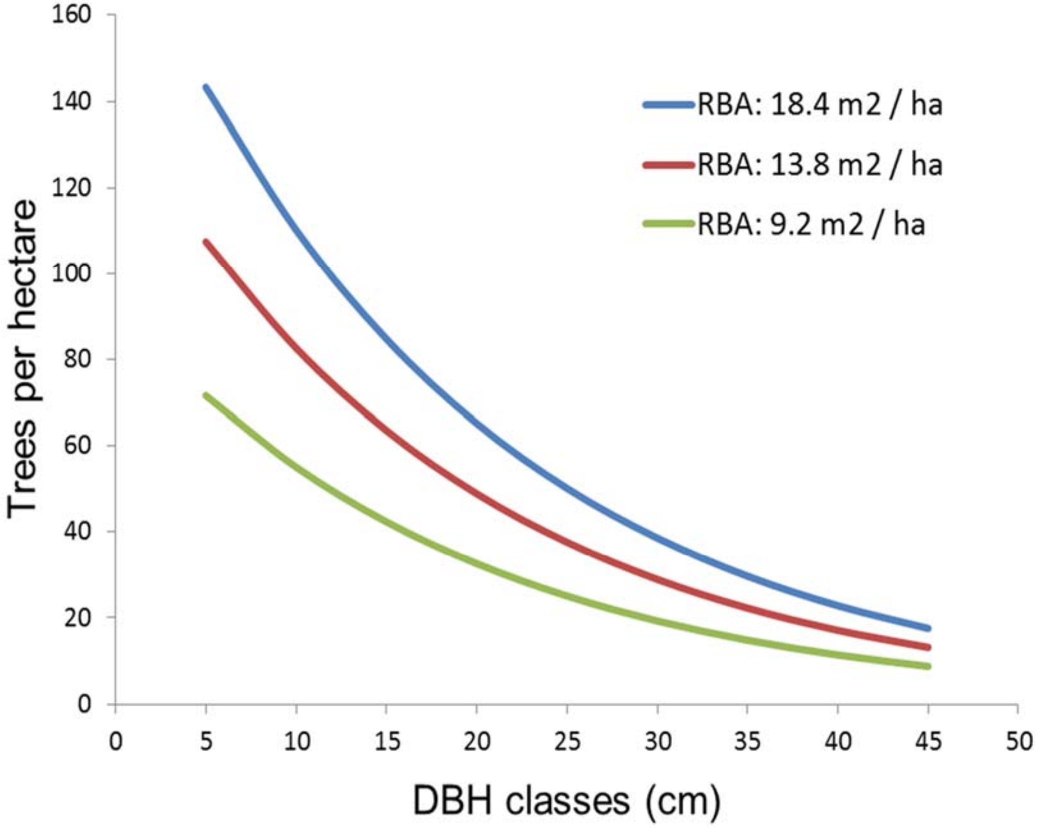

Figure 3.8: Target stand structures based on RBA created using the Pro-B method.

CHAPTER IV – A GINGRICH STYLE STOCKING CHART for LONGLEAF PINE (P*inus palustris* Mill.) AND ITS COMPARISON WITH BASAL AREA

Abstract: The dramatic decline in area dominated by longleaf pine (*Pinus palustris* Mill.) has generated a growing concern about the restoration of these forests. Stocking charts are useful silvicultural tools to allocate growing space to meet specific objectives; however, there has not been one created specifically for longleaf pine forests. Because successful management of longleaf pine is often associated with low-density management which is readily determined on a stocking chart, the development of one was needed. For this reason, a Gingrich style stocking chart was developed for longleaf pine forests by published approaches and models from the literature. Average maximum density was determined using forest inventory data while minimum density of full site occupancy was derived from a previously published open-growth crown width equation. Existing studies, physiological data, and longleaf pine silvical traits all support the accuracy of this stocking chart. We also examined two measures of stand density, stocking and basal area (BA), to determine which one is a better indicator of growing space allocation in longleaf pine forests. BA seems to be a better predictor than stocking with regard to germination; however, stocking better predicted overstory tree growth, growth of germinants, growth of planted seedlings, and survival of germinants and planted seedlings following a dormant-season fire.

***Keywords*:** A-line stocking, B-line stocking, longleaf pine, stand density, stocking chart.

1. INTRODUCTION

Stand density is an important ecological feature of forest structure (Sprintsin *et al.* 2009) because establishment, diameter growth, productivity and quality of trees are all affected (Zeide 2005), as are light regime beneath the canopy, respiration, evapotranspiration, and water consumption (Sprintsin *et al*. 2009). The growth rate and size of an individual tree is usually associated with available growing space which can be described in terms of stand density (Krajicek *et al.* 1961; Gingrich 1967). The number of trees on a unit area and individual tree size are strongly related; the smaller the tree size, the greater the number of trees that can potentially occupy a site (Zeide 1995). The maximum area that a tree can occupy is attained when the tree is open-grown and free from competition. Open-grown trees develop the largest crown possible (this relationship is species specific), relative to their diameter at breast height (DBH) (Krajicek *et al.* 1961). At the other end of the spectrum, the minimum tree area, which means that a tree has minimum necessary growing space to survive, is estimated from normally stocked stands (Gingrich 1967). Normal stocking is typical in undisturbed stands that are at or near maximum density for their age.

Stand density can be described with absolute or relative measures. Basal area per hectare (BA), trees per hectare (TPH) and volume per hectare are both quantitative and absolute measures of stand density. It should be noted that absolute measures are not comparable across stands; two stands with same TPH may not have necessarily same density if average tree size of the stands is different. On the other hand, relative density measures such as stocking refers to the availability of growing space among trees in a stand and is comparable (Gingrich 1967). A Gingrich style stocking chart combines measures of both absolute and relative density into one graph, and shows the average maximum density (A-line) as well as minimum density of full site occupancy (B-line) (Gingrich 1967). A-line stocking represents the average maximum density (N_{AMax}) of a stand, and refers to the minimum growing space required for a tree to survive under normally-stocked conditions. B-line stocking represents minimum density of full site occupancy (N_{MCA}), and refers to the maximum growing space that a tree can occupy under open-grown conditions (Lhotka and Loewenstein 2008). A stocking chart illustrates relationships between BA per hectare, TPH and quadratic mean diameter (QMD); stocking of a stand is obtained based on any two of these three measurements. Gingrich type stocking charts have been commonly used to determine relative density of stands in Eastern North America (Larsen *et al.* 2010).

BA alone is a commonly used measure of density when allocating growing space. However, Gingrich (1967) shows that growing space at a given BA varies with average tree diameter; stands with a larger average QMD represent lower stocking (fill less growing space) than stands with smaller average QMD at a given BA. Thus, it seems that stocking charts may offer a greater precision than BA alone when allocating growing space through silvicultural manipulation of a forest stand. This is likely important in stands that vary widely in tree diameters, and have non-normal diameter distributions such as UEA stands. In an EA plantation with a narrow normal distribution, stocking and BA may be interchangeable.

Growing space allocation in longleaf pine (*Pinus palustris* Mill.) forests is crucial for several reasons including the slow growth of longleaf pine seedlings under shade (Boyer 1993), its intolerance to competition under a high-density overstory (Brockway *et al.* 2006), and effects of residual BA on cone production (Croker and Boyer 1975). Therefore, deciding upon the optimal residual basal area (RBA) for successful regeneration, recruitment and growth of longleaf pine is vital, and consequently, a stocking chart for longleaf pine is needed. In this study, our objective was to develop a Gingrich style stocking chart for longleaf pine forests and compare it with BA in order to see which one is a better indicator in growing space allocation. We hypothesize that a stocking chart is a better indicator than BA for growing space allocation because of the reasons stated above.

2. METHODOLOGY

To fit the B-line stocking level, 105 open-grown longleaf pine trees that were free of competition were measured in Alabama. Maximum crown width (CW_{max}) and DBH were recorded. Because the crown of a tree will occupy the maximum area allocated to it up to a species specific physiological limit, the measurement of crown width is the best predictor of number of trees per unit area (Yang and Titus 2002). In addition, the correlation between crown width and diameter is known to be very strong (Zeide 1987) and their measurements are less subject to measurement errors (Yang and Titus 2002). Age and site quality were not recorded because it has been shown that these variables have negligible influence on tree area (Chisman and Schumacher 1940; Gingrich 1967). A linear regression between crown width and DBH were developed, and an equation to fit the B-line stocking was obtained. However, after comparing our B-line with a previously published equation (Smith *et al.* 1991), we found that the BA at our B-line was about 2 m^2 ha^{-1} higher suggesting that our open-grown trees had smaller crowns. Upon further investigation, we found that some of our open-grown trees had not been free of competition throughout their life span, thus, they may not have reached maximum crown expansion. For this reason, we decided to use the published equation (eq. 1) from Smith *et al.* (1992).

$$[1] \qquad CW_{max} = 0.113 + 0.259 * DBH \qquad (R^2=0.956)$$

Using equation 1, for each 5 cm DBH class, a CW_{max} was calculated in meters. Next, using equation 2 from Lhotka and Loewenstein (2008), the N_{MCA} was determined for each CW_{max}. BA (m^2 ha^{-1}) for each N_{MCA} was calculated using equation 3.

