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RESEARCH ARTICLE

Effects of basal area on survival and growth of longleaf pine when practicing selection silviculture

Ferhat Kara[1*], Edward F. Loewenstein[2] and Dale G. Brockway[3]

[1]Faculty of Forestry, Kastamonu University, Kastamonu, Turkey, 37100. [2]School of Forestry and Wildlife Sciences, 602 Duncan Drive, Auburn University, Auburn, AL, 36849, USA. [3]Southern Research Station, USDA Forest Service, 521 Devall Drive, Auburn, AL, 36849, USA.*

Abstract

Aim of study: Uneven-aged (UEA) management systems can achieve multiple-use objectives, however, use of UEA techniques to manage longleaf pine (*Pinus palustris* Mill.) forests are still open to question, because of the species' intolerance of competition. It was our aim to examine the influence of different levels (9.2, 13.8 and 18.4 m^2 ha^{-1}) of residual basal area (RBA) on longleaf pine seedling survival and growth following three growing seasons.

Area of study: This study was conducted at the Escambia Experimental Forest, located on the Southern Coastal Plain of Alabama, in the southeastern United States.

Material and Methods: Selection silviculture was implemented with the Proportional-Basal Area (Pro-B) method. Prescribed burning was conducted before seed dispersal and in the second year after germination. Photosynthetically active radiation (PAR) was measured under the canopy in the study plots. Survival and growth of longleaf pine seedlings were observed for three growing seasons.

Main results: An inverse relationship was found between the number of germinants and RBA, but the mortality of germinants and planted seedlings was not affected by RBA. At age three, an inverse relationship was observed between root-collar diameter (RCD) growth of the germinants and RBA, but RCD growth of planted seedlings was not affected by RBA. Most of the study plots contained more than the projected number of seedlings needed to sustain the target diameter structure.

Research highlights: Long-term continuous monitoring of seedling development and recruitment into canopy is required to determine the efficacy of UEA management. However, current data suggest that UEA methods may be a viable alternative to the use of even-aged (EA) methods in longleaf ecosystems.

Keywords: Prescribed burning; Recruitment; Single-tree selection; Sustainability; Uneven-aged management.

Abbreviations used: EA: even-aged, PAR: photosynthetically active radiation, Pro-B: Proportional-Basal Area method, RBA: residual basal area, RCD: root collar diameter, S-N: The Stoddard-Neel approach, UEA: uneven-aged, VGDL: volume guiding diameter limit.

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Correspondence should be addressed to Ferhat Kara: fkara@kastamonu.edu.tr

Introduction

Longleaf pine (*Pinus palustris* Mill.) ecosystems exhibit a rich species diversity containing more than 40 vascular plant species in 1 m^2 (Walker & Peet, 1983), produce wild game and forage grasses (Franklin, 1997), and provide high quality wildlife habitat (Brockway *et al.,* 2006). As a result of the historic decline (by 97%) in longleaf pine acreage (Boyer, 1990), concern about restoration and management of longleaf pine ecosystems has increased in recent years (Brockway & Outcalt, 2000). Achieving restoration and management goals for longleaf pine forests will require application of practical silvicultural methods that lead to sustainable production of goods and services. Even-aged (EA) methods, particularly shelterwood regeneration methods, have been successfully and effectively used to regenerate existing longleaf pine stands (Croker & Boyer, 1975). However, ecosystem services have been episodic due to complete overstory removal at the end of each rotation (Brockway *et al.,* 2006) and the intensity of logging during shelterwood harvesting appears to result in a sharp decline for native species such as wiregrass (*Aristida beyrichiana* Trin. & Rupr.) and silverthread goldaster (*Pityopsis graminifolia* (Michx) Nutt.) in the understory

(Brockway & Outcalt, 2015). Ecosystem services are the benefits people obtain from ecosystems, and they include provisioning (i.e. food, fresh water and wood), regulating (i.e. climate regulation, wildlife habitat and pollination) and cultural services (i.e. recreation, aesthetic and education) (Millennium Ecosystem Assessment, 2005). There is a need for an approach that ensures continuous ecosystem services while producing high quality timber.

Recently, more attention has been given to multiple-use objectives such as aesthetics, wildlife management, water quality, and recreation (Guldin, 2006). It has been suggested that uneven-aged (UEA) management techniques can meet multiple-use objectives, and achieve restoration of longleaf pine forests (Guldin, 1996) because of the continuous forest cover and multi-cohort structure provided by UEA systems (Moser *et al*., 2002). Field trials to demonstrate and assess the utility of UEA silviculture in these forests have been attempted to a limited degree. The Stoddard-Neel (S-N) approach to single-tree selection is one example of UEA silviculture in longleaf pine forests (Moser *et al*., 2002; Mitchell *et al*., 2006; Neel *et al.,* 2010). However, the S-N approach is not quantitative, and it cannot be systematically evaluated because there is no defined target residual structure. It can only be applied by experienced practitioners and training someone to properly apply this approach is time consuming. The S-N approach suggests that UEA systems work for longleaf pine; however, the implementation of the approach, and the required residual basal area (RBA) and number of seedlings are not explicit. Volume guiding diameter limit (VGDL) and BDq methods (Farrar, 1996) are more quantifiable than the S-N approach, but they still require a high degree of professional skill to properly apply in the field. It is also difficult to mark the stand in one pass when using these approaches. In this study, we used an easy-to-apply and scientifically-based tree-marking approach, the Proportional-Basal Area (Pro-B) method, to implement UEA management via single-tree selection in longleaf pine forests (Brockway *et al*., 2014). Pro-B is based on structural control, allows stand marking in one pass and does not require extensive field experience (Brockway *et al*., 2014).

The natural gap-phase regeneration pattern of longleaf pine can be closely achieved using group selection (Farrar & Boyer, 1991; Brockway & Outcalt, 1998; McGuire *et al*., 2001) since longleaf pine can regenerate by filling openings regardless of the gap size (Schwarz, 1907). Distribution of large longleaf pine seeds by wind may be a problem in larger canopy gaps (Boyer, 1963). An additional consideration is that small canopy gaps can become closed before regeneration is established (Guldin, 2006), and the spatial control of many small gaps may be difficult in the long-term (Roach, 1974). 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). However, there has not yet been enough long-term research in the use of UEA management to verify that selection silviculture can sustain these forests.

The degree of tolerance of longleaf pine to shade has been questioned (Samuelson & Stokes, 2012). Longleaf pine has been classified as shade intolerant species (Boyer, 1990), but its seedlings may survive under shaded conditions for a prolonged time during the grass stage (Croker & Boyer, 1975). During the grass stage, longleaf seedlings concentrate growth in their root system, and this stored energy in the taproot facilitates recovery after fire (Chapman, 1932). It has been suggested that longleaf pine is moderately tolerant to shade when young, and then becomes more intolerant of shade with increasing age (Bhuta *et al*., 2008). The RBA level at which seedling survival and development is acceptable under UEA silviculture is still open to question. This study aims to address such questions by assessing the influence of differing RBA levels on longleaf pine seedling survival and growth. Because regeneration of longleaf pine may be hindered by its intolerance to shade and competition (Croker & Boyer, 1975), canopy openness as measured by RBA seems to be an important factor in seedling establishment. Thus, it seems reasonable to test a range of RBAs (9.2, 13.8, and 18.4 m^2 ha^{-1}) to assess their effects on longleaf pine survival and growth. These RBA levels were selected to contrast this study with previous studies that examined rates of longleaf pine regeneration under varying stand densities (Croker & Boyer, 1975; Boyer, 1979; Brockway *et al*., 2014). The RBA suggested for shelterwood methods ranges from 6.9 to 9.2 m^2 ha^{-1}, because seed production usually peaks within this range of RBA (Croker & Boyer, 1975) and lower stand densities may, because of insufficient needle fall, inhibit the effectiveness of prescribed fire. Therefore, we selected an RBA of 9.2 m^2 ha^{-1}, the upper limit suggested for shelterwood, as our lowest RBA. Brockway *et al*. (2014) examined development of longleaf pine seedlings under an RBA of 11.5 m^2 ha^{-1} and noted encouraging levels of longleaf pine regeneration and stand development under that RBA. We selected an RBA of 13.8 m^2 ha^{-1} as our mid-level of RBA, somewhat higher than that observed by Brockway *et al*. (2014). Finally, an RBA of 18.4 m^2 ha^{-1} was chosen as the high level of RBA, to determine whether a dense stand of longleaf pine can be managed to obtain adequate numbers of well-developed seedlings through selection silviculture.

Longleaf pine is adapted to survive in ecosystems that are subjected to frequent surface fires (Landers, 1991). Prescribed fire prepares a seedbed for longleaf pine seedlings, facilitates germination by exposing the mineral soil (Boyer & White, 1990), decreases the competition for longleaf pine seedlings from other species (Heyward, 1939) and reduces the risk of brown-spot needle blight disease (Chapman, 1932). Periodic fire is also necessary for restoring and maintaining native groundcover plants and wildlife communities (Brockway & Outcalt, 2000). Even though prescribed fire is an essential silvicultural tool in longleaf pine forests, it may be partly responsible for seedling mortality, especially when seedlings are newly germinated (Boyer, 1963). For this reason, we included an examination of fire-inducted mortality during the establishment phase to quantify its magnitude.

In examining the efficacy of selection silviculture with the Pro-B method in longleaf pine ecosystems, our primary objectives were to (1) assess the effects of RBA on longleaf pine seedlings survival and growth following three growing seasons, (2) estimate future seedling abundance across varying levels of RBA, and (3) evaluate the influence of RBA on the interaction between a dormant season prescribed fire and survival of planted longleaf pine seedlings.

Materials and methods

Study Site

This study was conducted on the Escambia Experimental Forest, which is located in the Gulf Coastal Plain of the southeastern United States (USDA, 2014) (Fig. 1a). The Escambia Experimental 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, occurring mostly along small streams. Average site index for longleaf pine is 22 m (base age 50). Soils are coarse to fine, loamy, siliceous thermic Paleudults (Mattox, 1975). Annual precipitation is about 1520 mm and average temperatures range from 5 to 33 °C. Topography is flat to rolling with slopes mostly less than 10%. At this experimental forest, various age classes are present, ranging from new germinants to trees up to 160 years old. Prior to harvesting in our study area, average tree diameter ranged from 19 to 29 cm, while average density ranged from 200 to 680 tree ha^{-1} across all plots. Basal area ranged from 11.5 to 30 m^2 ha^{-1}. Stand structures varied across all plots. In general, plots contained trees of all diameter classes representing UEA conditions; however, they did not exhibit an explicit reverse j-shaped distribution typical of balanced UEA stands.