[2] $$N_{MCA} = 10000 / (CW_{max} * (\Pi / 4))$$

[3] $$BA = QMD^2 * 0.00007854 * N_{MCA}$$

To fit A-line stocking, the USDA Forest Service's Forest Inventory and Analysis (FIA) database for years 2000 through 2010 was used. Data plots from the States of Alabama, Georgia, Florida, South Carolina and Mississippi were downloaded from http://www.fia.fs.fed.us/tools-data/. Only fixed-radius plots were used. Each plot consists of four 7.3-m radius subplots in which all trees with a DBH of 12.7 cm and greater were measured (Woudenberg *et al.* 2010). Pure longleaf pine plots were selected in the database, and among those plots, the most fully-stocked plots were chosen using the following approach (data included in Appendix E). Stand density index (SDI) was calculated for each plot using Reineke's formula (eq.4).

[4] $$SDI = N \times (QMD / 25)^{1.605}$$

where N is number of trees per hectare. Relative density (RD), which is defined as the ratio of actual SDI to the max SDI (Drew and Flewelling 1979), was calculated for each plot. Plots with RD > 0.7 were selected as suggested by Solomon and Zhang (2002) because they state that self-thinning and density-related mortality should begin in stands with RD > 0.7. Another reason for choosing RD > 0.7 is to obtain sufficient number of plots to fit the A-line (Solomon and Zhang 2002).

Twenty-six plots were identified as fully-stocked plots. Given the number of plots used to determine the average maximum density for different tree species (Solomon and Zhang 2002; Pretzsch and Biber 2005; Lhotka and Loewenstein 2008; Comeau *et al.* 2010; Larsen *et al.* 2010), 26 plots seems to be acceptable. The number of plots used in these studies varies from 9 to 50 to fit the average maximum density line. The fitted A-line on the chart spans the range between QMD of 15 cm and 55 cm. It should be noted that the 26 fully-stocked plots are in the range of QMD of 21 cm and 40 cm. Table 4.1 gives the estimated slope and intercept for A-line and B-line.

Reineke (1933) suggests that the relationship between number of trees per unit area (N) and QMD is linear on a log-log scale (eq. 5).

$$[5] \qquad \ln(N) = b_0 - b_1 . \ln(QMD)$$

where b_0 and b_1 are coefficients. Thus, TPH and their QMD from fully-stocked plots were plotted on a log-log scale to estimate the coefficients for longleaf pine.

In forestry studies, fitting a line through a data set using regression techniques is a common means of analysis for prediction of one variable when another is known (Leduc 1987). In order to determine A-line stocking, both ordinary least square (OLS) regression and reduced major axis (RMA) regression have been used in several studies (Solomon and Zhang 2003;VanderSchaaf and Burkhart 2007; Lhotka and Loewenstein 2008; Comeau *et al.* 2010). Solomon and Zhang (2002) suggest that RMA regression gives less biased and efficient estimates than OLS when fitting size-density relationships. They state that when the variability of an independent variable (such as mean DBH) is as high as the variability of the response variable (such as density), RMA regression provides unbiased estimates. In addition, Leduc (1987) states that RMA is often the most appropriate method in forestry research for fitting a line to the data. He further mentions that OLS regression is not appropriate for fitting lines if the main interest is in the values of the equation parameters. Moreover, we compared OLS and RMA regressions, and decided to use RMA regression due to an extreme increase in stand BA at larger tree diameters when OLS regression was used. Mature longleaf pine trees grow more slowly after reaching 80 years (Chapman 1909;

Platt *et al.* 1988). When stands reach approximately 120 years, growth slows markedly and equals mortality (Chapman 1909). In dense stands (such as those growing at or near A-line stocking), and with increasing age, we do not believe that BA would increase at the rate predicted by the OLS regression.

Slope (β_{RMA}) and intercept (α_{RMA}) of RMA regression were calculated using equation 6 and equation 7 after Solomon and Zhang (2002).

[6] $$\beta_{RMA} = \beta_{OLS} / |Corr_{x,y}|$$

[7] $$\alpha_{RMA} = \mu N - \beta_{RMA}(\mu QMD)$$

where β_{OLS} is the slope of OLS, $Corr_{x,y}$ is the Pearson correlation between number of trees and QMD, μN is the mean density of plots with a RD > 0.7, and μQMD is the mean QMD of plots with a RD > 0.7.As a result, TPH and BA for each 5 cm diameter class were calculated after natural log transformation of the TPH and QMD. Finally, B-line and A-line stocking levels were fit on the same chart using the trend equation 8 as suggested by Lhotka and Loewenstein (2008). Stocking levels below A-line were determined as a proportion of average maximum density.

[8] $$BA = b_0 * (QMD)^{b1}$$

where b_0 and b_1 are coefficients.

2.1. Statistical analysis for the comparison of BA and stocking

BA and stocking were compared using structural equation models (SEM) that are multiple equation regression models (Fox 2002). SEMs are used for testing the overall causal structure of a path model (Karels *et al.* 2008). Path analysis can be used when a variable is influenced by other variables (Karels *et al.* 2008). Since stocking and BA influence each other, we used path analysis to test which one has more influence on germination, growth and survival. Standardized partial regression coefficients (r) were calculated for 1) overstory tree growth, 2) number of germinants, 3) growth of germinants, 4) survival of germinants following fire, 5) growth of planted seedlings, and 6) survival of planted seedlings following fire, regressed on each of the two variables; BA and stocking (Karels *et al.* 2008). These coefficients are the increase of the standard deviation of the dependent variable with one unit increase in the standard deviation of the independent variable (Karels *et al.* 2008). A smaller "r" (absolute value) means less influence of the independent variable on the dependent variable. Path coefficients are usually between -1 and +1; however, the coefficients can be larger (or smaller) when there is a high degree of multi-collinearity among variables (Joreskog 1999).

In addition, in order to observe statistically the significance of differences between BA and stocking, bootstrapping was used (Steury 2003; Higgins 2005). Bootstrapping is a statistical technique of resampling with replacement. In this method, random samples from a dataset are chosen with replacement, and each sample is analyzed the same way (Singh and Xie 2010). Bootstrapping procedure was repeated 1000 times for each relationship, and the confidence interval of the distribution of the differences in correlation coefficients was calculated using R-Statistical software (Steury 2003; R-Project 2008). If zero was not contained in the intervals, it was concluded that influence of the two variables was statistically significant (Steury 2003).

2.2. Additional data description

In order to validate the stocking chart, and compare it with BA, additional long term data from the U.S. Forest Service's Laboratory at Pineville, Louisiana was used (Goelz and Leduc 2001). Ninety six permanent longleaf pine plots were chosen from the dataset. The permanent plots in a combination of several studies have been regularly re-measured to monitor influence of spacing and thinning in longleaf pine plantations (Goelz and Leduc 2001). Plantations are located on both old field and cutover sites (Gonzalez-Benecke *et al*. 2012). Silt loams and sandy loams are the main soil textures on the plantations. Basal area (m^2 ha^{-1}), number of trees per hectare, and average tree diameter were determined for each plot. Basal area ranged from 10 to 50 m^2 ha^{-1} across all plots while number of trees ranged from 70 to 1500 trees, and average tree diameter ranged from 14 to 46.5 cm across all plots. Average tree diameter growth which is the mean diameter growth of all individual trees for a given plot was calculated for each plot. Growth was calculated for 5-year measurement periods for each plot where there was no thinning or tree mortality. Same statistical procedures (SEM and Bootstrapping) were used to compare stocking and BA for overstory tree growth.

3. RESULTS

3.1. Stocking chart of longleaf pine

Slope of our A-line fit with OLS regression (-1.6244) was close to Reineke's (1933) universal slope of -1.605. However, RMA regression was used due to reasons stated above. Based on the RMA regression, the slope on a log-log scale is -1.754, steeper than Reineke's slope (Table 5.1). Maximum SDI was calculated at 413, which is slightly greater, but similar to Reineke's (1933) maximum SDI of 400 for longleaf pine.

Gingrich style stocking charts for longleaf pine are presented in Figure 4.1(metric units) and in Figure 4.2 (English units). The A-line represents the average maximum density where trees, on average, have the minimum growing space needed to survive. The B-line represents the lowest density where canopy closure can occur and is the minimum stocking necessary for full site occupancy. In general terms, stands falling above the A-line are considered overstocked and tend toward the A-line as additional growth and density dependent mortality occur. Stands falling anywhere within the area between the A and B-lines are considered full-stocked; all of the available growing space is being utilized and approximately equal total volume is being added to the stand. Stands below B-line stocking are understocked (Gingrich 1967).

3.2. Comparison of stocking and basal area in growing space allocation

Percent stocking was calculated for each study plot (Table 5.2). Stocking values ranged from 22.5 to 44.7 % across all plots. Low RBA plots were below canopy closure (B-line) while mid-RBA plots were near or at B-line stocking and high-RBA plots were spread above the 40% stocking level (Figure 4.3).

There was a statistically significant inverse relationship between stocking and cumulative number of germinants through year 3 (p=0.0098). Higher number of germinants was observed under lower stocking conditions. No relationship was found between stocking and survival of germinants (p=0.94) and underplanted seedlings (p=0.93). Stocking level significantly accounted for cumulative RCD growth of both germinants (p=0.0031) and planted seedlings (p=0.006) at the end of the third growing season. Stocking significantly explained the impacts of a dormant-season burning on the survival of germinants (p=0.007) and planted seedlings (p=0.022). Higher survival was observed under lower stocking conditions.