Study Design

The study was installed as a completely randomized design. In the winter of 2010, nine 2-ha square plots were established, and randomly assigned to one of three RBA levels: 9.2, 13.8, and 18.4 m^2 ha^{-1} (40, 60, and 80 ft^2 ac^{-1}, respectively). Plots were designated 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, with each RBA treatment 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 contained six 100-m^2 square overstory measurement subplots (Fig. 1b), and each overstory measurement subplots contained three 10-m^2 circular regeneration subplots (Fig. 1b). Overstory and understory subplots were systematically located within each plot (Fig. 1b).

Harvest operations were completed during May 2011, after stands were marked to the defined treatment RBA using single tree-selection implemented with the Pro-B method (Brockway *et al*., 2014). 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) was used. This structure apportions RBA 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). Given a properly selected RBA, this distribution has been shown to allocate sufficient growing space for the recruitment of new cohorts in studies with longleaf pine (Dyson *et al*., 2009) and with various hardwood species (Loewenstein, 2005).

Longleaf pine seedlings were planted in the event that seed production was poor or failed during 2011-2012, since longleaf pine exhibits a high degree of annual variation in seed production. Three longleaf pine seedlings were hand-planted, in early December 2011, in each regeneration subplot (486 total) following a growing-season prescribed fire. Seedlings were 15-cm deep-plug containerized planting stock with a rooting volume of 100 cm^3. Planting was performed following a rainy period. Seedlings were planted approximately 1-m away from plot center and equidistant from each other to minimize intraspecific competition. Seedlings were tagged and numbered after planting in order to monitor their survival and growth.

A dormant-season fire was applied in January-February 2014 to reduce competition for longleaf pine seedlings from hardwoods, and note the influence of

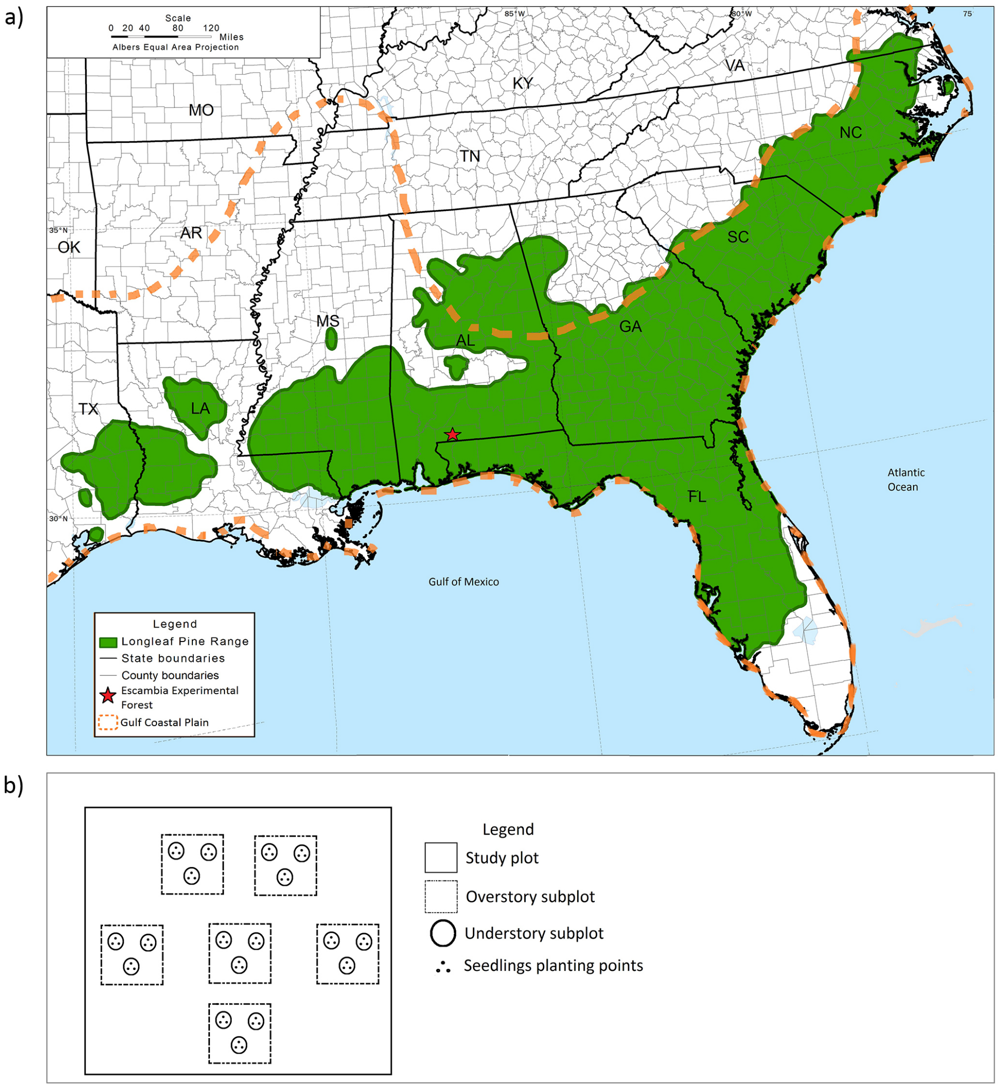

Figure 1. (a) Escambia Experimental Forest within the native range of longleaf pine in the southeastern United States (USDA, 2014). (b) Study plot design.

RBA on the interaction between burning and survival of planted seedlings. During the dormant-season fire, the air temperature ranged from 11 to 23 0C, while relative humidity ranged from 23 to 47 percent. Within the study plots, most of the understory vegetation was consumed and resulted in more than 93% of topkill for hardwoods during the growing-season and dormant-season prescribed fires. Hardwood seedlings larger than 5 cm in their root-collar diameters (RCD) mostly survived.

Data collection and analysis

Following the dormant-season prescribed fire at age 2 (January-February 2014), three germinants among those that survived were randomly selected in each regeneration subplot, and their RCDs were measured to the nearest millimeter to record their growth at the end of the third growing season (August 2014). In addition, the number of germinants was also counted at the end of the third growing season in each regeneration subplot.

The RCD growth of the planted seedlings were recorded in the second (July 2013) and third (August 2014) growing seasons to calculate the growth of planted seedlings. Mortality of planted seedlings was recorded at the end of each growing season (i.e. July 2013 and August 2014). Survival of the planted seedlings from the dormant-season fire was also observed two months after the fire, in the first week of April (2014) when the new needles begin to emerge.

Photosynthetically active radiation (PAR) was measured under the canopy in each regeneration subplot, on nearly cloudless days between 11:00 and 14:00 hours, during each measurement period, using an AccuPar Linear PAR/LAI Model PAR-80 ceptometer (Decagon

Devices, Inc., Pullman, WA). PAR measurements from regeneration subplots were averaged in each treatment plot. A HOBO weather station PAR sensor (Onset Computer Corporation, 2009) was also installed in a treeless area of about 8 ha. Intercepted PAR (IPAR) was calculated using the following formula;

$$IPAR = 1 - \left(\frac{PAR\ under\ canopy}{PAR\ in\ open}\right) \times 100$$

Since PAR measurement is affected by factors such as topography IPAR=y, elevation and solar zenith angle, readings were corrected for zenith angles and topography elevations using the correction formula suggested by Liang *et al*. (2012). The change in PAR values, following the correction, was negligible.

Rather than using ANOVA to test difference among treatments, because of deviation from the target RBA levels (Kara & Loewenstein, 2015a) we decided that simple linear regression (α-level=0.05) would be preferable for testing the relationships between RBA and the (1) number of germinants, (2) growth of germinants, (3) growth of planted seedlings, (4) survival of planted seedlings in the absence of fire, and (5) survival of planted seedlings following fire. Relationships between IPAR and the same variables were also examined using simple linear regression (α-level=0.05). In order to more appropriately model the relationship between RBA and number of germinants, Poisson regression was used. For count data, such as the number of germinants, a Poisson regression model is usually recommended (Rodriguez, 2007). Seedling survival percentages were averaged for each plot and these percentages were arcsine transformed before regression analysis (Davis *et al*., 1999). Growth data were 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. It should be noted that a wildfire occurred during May 2012 on one of the mid-level BA plots, M_2 (13.8 m^2 ha^{-1}), and all new germinants were consumed. Therefore, data from this plot were not included in the analysis.

Reliable Recruitment

When a seedling bank is created across the observed range of RBA, the concern at this point becomes whether the stand conditions are suitable for providing reliable recruitment into the overstory. Three-year observations and data from the literature provide some evidence as to whether the current stand conditions are adequate for contributing to the sustainable management of these stands when implementing selection silviculture. Although views concerning the stated assumptions might vary (in particular the q-value of our defined target diameter structure), our predictions are presented to provide a rough idea concerning the number of seedlings that may be expected to recruit into the overstory.

Longleaf pine seedlings typically bolt from the grass stage (i.e. begin rapid height growth) and recruit into the overstory, after they reach an RCD of approximately 25 mm (Boyer, 1990). The age required to reach the RCD of 25 mm for each level of RBA was projected using the 3-year growth rates, and the growth rates reported by Boyer (1963). The number of seedlings that reach the RCD of 25 mm was determined using the mortality rates measured: (1) following the prescribed fire, (2) in the absence of fire, and (3) following the logging operation.

Longleaf pine seedlings become more resistant to fire when they reach an RCD of 13 mm (Boyer, 1974). For this reason, average mortality rates observed during the prescribed fire at age 2 were assumed for subsequent fires until the seedlings reach the RCD of 13 mm. In addition, during the prescribed fire at age 2, planted seedlings were already larger than the RCD of 13 mm, thus, for the fires after seedlings reach the RCD of 13 mm, we used the mortality rates of planted seedlings observed during the prescribed fire at age 2. Moreover, average mortality rates observed in the absence of fire were assumed for subsequent years when no burning is conducted. An average mortality of 50 % during logging operations at age 10 was assumed as suggested by Maple (1977) and Boyer (1990).

Results

IPAR

IPARs ranged from 77 to 88% across all study plots before the harvest operations. Average IPARs following the harvesting ranged from 57 to 78% across the study plots. PAR levels ranged from 192 to 536 µmol m-2 s-1 across all plots before harvesting, and higher PAR levels were measured following the harvesting ranging from 557 to 1087 µmol m^{-2} s^{-1}. There was a statistically significant inverse relationship between RBA and IPAR following the harvest operations (p = 0.0025).