Stocking had more influence than BA on the cumulative growth of germinants at the end of the third growing season (Table 4.3). In addition, the effects of stocking on the cumulative growth of planted seedlings were larger than the effects of BA during three-year period. As stated before, if zero is not within the confidence interval following the bootstrapping procedure, it means that difference between BA and stocking is significantly different. For this reason, the difference between BA and stocking on the seedling growth was statistically significantly different (Table

4.4). Compared to BA, stocking level had more effect on the survival of both germinants and planted seedlings following burning (Table 4.3). However, the difference between BA and stocking on the seedling survival was not statistically significant (Table 4.4).

It should be noted that our nine study plots were not well distributed across the range of average tree diameter on the stocking chart (Figure 4.3). For this reason, we used a long term dataset provided by the U.S. Forest Service's Laboratory at Pineville to compare influence of BA and stocking on the diameter growth of longleaf pine trees. Ninety six plots from the dataset were well distributed across the average tree diameter (from 14 to 46.5 cm), and across the BA (from 10 to 50 m^2 ha^{-1}). Influence of stocking on the diameter growth of longleaf pine trees was larger than influence of BA (Table 4.3). However, difference between the influences of BA and stocking on diameter growth was not statistically significantly different (Table 4.4).

Although stocking seemed to have more influence than BA on the growth and survival of longleaf pine seedlings, and on the growth of overstory trees, BA had more effect than stocking on the germination of longleaf pine across all plots (Table 4.3). However, influence of BA on the germination was not statistically significant than influence of stocking on the germination (Table 4.4).

4. DISCUSSION

4.1. Stocking chart of longleaf pine

A-line on our stocking chart ranges between 36-50 m^2 ha^{-1}. This high amount of BA in the range of A-line demonstrates that mature longleaf pine trees can maintain growth even in dense stands (Platt *et al.* 1988). Although longleaf pine seedlings are very intolerant of competition (Brockway and Outcalt 1998), mature and large longleaf trees become very tolerant of competition due to well-developed root systems and heavy stems developed at an early age (Strauss and Ledig 1985). Known as a long-lived tree species, longleaf pine continues to grow after 80-100 years of age (Chapman 1909; Platt *et al.* 1988), and are able to reach 500 years (Boyer 1999). Meldahl *et al.* (1999) observed continued growth even among suppressed trees, and pointed out the tolerance of longleaf pine at older ages as well. Self-thinning usually begins at approximately 80 percent stocking (Shaw and Long 2007). The threshold of self-thinning (SDI of 250) from Shaw and Long's (2007) density diagram for longleaf pine coincide with our 75-80 percent stocking levels. This would seem to support the accuracy and utility of our stocking chart.

The B-line on our chart appears nearly flat, suggesting that the crown width of longleaf pine trees continue to increase in direct relation to BA as trees get older and larger. Smith *et al.* (1992) examined the relationship between crown width and DBH for three pine species (longleaf, loblolly, and slash pines), and fitted the regression lines for each species. They note that the relationship for longleaf pine was significantly different than for loblolly and slash pines; the slopes decrease for loblolly and slash pines as DBH increases (Smith *et al.* 1992). The curved B-line on the Gingrich (1967) stocking chart for upland oaks shows a similar relationship. This is in contrast with the slope of the B-line for longleaf pine which is linear, demonstrating that crown width continuously increases with increasing DBH (Smith *et al.* 1992). Schwarz (1907) also notes this relationship between crown and DBH, observing that larger crowns are developed as diameter increases in open stands. Thus, in stands with large trees, canopy closure occurs with fewer trees and at a lower BA than is typical in other species. This is what makes the B-line nearly flat. Examining our B-line in relation to Shaw and Long's (2007) density diagram for longleaf pine, it falls within the range between their lower limit of full site occupancy and the transition from open-grown conditions to competing state.

On the chart, curved stocking lines may span a substantial range of BAs, especially as stocking percentage increases, thus, the chart should be very useful when allocating growing space to manage a trait that is tied to some specific level of stocking. However, unlike other southern pine species like loblolly pine and slash pine (Smith *et al.* 1992) or upland central hardwood (Gingrich 1967) where canopy closure, the B-line, closely parallels a given stocking percentage, the B-line for longleaf pine is fairly flat. Across a QMD from 15-55 cm DBH, the BA at which canopy closure occurs varies by less than 1 m^2 ha^{-1} whereas stocking percentage varies by nearly 10% (Figure 4.1). Thus, BA may be a better indicator than stocking when managing for an objective that requires manipulation of a longleaf stand in relation to canopy closure.

4.2. Comparison of stocking and basal area in growing space allocation

As stated before, two stands with same BA may have different amount of growing space depending on the average size of the trees (Martin 1996). Gingrich (1967) concluded that a stand with larger QMD will provide more growing space than a stand with smaller QMD for a given BA, suggesting that available growing space can be explained better by stocking rather than BA. Our analysis substantiates Gingrich's statement with one exception. We found that stocking was a better indicator than BA for seedling growth and seedling survival. However, it was observed that BA had more influence than stocking on the germination of longleaf pine across all plots (Table 5.3). This may suggest that, in addition to growing space, there are other factors that influence the number of germinants in longleaf pine stands. Number of germinants is related to cone production per tree, while cone production of a tree is affected by tree size, crown class, stand density, and genetics (Wahlenberg1946; Boyer 1990; Brockway *et al.* 2006). Boyer (1990) stated that trees with 38 cm or larger in diameter are the best cone producers. Trees in this diameter range produce an average of 65 cones per tree while trees from 25 to 33 cm in diameter produce about 15 cones per tree (Boyer 1990). The chart shows that, for a given stocking level, average size of the trees is increasing with increasing BA. For example; consider two stands at 30% stocking level, and one with 12 m^2ha^{-1} of BA while the other with 15 m^2ha^{-1} of BA. Between these stands, the one with higher BA will have larger trees in diameter, and potentially better cone producer suggesting that BA may have more influence than stocking on germination. However, it should be noted that the influence of BA on the germination was not statistically significant than the influence of stocking on the germination.

As stated above, although stocking had more influence than BA on the diameter growth of longleaf pine trees, the differences between BA and stocking were not statistically significantly different (Table 4.4). This may be due to the very high correlation between stocking and BA in the plantation plots (Figure 4.4). Plantations are usually more uniform in terms of diameter distribution and tree spacing. This uniformity might have probably increased the correlation relationship between BA and stocking in plantations, and consequently an insignificant relationship between the influence of BA and stocking was obtained. As stated before, in an EA plantations with a narrow normal distribution, stocking and BA may be interchangeable.

5. CONCLUSIONS

A Gingrich style stocking chart was developed for longleaf pine forests. An average maximum density equation was created from forest inventory data obtained from normally stocked stands using generally accepted methodology. In addition, a published equation developed from open-grown trees was used to determine minimum density of full site occupancy.

In practice, foresters commonly use BA when prescribing residual stand density since it is a commonly used and understood measure. However, it is believed that stocking is a better description of residual stand density than BA because the amount of available growing space changes based on average tree diameter at a given BA. Our findings show that stocking usually has more influence than BA, but this may not be the case for processes influenced by canopy closure due to the unique nature of open grown canopy dynamics in longleaf pine. Due to its ease of use, this chart will be a handy tool for managing longleaf pine forests within their natural range. The chart can be used to determine average growing space of a stand based on any two of three measurements; BA, TPH and QMD. As a result, growing space will be fully and more effectively used to achieve specific objectives including regeneration, timber production, and thinning and wildlife purposes.

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Table 4.1: Summary of data sources for the stocking chart.

Stocking Level	Number of Plots	Source of Data	Slope	Intercept	R^2
A-Line	26	FIA database	-1. 754	5. 377	0.85
B-Line	81	Smith *et al.* (1992)	0.259	0.113	0.96

Table 4.2: Percent stocking of study plots.

Study plot	Final BA (m^2/ha)	Stocking (%)
H_1	17.6	42.2
H_2	18.2	43.2
H_3	18.0	44.7
M_1	14.7	35.0
M_2	14.5	34.5
M_3	13.8	32.6
L_1	8.0	20.8
L_2	9.3	22.8
L_3	10.8	25.0

Table 4.3: Influences of basal area and stocking on the number of germinants, growth of germinants, survival of germinants during fire, growth of planted seedlings, and survival of planted seedlings during fire. Effects are the path coefficients (r). A larger |r| indicates greater influence.

	Basal area	Stocking
Overstory growth	0.13	-0.89
Number of germinants	-1.56	0.72
Growth of germinants	2.87	-3.75
Survival of germinants during fire	1.83	-2.74
Growth of planted seedlings	2.77	-3.37
Survival of planted seedlings during fire	3.32	-4.01

Table 4.4: Confidence intervals (CI) of bootstrapping analysis. If zero is not within the CI, the differences between the two independent variables, stocking and BA, is significant.

	Confidence Intervals
Overstory growth	(-54.03 , 24.43)
Number of germinants	(-1.97 , -0.34)
Growth of germinants	(-0.70 , -0.34)
Survival of germinants during fire	(-1.59 , 0.78)
Growth of planted seedlings	(-1.30 , -0.47)
Survival of planted seedlings during fire	(-1.77 , 0.43)

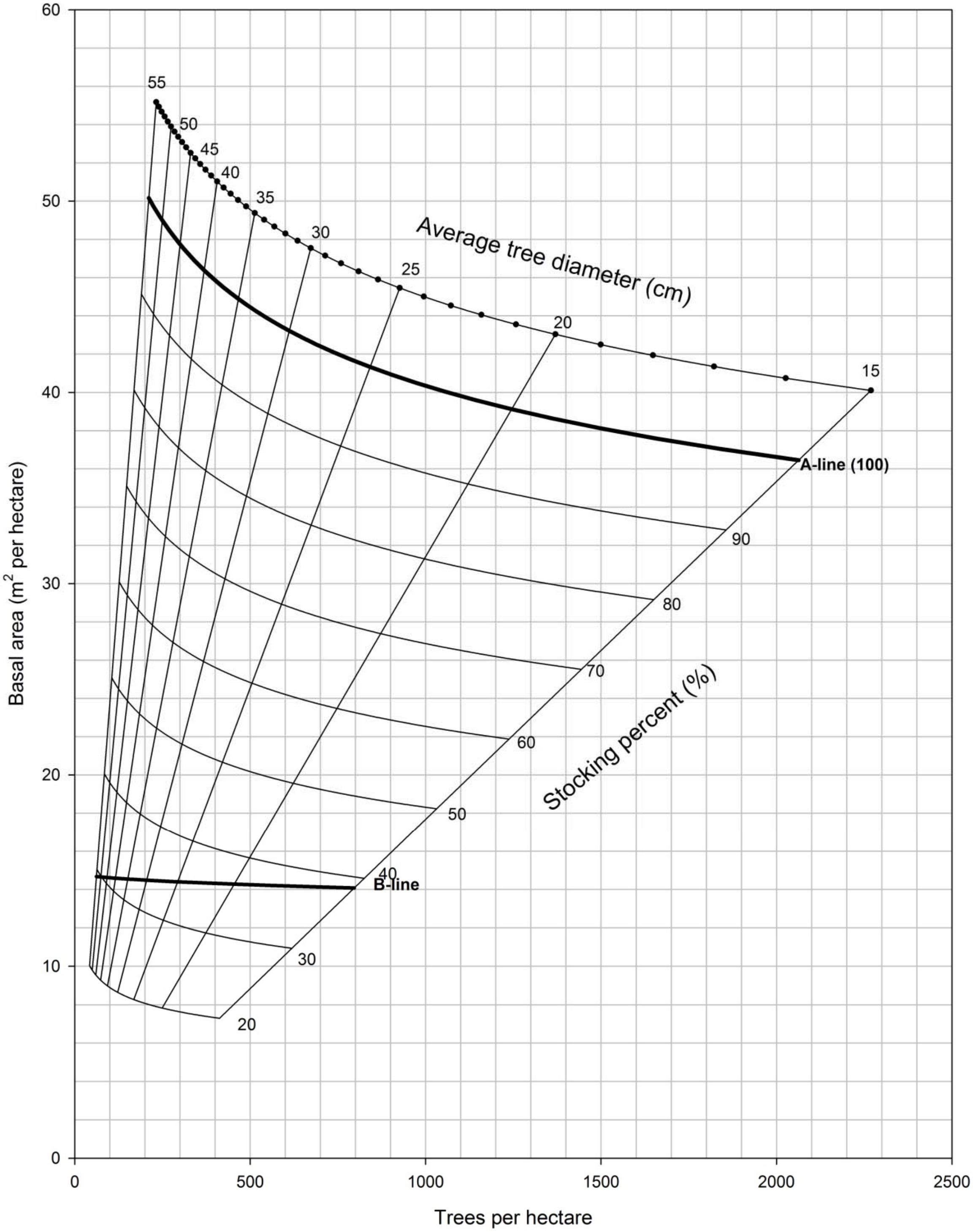

Figure 4.1: Gingrich style stocking chart for longleaf pine in metric units.

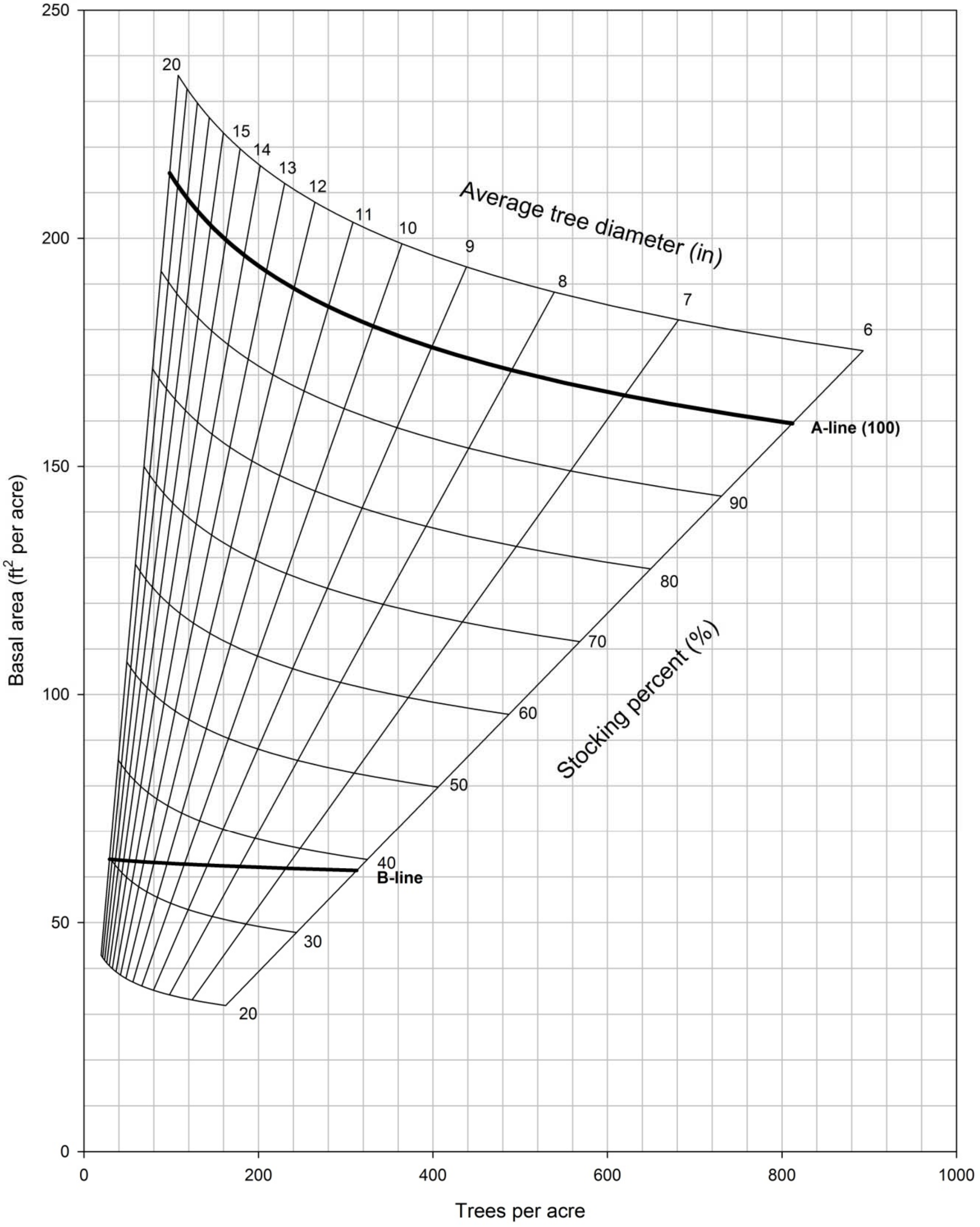

Figure 4.2: Gingrich style stocking chart for longleaf pine in English units.