Seedling survival and growth

At the end of the second growing season (July 2013), there was no significant relationship between RBA and the mortality of germinants (p=0.85). Nor did IPAR affect the survival of germinants in the second growing season

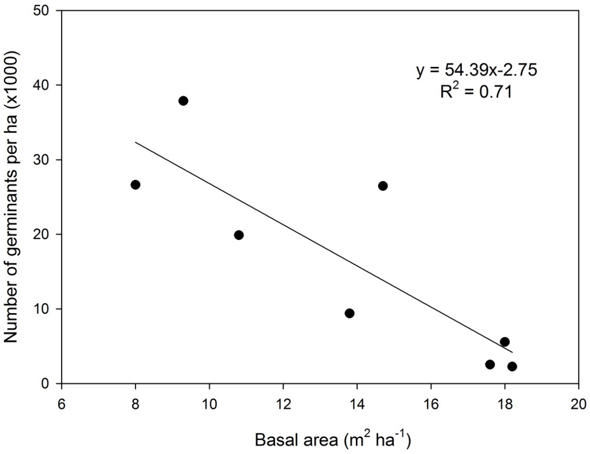

Figure 2. Relationship between the number of germinants and RBA during the third growing season.

(p=0.79). Survival rate of germinants was high across all plots in the absence of fire (i.e. in the second growing season), ranging from 95 to 98%. At the end of the third growing season (August 2014), following the dormant-season fire at age 2, the number of germinants ranged from 2,270 to 37,870 per hectare across all study plots. There was a statistically significant inverse relationship between RBA and the number of germinants in the third growing season (p<0.0001) (Fig. 2) as well as a significant relationship between IPAR and the number of germinants (p<0.0001). Higher numbers of germinants were observed from the lower RBA plots. Although stand density is known to impact cone production in longleaf pine forests (Croker & Boyer, 1975) and consequently may influence the number of germinants, there was no statistically significant effects of initial basal area on the number of germinants (p=0.94) nor was there an effect from the interaction of initial basal area with RBA on the number of germinants (p=0.93).

Mortality among planted seedlings was not affected by RBA or IPAR during the second year following planting (p=0.87 and p=0.76, respectively) (Fig.3a). Survival was high during the first two growing seasons, ranging from 96 to 100 % across all plots. In addition, a statistically significant negative relationship was noted between RBA and the survival of planted seedlings following the dormant-season prescribed fire at age 2 (p=0.04) (Fig.3b). The survival rate ranged from 39 to 85% across all plots and increased with decreasing RBA following the dormant-season fire (Fig.3b).

At the end of the third growing season (August 2014), following the dormant-season prescribed fire, there was a statistically significant relationship between RCD size of germinants and RBA (p=0.006) (Fig. 4a), and a significant relationship between IPAR and RCD size of germinants (p<0.0001). Average RCD of germinants at the end of the third growing season ranged from 4.11 to 5.90 mm across all plots (Fig. 4a). It should be noted that the RCD of the germinants was measured only in the third growing season, thus, the growth of germinants was cumulative growth during the three-year period.

As for the planted seedlings, it should be noted that seedling growth in the second and third growing seasons (i.e. July 2013 and August 2014, respectively) was cumulative growth during the two-year and three-year periods, respectively. There was no statistically significant relationship between RBA and the RCD of planted seedlings in the second growing season (p=0.41) (Fig. 4b). Nor did we observe a significant relationship between IPAR and RCD (p=0.54). Average RCD at the end of the second growing season ranged from 2.48 to 4.37 mm across all plots (Fig. 4b). RBA did not significantly affect the RCD of planted seedlings at the end of the third growing season either (p=0.13) (Fig. 4c). However, the relationship between RBA and RCD growth in the third year itself (i.e. RCD growth between the second and the third growing seasons) was significant (p=0.0009) (Fig. 4d). Average RCD ranged

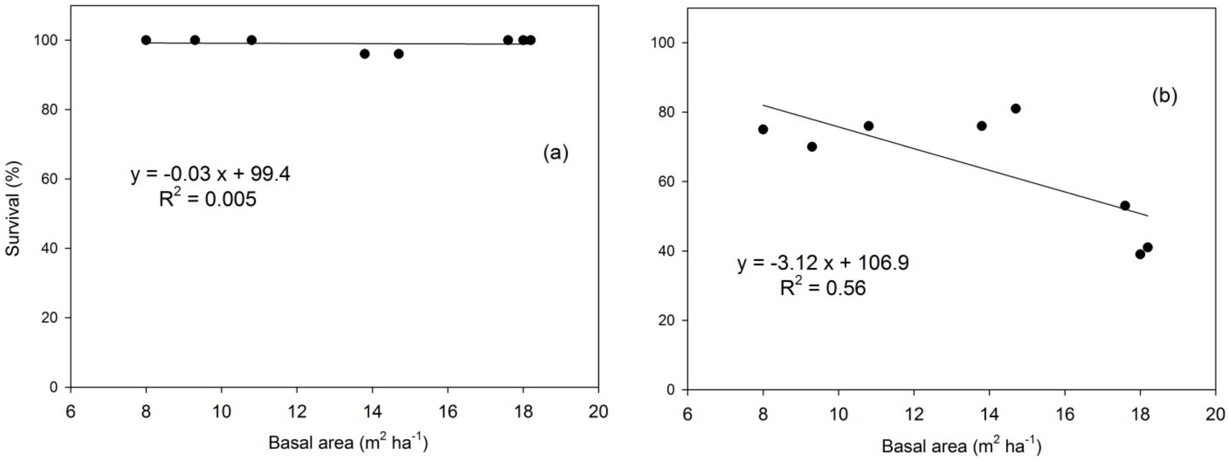

Figure 3. Relationships between RBA and survival (%) of planted seedlings in the (a) second growing season, and (b) following dormant-season fire.

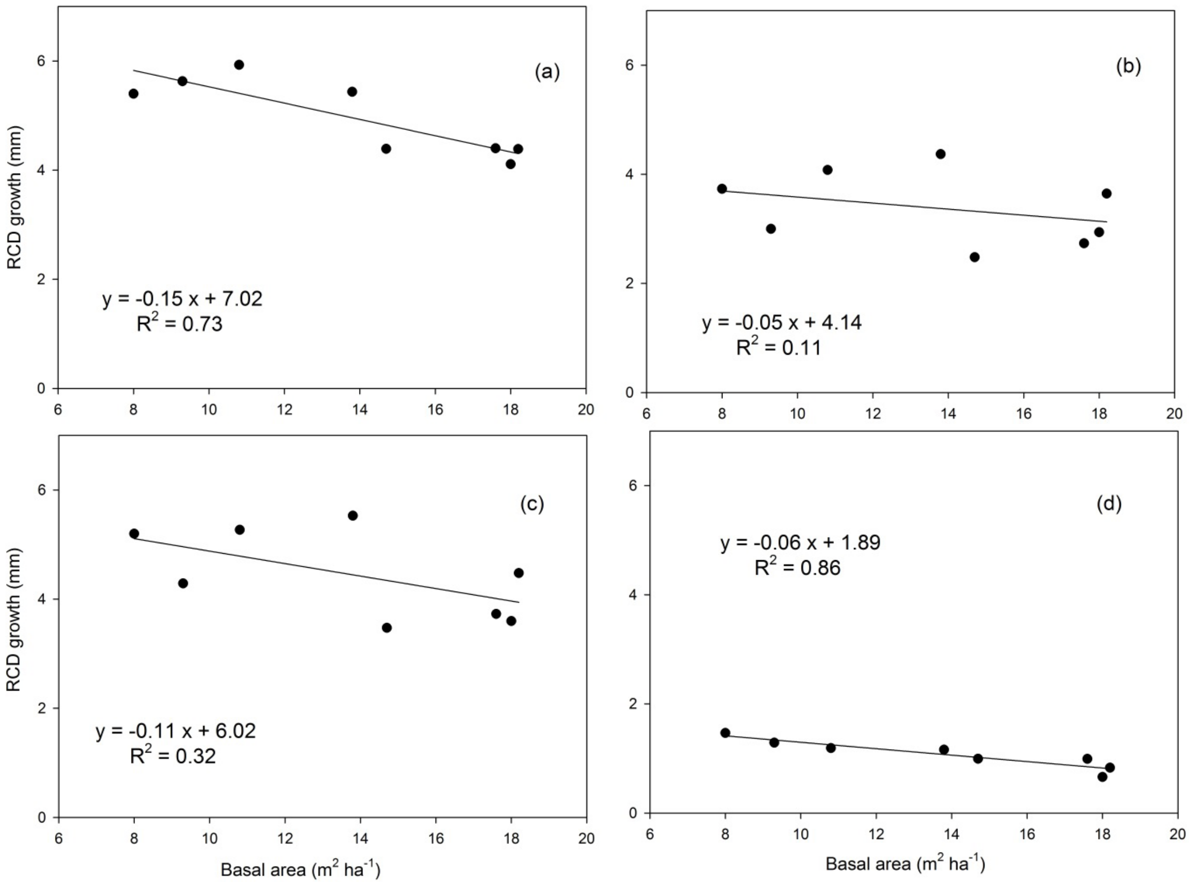

Figure 4. Relationship between RBA and RCD growth of germinants at end of the third growing season (a). Relationship between RBA and RCD growth of planted seedlings in the (b) second growing season and (c) third growing season. Growth in the second and third growing seasons was cumulative growth during the two-year and three-year periods, respectively. Relationship between RBA and RCD growth of planted seedlings in the third growing season itself (d).

from 3.47 to 5.27 mm across all plots during three-year period (Fig. 4d).

Reliable Recruitment

Average mortality rates of germinants observed during the prescribed fire at age 2 were 20, 44, and 72 % in the low, mid and high-RBA plots, respectively (Kara & Loewenstein, 2015b). It should be noted that these rates were assumed for subsequent fires until the seedlings reach the RCD of 13 mm. For the fires after seedlings reach the RCD of 13 mm, the mortality rates were 20, 20, and 46 % in the low, mid and high-RBA plots, respectively (Fig. 3b). Average mortality in the absence of fire was 3, 2, and 3 % in the low, mid and high-RBA plots, respectively (Fig. 3a).

In low-RBA plots (9.2 m^2 ha^{-1}), our average RCD growth was 1.88 mm per year. If the seedlings under this RBA follow a similar trend, seedlings would reach a RCD of 25 mm and bolt to breast height by age 14 or sooner, thereafter eventually recruiting into the forest canopy. In low-RBA plots, the average number of germinants in the third growing season was 28,000 per hectare. Until age 14, these plots would be burned every two years (at ages 4, 6, 8, 10 and 12). RBA is once again adjusted to its target (i.e., 9.2 m^2 ha^{-1}) during the next cutting cycle, by removing trees across a broad range of diameter-classes in year 10. It should be noted that this 10-year cutting cycle may be modified due to operational constraints. If the growth of the residual stand is not sufficient to produce a merchantable harvest, the cutting cycle may be extended. If we assume a mortality of 20 % from each prescribed fire before seedlings reach the RCD of 13 mm (at age 8), 20 % from each prescribed fire after they reach the RCD of 13 mm, 3 % in the absence of fire, and 50 % during logging operations at age 10, then there would be about 3900 seedlings per hectare when seedlings reach the RCD of 25 mm at age 14.