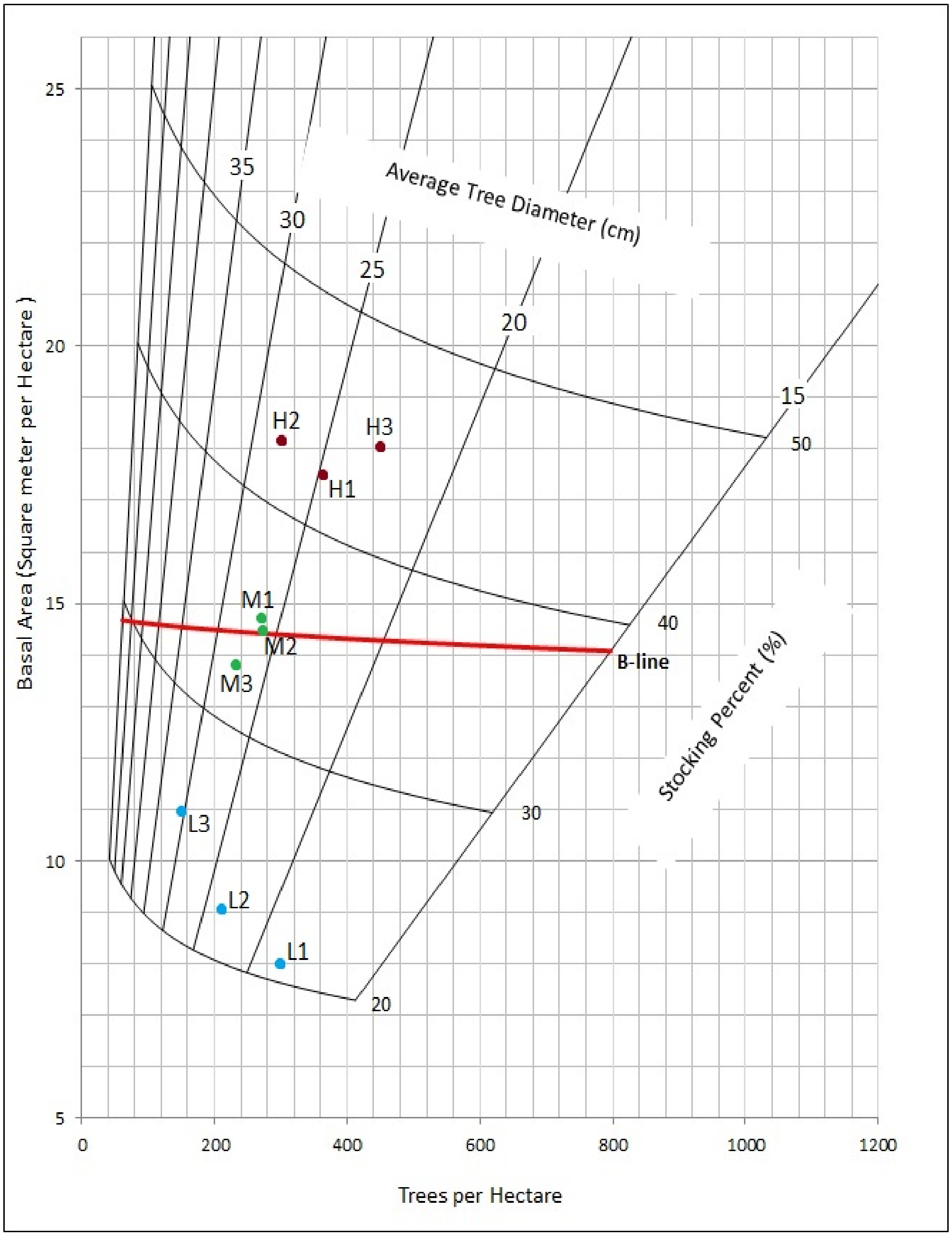

Figure 4.3: Distribution of each study plot on the stocking chart.

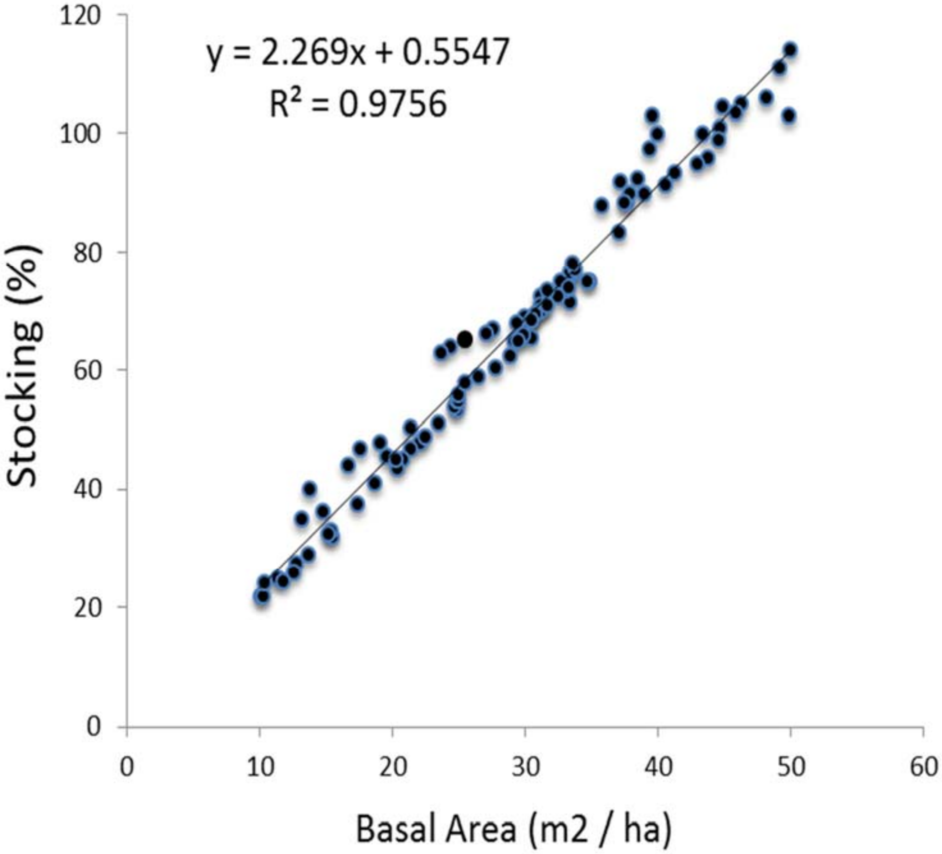

Figure 4.4: Relationship between basal area and stocking of the plantation plots.

CHAPTER V – CONCLUSIONS

1. Project summary

Because uneven-aged silviculture may better fulfill some stewardship objectives than EA systems, it appears to be a valuable tool for managing longleaf pine stands under multiple-use management. However, the influences of stand density on the successful regeneration of longleaf pine forests under uneven-aged methods are not fully understood. The success of an uneven-aged system relies on episodic recruitment of new cohorts into the overstory. Thus, successful development and implementation of uneven-aged systems requires understanding the linkage between overstory density and its influence on the response of seedlings. The goal of this project was to expand the current understanding of the relationship between stand density, IPAR, seed germination, seedling growth and survival across a gradient of overstory density ranging from 9.2 to 18.4 m^2 ha^{-1}.

This study was initiated on the Escambia Experimental Forest which is dominated by longleaf pine. The RBA gradient was created by randomly assigning one of three levels of overstory density to nine 2-hectare square plots. The relationships between stand density, IPAR, seed germination, seedling survival and growth were observed by direct measurements of seedling numbers, root collar diameter, IPAR and basal area. Linear regression analysis was used to examine the relationships.

Number of germinants increased with decreasing stand density. This seems to be primarily due to higher levels of light penetration to the ground with decreasing stand density. Stand density did not influence mortality of germinants. Most of the germinants survived under varying levels of stand densities. This substantiates the fact that new longleaf seedlings may remain and survive in its well-known grass stage for a prolonged period of time. Growth of germinants was affected by stand density; larger root collar diameters were recorded under lower stand density by the end of third growing season. Stand density also influenced the impact of a dormant-season burning on germinants, following their second growing season. Higher stand density resulted in higher fuel accumulation, and consequently higher mortality of germinants. Germinant size influenced survival following prescribed burning. Germinants with larger root collar diameter seem to be more resistant to burning. In addition, stand density did not have any effect on the mortality of seedlings. Most of the seedlings survived under varying levels of stand densities during three growing seasons. Overstory density did not influence the growth of seedlings in the first two growing seasons, but, larger root collar diameters were recorded under lower stand densities by the third growing season. The lack of significance between stand density and seedling growth for the first two years may be explained by transplant shock in the first year of planting. Moreover, stocking level had more influence than basal area on growth and survival of seedlings.

This study aimed to extend the current understanding of the stand density-germination, stand density-growth, and stand density-mortality relationships within longleaf pine forests of southeastern USA. The results presented in this study reflect how stand density influences regeneration success in longleaf pine forests. Stand density has produced variable effects on seedling number, mortality, and seedling size across longleaf pine stands. Data indicate that variability of overstory density and periodic fire influence the existence of longleaf seedlings and their competitors in the understory.

2. Management Implications

This study documented the linkage between stand density and longleaf pine reproduction. Determining optimum overstory density under uneven-aged systems is important for survival establishment, and recruitment of longleaf pine seedlings. Results show that decreasing basal area increased germination, survival, and growth of seedlings. However, regression equations presented in this study should not be used in the direct estimate of germination, survival, or growth of seedlings in all longleaf pine ecosystems, because other factors such as moisture and soil may influence regeneration success of longleaf pine as well.

Basal area is a practical and easily understood approach, thus, it is commonly used by foresters and silviculturists when manipulating stand density. However, stocking may be a more precise and appropriate index to use. The stocking chart created in this project seems to be a useful tool when making density-related management decisions. Above all, results highlight the importance of considering the potential effects of stand density on the development of longleaf pine reproduction.

2.1. A prediction of seedling recruitment

We simply projected seedling recruitment into the overstory for each level of stand density using the current observations and suggestions in the literature. Although it is controversial, this prediction may roughly give some idea on the number of seedlings that we may expect to recruit into the overstory.

Low density plots- Average number of germinants in the third growing season was 28000 per hectare. Average RCD growth was 1.88 mm per year on low RBA plots. Similarly, Boyer (1963) found that average RCD growth was 1.7 mm per year under same level of stand density (9.2 m^2 ha^{-1}). This growth rate is also consistent with some other studies (Gagnon *et al*. 2003; Dyson 2010). In addition, Boyer (1963) found an average survival of 72% by age 7 under varying levels of stand densities, and stated that fire was mostly responsible for the mortality (two burnings were conducted at age 3 and 6) and survival was as high as 90% in the absence of fire. Our three year observation on the mortality substantiate the mortality rates suggested by Boyer (1963); average mortality during fire was 20% during the first dormant season fire conducted at age 2, and average survival was 97% in the absence of fire. As stated before, longleaf pine seedlings bolt from grass stage, begin rapid height growth, and recruit into the overstory when they reach a RCD of 25 mm. With the growth rate that we observed during 3-year period and suggested by the literature studies (Boyer 1963; Gagnon *et al*. 2003; Dyson 2010), seedlings would reach the RCD of 25 mm at age 13 under low RBA plots. In addition, using the mortality rate that we observed during 3-year period and suggested by the literature studies (Boyer 1963), we would expect to have an average of 7000 seedlings per hectare under low stand densities. It should be noted that plots will be burned every two years, and plots will be cut to the target RBA at year 10 before seedlings reach age 15. It is suggested that an average mortality of 50% during logging operations is common (Maple 1977; Boyer 1990). Our target stand structure recommend ~70 seedlings per hectare which is substantially higher than we project in the smallest diameter class (0-5 cm in DBH).