With an average RCD growth of 1.50 mm per year under the mid-RBA plots (13.8 m^2 ha^{-1}), seedlings would reach a RCD of 25 mm at age 17. In mid-RBA plots, the average number of germinants in the third growing season was 18000 per hectare. With the 44 % mortality during fires before they reach a RCD of 13 mm (at age 9), 20 % mortality during fires after they reach a RCD of 13 mm, 2 % in the absence of fire, and 50 % during logging operations at age 10, there would be about 1000 seedlings per hectare when seedlings reach the RCD of 25 mm at age 17.

Under our high-RBA (18.4 m^2 ha^{-1}), the average RCD growth was 1.43 mm per year. If the seedlings under this RBA follow a similar trend, an RCD of 25 mm would be reached at age 18. In high-RBA plots, the average number of germinants in the third growing season was 3500 per hectare. Assuming the 72 % mortality during fires before they reach a RCD of 13 mm (at age 9), 46 % mortality during fires after they reach a RCD of 13 mm, 3 % in the absence of fire, and 50 % during logging operations at age 10, there would be about 3 seedlings per hectare when seedlings reach the RCD of 25 mm at age 18.

Discussion

IPAR

Few light measurements have been reported for longleaf pine forests (Battaglia *et al*., 2003), and scientists came to different conclusions using different approaches (Palik *et al*., 1997; Brockway & Outcalt, 1998; McGuire *et al*., 2001). This inconsistency has been explained by highly variable light availability temporally and spatially in longleaf pine ecosystems (McGuire *et al*., 2001). Other reasons for these differences in light transmittance are the differences in forest canopy structures (Battaglia *et al*., 2003) and differences in the densities of surrounding stands in longleaf pine forests (Gagnon *et al*., 2003). Palik *et al*. (1997) stated that the relationship between stand density and light availability was curvilinear, while Brockway & Outcalt (1998) suggested that the distribution of solar radiation was relatively uniform across canopy gaps. Using a similar approach, Brockway & Outcalt (1998) investigated gap-phase regeneration in an UEA longleaf pine forest, and measured relatively lower amounts of light transmittance ranging from 500 to 900 µmol m^{-2} s^{-1} depending on the four cardinal directions that the measurements were taken. Following the harvest operations, our PAR measurements ranged from 557 to 1087 µmol m^{-2} s^{-1} under varying levels of RBA during midday and seemed to be consistent with that measured by Brockway & Outcalt (1998).

Seedling survival and growth

The higher number of longleaf pine germinants observed in stands of lower RBA was a result of 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. The level of soil disturbance was proportional to the amount of timber skidded from the stand because the higher amount of removal usually requires more skid trails and causes more disturbances (Whitford & Mellican, 2011). Although a greater amount of timber was usually removed from the mid-RBA and high-RBA plots (Table 1), fewer germinants were observed in these stands suggesting that light penetration had more influence than soil disturbance on germination.

Survival rates of the planted seedlings in this study were consistent with reports from previous studies. South *et al*. (2005) observed 87% survival two years after planting on a nearby cutover site in 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. Franklin (2008) suggests that early planting, as early as October with adequate soil moisture, usually results in a better developed root system, more drought tolerance and improved competitiveness with other vegetation in spring and summer. Therefore, our planting following a rainy period in early December favored seedling survival during their first two years. In addition, the higher survival was also related to the fact that containerized longleaf pine seedlings have much lower mortality rates in comparison to bare-root seedlings, as observed by previous studies (Barnett *et al*., 1996; Rodriguez-Trejo *et al*., 2003). Several studies support our observations that seedling survival is not influenced by overstory density in the absence of prescribed fire (Boyer, 1993; Palik *et al*., 1997; McGuire *et al*., 2001). However, higher litter accumulation occurs in denser stands, and it results in fires of higher intensity, and thus, higher mortality rates among understory seedlings occurring within these plots during fire (Boyer, 1963;

Table 1. Residual basal areas for pre-harvest, target and post-harvest conditions in each study plot.

Plot	Pre-harvest (m^2 ha^{-1})	Target (m^2 ha^{-1})	Post-harvest (m^2 ha^{-1})
L_1	11.5	9.2	8.0
L_2	13.7	9.2	9.3
L_3	15.9	9.2	10.8
M_1	24.9	13.8	14.7
M_2	29.6	13.8	14.5
M_3	19.2	13.8	13.8
H_1	30	18.4	17.6
H_2	29.8	18.4	18.2
H_3	21.8	18.4	18.0

Platt *et al*., 1988; Grace & Platt, 1995; Brockway & Outcalt 1998). Our findings during dormant-season prescribed fire substantiate this expectation as well. Another consideration for explaining fire-inducted mortality is the relationship between RCD of seedlings and RBA observed in the third growing season. Seedling size positively affects the survival rate of longleaf pine seedlings following burning (Croker & Boyer, 1975; Brockway *et al*., 2006), thus, seedlings under the lower stand densities reached relatively larger size, had better root development, and were better able to tolerate fire.