Middle density plots- Average number of germinants was 18000 per hectare by age 3. Average RCD growth was 1.63 mm per year on middle RBA plots. Similarly, Boyer (1963) found an average RCD growth of 1.6 mm per year under same level of stand density (13.8 m^2 ha^{-1}). Average mortality during fire was 44% during the first dormant season fire conducted at age 2, and average survival was 98% in the absence of fire. Based on the growth and mortality rates from 3-year measurements and literature studies, we expect to have an average of 1000 seedlings per hectare that would reach the RCD of 25 mm at age 14 under middle RBA plots. The target stand structure recommends 110 seedlings per hectare which is again higher than we project in the smallest diameter class (0-5 cm in DBH).

High density plots- Average number of germinants was 3500 per hectare by age 3 in high density plots. Average RCD growth was 1.43 mm per year. Similarly, Boyer (1963) found an average RCD growth of 1.4 mm per year under same level of stand density (18.4 m^2 ha^{-1}). Average mortality during fire was relatively higher (72%) during the first dormant season fire conducted at age 2, and average survival was 97% in the absence of fire. The growth and mortality rates from 3-year measurements and literature studies suggest that we would expect to have an average of 47 seedlings per hectare when they would reach the RCD of 25 mm at age 17 under middle RBA plots. For the higher density plots, required number of seedlings per hectare in the smallest diameter class (0-5 cm in DBH) is 145 seedlings per hectare which is lower than required.

3. Future Recommendations

Although this study suggests that uneven-aged silviculture may work in longleaf pine forests, more potential avenues of applied research remain. Long-term monitoring of these seedlings is needed. Because the study cannot be concluded until recruitment of the seedlings into the overstory is observed, additional measurements are required to gain a better understanding of the applicability of single-tree selection in longleaf pine forests. The present data are not sufficient to state unequivocally that the single-tree selection system works in longleaf pine forests. However, at the same time, present data does not show any evidence that this approach cannot be successful in sustaining an uneven-aged longleaf pine stands.

Inferences gained from this research will inform future discussions about the applicability of uneven-aged systems in longleaf pine forests. Seedling recruitment prediction suggests that 9.2 m^2 ha^{-1} RBA may be too low to sustain a longleaf pine forest under selection silviculture because substantial number of seedlings may be obtained when they recruit into the overstory. On the other hand, under high density plots, it may be expected to have inadequate number of seedlings to sustain a longleaf pine forest because less than required number of seedlings may be recruited into the overstory. Middle level of RBA may also recruit more than required seedlings. Thus, as a future hypothesis, levels of RBA can be chosen between 13.8 and 18.4 m^2 ha^{-1} to determine the optimum stand density to sustain a longleaf forest under selection silviculture. Future research should also include investigating the recruitment of longleaf seedlings in stands of varying soil types and soil moisture. In addition, several studies suggested that distance from adult trees effects the growth of longleaf pine trees (Brockway *et al*. 2006). However, we were not able to measure distance between seedlings and overstory trees in this study. In future studies, stem-map of seedlings can be generated to better observe their relationship with overstory trees. Moreover, carbon sequestration of longleaf pine seedlings under varying levels of stand densities can be monitored in long term. Influence of varying stand densities on the development of root system, and below and above ground biomass of longleaf pine seedlings can be investigated. Furthermore, physiological responses of longleaf pine seedlings to seasonal prescribed fires can be evaluated in future studies. Such work may develop alternative silvicultural strategies for continuous cover multiple-use management in longleaf pine forests.

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APPENDICES

APPENDIX A

MARKING GUIDE OF EACH STUDY PLOT

	DBH					PLOTS				
	Classes	L_1	L_2	L_3	M_1	M_2	M_3	H_1	H_2	H_3
	(cm)	9.2	9.2	9.2	13.8	13.8	13.8	18.4	18.4	18.4
		m^2/ha	m^2/ha	m^2/ha	m^2/ha	m^2/ha	m^2/ha	m^2/ha	m^2/ha	m^2/ha
Inventory	0-15 dbh	1.5	0.96	0.3	0.4	1.8	0.4	1.8	0	1.6
(m2/ ha)	15-30 dbh	4.5	3.72	3.3	15.5	10.8	11.7	18.3	18.8	15
	30 + dbh	5.6	9.07	12.3	9	17.1	7.2	9.9	11	5.3
Target	0-15 dbh	1	1	1	1.5	1.5	1.5	2	2	2
(m2/ ha)	15-30 dbh	3.6	3.6	3.6	5.4	5.4	5.4	7.2	7.2	7.2
	30 + dbh	4.6	4.6	4.6	6.9	6.9	6.9	9.2	9.2	9.2
Cut	0-15 dbh	0.5	-0.04	-0.7	-1.1	0.3	-1.1	-0.2	-2	-0.4
(m2/ ha)	15-30 dbh	0.9	0.12	-0.3	10.1	5.4	6.3	11.1	11.6	7.8
	30 + dbh	1	4.47	7.7	2.1	10.2	0.3	0.7	1.8	-3.9
Cut %	0-15 dbh	0.33	-0.05	-2.33	-2.75	0.17	-2.75	-0.11	0.00	-0.25
	15-30 dbh	0.20	0.03	-0.09	0.65	0.50	0.54	0.61	0.62	0.52
	30 + dbh	0.18	0.49	0.63	0.23	0.60	0.04	0.07	0.16	-0.74
Marking	0-15 dbh	1 of 3	None	None	None	1 of 5	None	None	None	None
Guide	15-30 dbh	1 of 5	None	None	2 of 3	1 of 2	1 of 2	3 of 5	3 of 5	1 of 2
	30 + dbh	1 of 5	1 of 2	3 of 5	1 of 4	3 of 5	None	None	1 of 5	None

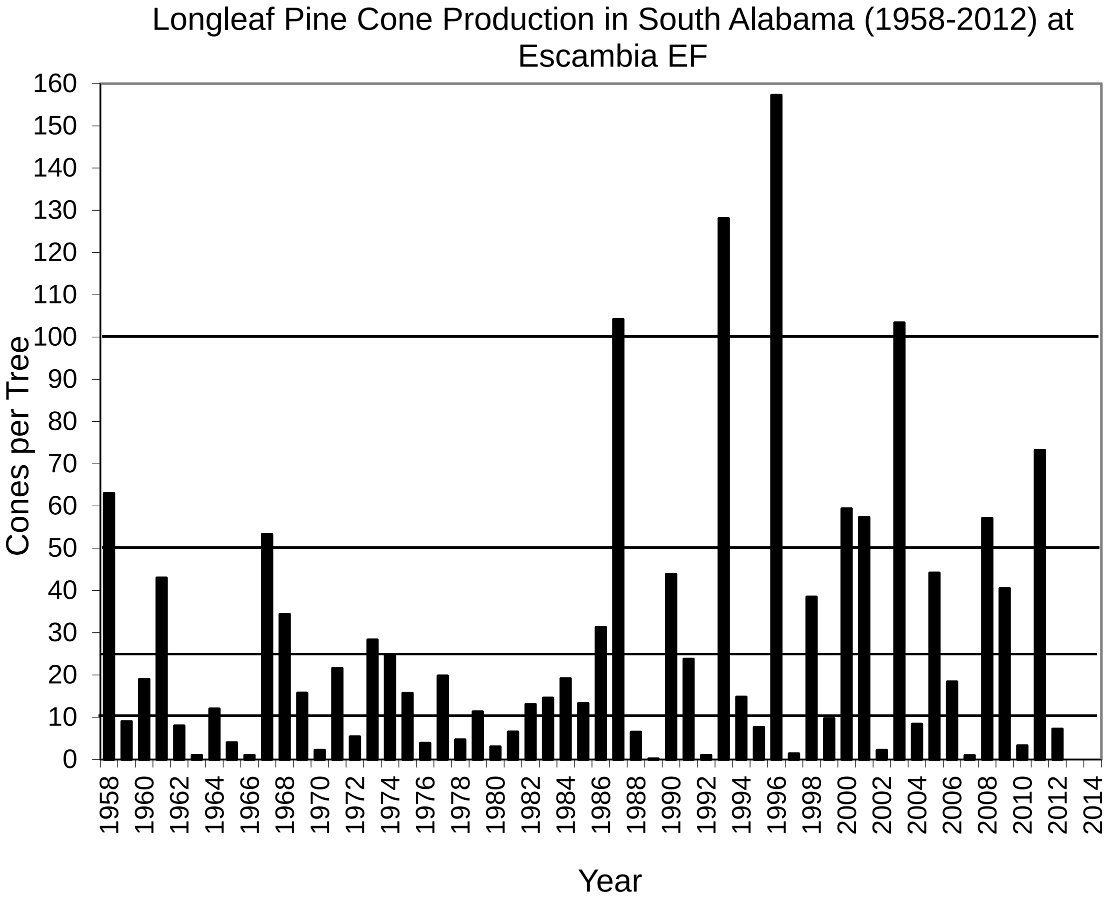
Summary table of the marking guide for the study plots

	DBH					PLOTS				
	Classes (cm)	L_1	L_2	L_3	M_1	M_2	M_3	H_1	H_2	H_3
Marking	0-15 dbh	1 of 3	None	None	None	1 of 5	None	None	None	None
Guide	15-30 dbh	1 of 5	None	None	2 of 3	1 of 2	1 of 2	3 of 5	3 of 5	1 of 2
	30 + dbh	1 of 5	1 of 2	3 of 5	1 of 4	3 of 5	None	None	1 of 5	None

Final marking guides for the study plots

APPENDIX B

CONE CROP REPORT of 2011 and 2012 for LONGLEAF PINE



Classification of longleaf pine cone crops*

Crop Quality	Cones per Tree	Cones per Acre (on 25 trees per acre)
Bumper crop	≥ 100	≥ 2500
Good crop	50 to 99	1250 to 2475
Fair crop	25 to 49	625 to 1225
Poor crop	10 to 24	250 to 600
Failed crop	< 10	< 250

---

* Cones on mature (14 to 16 inches DBH) trees in low-density stands (< 40 feet^2/acre basal area).

APPENDIX C

REGRESSION MODELS FOR LONGLEAF PINE GERMINANTS AND PLANTED SEEDLINGS FOR THREE GROWING SEASONS FOLLOWING GERMINANTION AND PLANTING

Appendix C.1: Poisson regression model for the influence of RBA on longleaf pine germination

```
glm(formula = Germi ~ RBA, family = poisson, data = datum)

Deviance Residuals:
   Min      1Q  Median      3Q     Max
-93.32  -68.00  -47.11   21.52  189.41

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept) 12.3596643  0.0055037  2245.7   <2e-16 ***
RBA         -0.1227078  0.0004307  -284.9   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 146688  on 8  degrees of freedom
Residual deviance:  63458  on 7  degrees of freedom
  (13 observations deleted due to missingness)
AIC: 63573
```

Appendix C.2: Poisson regression model for the influence of RBA on the number of longleaf pine germinants in the first growing season

```
glm(formula = Germ1 ~ RBA, family = poisson, data = datum)

Deviance Residuals:
   Min      1Q  Median      3Q     Max
-59.59  -56.04  -31.97   24.65  138.79

Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) 11.515963   0.007494  1536.7   <2e-16 ***
RBA         -0.102244   0.000582  -175.7   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 64990  on 7  degrees of freedom
Residual deviance: 33218  on 6  degrees of freedom
  (14 observations deleted due to missingness)
AIC: 33317
```

Appendix C.3: Linear regression model for the influence of RBA on the survival of longleaf pine germinants in the first growing season

```
lm(formula = GermSurv1A ~ RBA, data = datum)

Residuals:
     Min       1Q   Median       3Q      Max 
-0.10787 -0.06749 -0.01176  0.02466  0.19679 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)  
(Intercept)  0.40223    0.14623   2.751   0.0333 *
RBA          0.01368    0.01022   1.339   0.2290  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.1096 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.2301,    Adjusted R-squared:  0.1018 
F-statistic: 1.794 on 1 and 6 DF,  p-value: 0.229
```

Appendix C.4: Poisson regression model for the influence of RBA on the number of longleaf pine germinants in the second growing season

```
glm(formula = Germ2 ~ RBA, family = poisson, data = datum)

Deviance Residuals:
   Min      1Q  Median      3Q     Max
-58.15  -54.44  -31.69   22.97  136.73

Coefficients:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) 11.487844   0.007608  1509.9   <2e-16 ***
RBA         -0.102433   0.000591  -173.3   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 62931  on 7  degrees of freedom
Residual deviance: 32001  on 6  degrees of freedom
  (14 observations deleted due to missingness)
AIC: 32100
```

Appendix C.5: Linear regression model for the influence of RBA on the survival of longleaf pine germinants in the second growing season

```
lm(formula = GermSurv2A ~ RBA, data = datum)

Residuals:
      Min        1Q    Median        3Q       Max
-0.072852 -0.008553  0.003302  0.015699  0.047701

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept) 1.3118270  0.0561016  23.383 4.01e-07 ***
RBA         0.0007923  0.0039199   0.202    0.847
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.04206 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.006763,  Adjusted R-squared:  -0.1588
F-statistic: 0.04085 on 1 and 6 DF,  p-value: 0.8465
```

Appendix C.6: Linear regression model for the influence of RBA on the survival of longleaf pine germinants following dormant season burning

```
lm(formula = FireSurvGA ~ RBA, data = datum)

Residuals:
     Min       1Q   Median       3Q      Max 
-0.23122 -0.06321 -0.01279  0.06902  0.24252 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  1.56071    0.19955   7.821 0.000231 ***
RBA         -0.06926    0.01394  -4.968 0.002533 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 0.1496 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.8044,    Adjusted R-squared:  0.7718 
F-statistic: 24.68 on 1 and 6 DF,  p-value: 0.002533
```

Appendix C.7: Poisson regression model for the influence of RBA on the number of longleaf pine germinants in the third growing season

```
glm(formula = Germ3 ~ RBA, family = poisson, data = datum)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-58.666  -53.664  -24.953    5.775  122.520

Coefficients:
              Estimate Std. Error z value Pr(>|z|)
(Intercept) 11.8993036  0.0095029  1252.2   <2e-16 ***
RBA         -0.1752560  0.0007997  -219.1   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for poisson family taken to be 1)

    Null deviance: 82421  on 7  degrees of freedom
Residual deviance: 28451  on 6  degrees of freedom
  (14 observations deleted due to missingness)
AIC: 28544
```

Appendix C.8: Linear regression model for the influence of RBA on the growth of longleaf pine germinants in the third growing season

```
lm(formula = GermGroL ~ RBA, data = datum)

Residuals:
     Min       1Q   Median       3Q      Max 
-0.03716 -0.02580  0.00066  0.01687  0.04361 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.873415   0.045202   19.32 1.24e-06 ***
RBA         -0.013170   0.003158   -4.17  0.00588 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 0.03389 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.7435,	Adjusted R-squared:  0.7007 
F-statistic: 17.39 on 1 and 6 DF,  p-value: 0.005879
```

Appendix C.9: Linear regression model for the influence of RBA on the growth of planted longleaf pine seedlings in the first growing season

```
lm(formula = PlantGrowth1L ~ RBA, data = datum)

Residuals:
      Min        1Q    Median        3Q       Max 
-0.184624 -0.004614  0.015155  0.030451  0.110708 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.226186   0.121539   1.861    0.112
RBA         -0.001669   0.008492  -0.196    0.851

Residual standard error: 0.09112 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.006394,  Adjusted R-squared:  -0.1592 
F-statistic: 0.03861 on 1 and 6 DF,  p-value: 0.8507
```

Appendix C.10: Linear regression model for the influence of RBA on the survival of planted longleaf pine seedlings in the first growing season

```
lm(formula = PlantSurv1A ~ RBA, data = datum)

Residuals:
      Min        1Q    Median        3Q       Max 
-0.182345 -0.099461  0.003779  0.078270  0.193594 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept) 1.253486   0.197772   6.338 0.000722 ***
RBA         0.008416   0.013819   0.609 0.564831    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 0.1483 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.05822,   Adjusted R-squared:  -0.09874 
F-statistic: 0.3709 on 1 and 6 DF,  p-value: 0.5648
```

Appendix C.11: Linear regression model for the influence of RBA on the growth of planted longleaf pine seedlings in the second growing season

```
lm(formula = PlantCumGrow2ndL ~ RBA, data = datum)

Residuals:
      Min        1Q    Median        3Q       Max 
-0.119177 -0.060551 -0.005989  0.069802  0.120283 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)   
(Intercept)  0.621199   0.119541   5.197  0.00202 **
RBA         -0.007319   0.008353  -0.876  0.41460   
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.08963 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.1135,    Adjusted R-squared:  -0.03431 
F-statistic: 0.7678 on 1 and 6 DF,  p-value: 0.4146
```

Appendix C.12: Linear regression model for the influence of RBA on the survival of planted longleaf pine seedlings in the second growing season

```
lm(formula = PlantSurvival2 ~ RBA, data = datum)

Residuals:
    Min      1Q  Median      3Q     Max 
-3.0000  -0.1290  0.8828  1.1219  1.1376 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept) 99.43147    2.66131  37.362 2.45e-08 ***
RBA         -0.03127    0.18595  -0.168    0.872    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.995 on 6 degrees of freedom
  (1 observation deleted due to missingness)
Multiple R-squared:  0.00469,   Adjusted R-squared:  -0.1612 
F-statistic: 0.02827 on 1 and 6 DF,  p-value: 0.872
```

Appendix C.13: Linear regression model for influence of RBA on the survival of planted longleaf pine seedlings following dormant season burning

```
lm(formula = FireSurvP ~ RBA, data = datum)

Residuals:
   Min     1Q Median     3Q    Max 
-14.53 -11.09  -4.51   6.62  26.97 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)   
(Intercept)  124.693     21.219   5.877  0.00108 **
RBA           -3.894      1.483  -2.627  0.03923 * 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 15.91 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.5349,    Adjusted R-squared:  0.4574 
F-statistic:   6.9 on 1 and 6 DF,  p-value: 0.03923
```

Appendix C.14: Linear regression model for influence of RBA on the growth of planted longleaf pine seedlings in the third growing season

```
lm(formula = PlantCumGroL ~ RBA, data = datum)

Residuals:
      Min        1Q    Median        3Q       Max 
-0.090447 -0.043445 -0.009206  0.049485  0.101524 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.798062   0.094307   8.462 0.000149 ***
RBA         -0.011338   0.006589  -1.721 0.136095    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 0.07071 on 6 degrees of freedom
  (14 observations deleted due to missingness)
Multiple R-squared:  0.3304,    Adjusted R-squared:  0.2188 
F-statistic: 2.961 on 1 and 6 DF,  p-value: 0.1361
```