Average RCD growth rates of the seedlings in this study were consistent with several studies in the literature (Gagnon *et al*., 2003; Dyson, 2010; Hu *et al*., 2012; Knapp *et al*., 2013). Longleaf pine seedling growth usually decreases as overstory stocking increases (Pecot *et al*. 2007). Although the early growth of longleaf seedlings is quite slow, even under low levels of overstory RBA (Boyer, 1993), it is usually expected that higher rates of RCD growth would be observed under low RBA (Palik *et al*., 1997; Palik *et al*., 2003). Larger RCD is usually measured near the gap centers, while smaller RCD is noted along the gap edges (Gagnon *et al*., 2003). The significant relationship between RBA and the RCD of germinants in this study substantiates this expectation. Although the relationship between RBA and RCD growth for planted seedlings during the three-year period was insignificant, the statistically significant relationship between RBA and RCD growth during the third year itself (i.e. between the second and third year) can also be attributed to the influence of RBA on RCD growth of longleaf pine seedlings.

Reliable Recruitment

Boyer (1963) stated that longleaf seedlings reached an average RCD of 12.2 mm at age 7, under the same low-RBA (9.2 m^2 ha^{-1}) as in our study. This growth rate is consistent with our average RCD growth of 1.88 mm per year, and with other studies (Gagnon *et al*., 2003; Dyson, 2010). In addition, Wahlenberg (1946) noted that longleaf pine seedlings typically reach breast height within 13 years, depending on stand density. In our projection, the age required to reach the RCD of 25 mm under the low-RBA (i.e., age 14) was also consistent with that stated by Wahlenberg (1946). The projected number of seedlings under the low-RBA (i.e., 3900 seedlings ha^{-1}) is substantially higher than the recommended target stand structure of ~70 seedlings per hectare for the smallest diameter class (0-5 cm in DBH) (Fig. 5).

The growth rates observed under the mid-RBA (13.8 m^2 ha^{-1}) and high-RBA (18.4 m^2 ha^{-1}) were also consistent with those reported by Boyer (1963). Under the same mid-RBA as in our study, Boyer (1963) found that seedlings reached an average RCD of 10.2 mm at age 7, while it was 9.6 mm under the same high-RBA as in our study. The projected number of seedlings under the mid-RBA (i.e., 1000 seedlings ha^{-1}) also exceeds the recommended target stand structure of 110 seedlings per hectare (Fig. 5). For the high-RBA plots, the required number of seedlings per hectare in the smallest diameter class (0-5 cm in DBH) is 145 seedlings per hectare (Fig. 5). Thus, the number of seedlings projected (i.e., 3 seedlings ha^{-1}) to recruit into the smallest diameter class is substantially lower than required to maintain the target diameter structure of longleaf pine forests under the high-RBA.

In summary, our seedling projection suggests that an RBA of 9.2 m^2 ha^{-1} is lower than necessary, because the predicted number of seedlings far exceeds the recommended target stand structure (Fig. 5). At the other end of the spectrum, the 18.4 m^2 ha^{-1} is too high to ensure reliable recruitment into the canopy of longleaf pine forests when implementing selection silviculture. Therefore, the mid-RBA (13.8 m^2 ha^{-1}), providing 1000 seedlings ha^{-1}, is closer to an optimal target for reliably recruiting enough seedlings into the canopy of longleaf pine forests, thus contributing to sustainability of the composition, structure and function of these ecosystems.

Conclusions

Fire is one of the primary factors in longleaf pine growth and survival. Modeling the fire effects is considered difficult because the influence of fire on growth and survival is usually associated with several

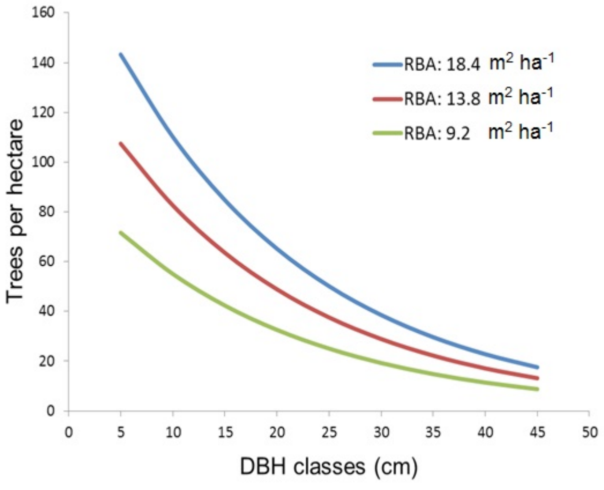

Figure 5. Target stand structure, based on RBA, calculated via the Pro-B method using a LDT = 45 cm and a q-value = 1.3 (5 cm).

factors such as the timing of burn, weather conditions, fuel conditions, stand conditions, methods of burning, fire behavior, etc. We usually have no control over what a burning will do or how it will behave. Thus, our approach of seedling projection may have some shortcomings in predicting the mortality and growth of longleaf pine seedlings. However, our assumptions are based on the data available, and our observations confirm those prior publications. The assumption that these mortality rates should persist going forward seems reasonable. Despite its shortcomings, the predictions provide a rough idea concerning the number of seedlings that may be expected to recruit into the overstory.

Successful development and implementation of UEA management systems requires an understanding of the linkage between overstory density and its influence on seedling responses. As research demonstrates successful management of longleaf pine forests with selection silviculture, UEA systems may become an increasingly used alternative relative to EA methods, especially under circumstance where UEA management better fulfills a land owner's objectives. Additional study is required to improve our understanding of the applicability and efficacy of single-tree selection in longleaf pine forests. Current data are yet insufficient to fully address the matter of reliable recruitment into the overstory. However, nothing in these data suggests that this approach cannot be successful in establishing a new cohort of trees 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 the appropriate RBA and disturbance regime are considered. Current data also suggest that understory planting of longleaf pine may be an option for converting from an EA to UEA structure in longleaf pine forests, and for species conversion.

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