Appendix C.15: Linear regression model between RBA and IPAR in the first growing season

```
lm(formula = IPAR1 ~ RBA, data = datum)

Residuals:
    Min      1Q  Median      3Q     Max 
-1.6774 -1.3807 -1.0060  0.4188  3.5073 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  48.4691     2.7299  17.755 4.44e-07 ***
RBA           1.2905     0.1905   6.775 0.000259 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

Residual standard error: 2.048 on 7 degrees of freedom
  (13 observations deleted due to missingness)
Multiple R-squared:  0.8677,    Adjusted R-squared:  0.8488 
F-statistic:  45.9 on 1 and 7 DF,  p-value: 0.000259
```

Appendix C.16: Linear regression model between RBA and IPAR in the second growing season

```
lm(formula = IPAR2 ~ RBA, data = datum)

Residuals:
     Min       1Q   Median       3Q      Max 
-1.60674 -0.55106 -0.02595  0.55171  1.72721 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept) 65.23599    1.41631  46.061 5.94e-10 ***
RBA          0.97205    0.09881   9.837 2.38e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.062 on 7 degrees of freedom
  (13 observations deleted due to missingness)
Multiple R-squared:  0.9325,    Adjusted R-squared:  0.9229 
F-statistic: 96.77 on 1 and 7 DF,  p-value: 2.384e-05
```

Appendix C.17: Linear regression model for influence of RBA on the growth of overstory longleaf pine trees in the third growing season

```
lm(formula = OverCumGro ~ RBA, data = datum)

Residuals:
     Min       1Q   Median       3Q      Max
-0.28011 -0.06600  0.06064  0.09149  0.13256

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  1.78705    0.18714   9.549  2.9e-05 ***
RBA         -0.06092    0.01306  -4.666   0.0023 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.1404 on 7 degrees of freedom
  (13 observations deleted due to missingness)
Multiple R-squared:  0.7567,    Adjusted R-squared:  0.7219
F-statistic: 21.77 on 1 and 7 DF,  p-value: 0.002299
```

APPENDIX D

SUMMARY of FULLY STOCKED LONGLEAF PINE STANDS WITH RELATIVE DENSITY of 70 and ABOVE

State	Year	Plot #	BA (m2/ha)	TPH	QMD (cm)	LOG TPH	LOG QMD	SDI	RD
SC	2007	22	52.59	892.86	27.39	2.95	1.44	1033.48	1.000
SC	2007	22	54.39	773.81	29.91	2.89	1.48	1032.11	0.999
GA	2007	16	49.17	892.86	26.48	2.95	1.42	979.23	0.948
GA	2001	42	44.77	1130.95	22.45	3.05	1.35	951.57	0.921
GA	1997	16	45.30	1071.43	23.20	3.03	1.37	950.42	0.920
GA	1997	11	47.07	892.86	25.91	2.95	1.41	945.51	0.915
MS	2010	43	49.69	714.29	29.76	2.85	1.47	944.98	0.914
AL	2003	102	41.59	1190.48	21.09	3.08	1.32	906.16	0.877
GA	1997	42	40.47	1071.43	21.93	3.03	1.34	868.25	0.840
GA	2008	55	44.63	654.76	29.46	2.82	1.47	852.10	0.824
FL	2006	85	41.04	892.86	24.19	2.95	1.38	846.97	0.820
GA	2001	42	47.71	476.19	35.72	2.68	1.55	844.18	0.817
MS	2006	43	45.34	535.71	32.83	2.73	1.52	829.38	0.803
AL	2000	23	47.05	416.67	37.92	2.62	1.58	813.09	0.787
GA	2003	55	41.92	654.76	28.55	2.82	1.46	810.29	0.784
MS	2010	106	40.90	535.71	31.18	2.73	1.49	763.67	0.739
AL	2009	73	40.66	535.71	31.09	2.73	1.49	759.95	0.735
FL	2002	7	34.57	1011.90	20.86	3.01	1.32	756.55	0.732
AL	2004	126	39.27	595.24	28.98	2.77	1.46	754.56	0.730
SC	2006	22	38.09	654.76	27.22	2.82	1.43	750.43	0.726
FL	2006	85	38.38	595.24	28.65	2.77	1.46	740.84	0.717
AL	2001	176	33.62	952.38	21.20	2.98	1.33	730.94	0.707
GA	1997	163	34.71	833.33	23.03	2.92	1.36	730.35	0.707
GA	2010	64	41.03	416.67	35.41	2.62	1.55	728.44	0.705
AL	2006	79	32.56	1011.90	20.24	3.01	1.31	721.06	0.698
GA	1997	108	37.02	595.24	28.14	2.77	1.45	719.79	0.696

BA: Basal area
TPH: Trees per hectare
QMD: Quadratic mean diameter
SDI: Stand density index
RD: Relative density

APPENDIX E

STRUCTURAL EQUATION MODELS TO COMPARE THE INFLUNCES OF BASAL AREA AND STOCKING ON GERMINATION, GROWTH AND SURVIVAL

Appendix E.1: Structural equation model to compare the influences of BA and stocking on the germination of longleaf pine, and the confidence interval for the significance of the relationship

```
Std. Estimate
BaVar                BaVar     1.0000000            Ba <--> Ba
StockingVar   StockingVar     1.0000000 Stocking <--> Stocking
GermVar            GermVar     0.2860550        Germ <--> Germ
BaGerm              BaGerm    -1.5594398          Germ <--- Ba
StockingGerm StockingGerm     0.7192023    Germ <--- Stocking
BaStocking      BaStocking     0.9964576      Stocking <--> Ba
```

```
Confidence Intervals:

Level     Percentile            BCa
95%   (-1.864, 0.964)   (-1.875, 0.535)
```

Appendix E.2: Structural equation model to compare the influences of BA and stocking on the growth of longleaf pine germinants, and the confidence interval for the significance of the relationship

```
Std. Estimate
BaVar                  BaVar     1.0000000             Ba <--> Ba
StockingVar      StockingVar     1.0000000 Stocking <--> Stocking
GrowthVar          GrowthVar     0.1249621     Growth <--> Growth
BaGrowth            BaGrowth     2.8730106         Growth <--- Ba
StockingGrowth StockingGrowth   -3.7528223   Growth <--- Stocking
BaStocking        BaStocking     0.9953176       Stocking <--> Ba
```

```
Confidence Intervals:

Level     Percentile            BCa
95%   (-0.7021,-0.3403)   (-0.7486,-0.3567)
```

Appendix E.3: Structural equation model to compare the influences of BA and stocking on the survival of longleaf pine germinants during a dormant season fire, and the confidence interval for the significance of the relationship

```
                                  Std. Estimate
BaVar                       BaVar     1.0000000             Ba <--> Ba
StockingVar           StockingVar     1.0000000 Stocking <--> Stocking
SurvivalVar           SurvivalVar     0.1252509 Survival <--> Survival
BaSurvival             BaSurvival     1.8340518       Survival <--- Ba
StockingSurvival StockingSurvival    -2.7437900 Survival <--- Stocking
BaStocking             BaStocking     0.9953176       Stocking <--> Ba
```

```
Confidence Intervals:

Level     Percentile            BCa
95%   (-1.587, 0.781)   (-1.771, 0.393)
```

Appendix E.4: Structural equation model to compare the influences of BA and stocking on the growth of planted longleaf pine seedlings, and the confidence interval for the significance of the relationship

```
Std. Estimate
BaVar                   BaVar     1.0000000             Ba <--> Ba
StockingVar       StockingVar     1.0000000 Stocking <--> Stocking
GrowthVar           GrowthVar     0.5635991     Growth <--> Growth
BaGrowth             BaGrowth     2.7775302         Growth <--- Ba
StockingGrowth StockingGrowth    -3.3681177   Growth <--- Stocking
BaStocking         BaStocking     0.9953176       Stocking <--> Ba
```

```
Confidence Intervals:

Level     Percentile            BCa
95%   (-1.3003,-0.4719)   (-1.3166,-0.4849)
```

Appendix E.5: Structural equation model to compare the influences of BA and stocking on the survival of planted longleaf pine seedlings during a dormant season fire, and the confidence interval for the significance of the relationship

```
                                 Std. Estimate
BaVar                       BaVar     1.0000000            Ba <--> Ba
StockingVar           StockingVar     1.0000000 Stocking <--> Stocking
SurvivalVar           SurvivalVar     0.3904836 Survival <--> Survival
BaSurvival             BaSurvival     3.3224039       Survival <--- Ba
StockingSurvival StockingSurvival    -4.0184562 Survival <--- Stocking
BaStocking             BaStocking     0.9953176       Stocking <--> Ba
```

```
Confidence Intervals:

Level     Percentile            BCa
95%   (-1.773, 0.428)   (-1.792, 0.400)
```

Appendix E.6: Structural equation model to compare the influences of BA and stocking on the growth of overstory longleaf pine trees, and the confidence interval for the significance of the relationship

```
Std. Estimate
BaVar                   BaVar     1.0000000             Ba <--> Ba
StockingVar       StockingVar     1.0000000 Stocking <--> Stocking
GrowthVar           GrowthVar     0.4325848     Growth <--> Growth
BaGrowth             BaGrowth     0.1350820         Growth <--- Ba
StockingGrowth StockingGrowth    -0.8863966   Growth <--- Stocking
BaStocking         BaStocking     0.9877169       Stocking <--> Ba
```

```
Confidence Intervals:

Level     Percentile            BCa
95%   (-54.00, 23.47)   (-58.25, 20.37)
```