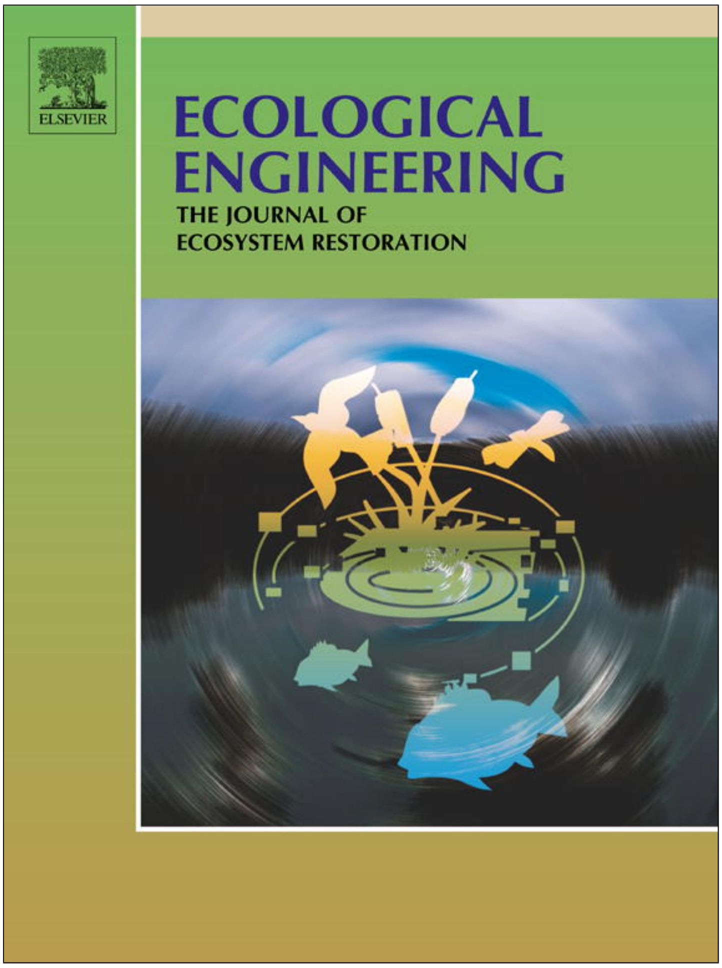
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Effects of canopy structure and cultural treatments on the survival and growth of *Pinus palustris* Mill. seedlings underplanted in *Pinus taeda* L. stands

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ABSTRACT

Longleaf pine restoration is a common management objective in the southeastern United States and requires artificial regeneration of longleaf pines on sites currently dominated by loblolly pine. In many cases, retention of canopy trees during stand conversion may be desirable to promote ecological function and meet conservation objectives. We tested the effects of seven harvesting treatments that varied residual canopy density and distribution, in conjunction with additional cultural treatments (herbicides and fertilizer), on the mortality and growth of longleaf pine seedlings underplanted in loblolly pine stands. We observed no change in the root collar diameter of longleaf pine seedlings planted in plots with no canopy removal (residual basal area of 16 m^2/ha) over three growing seasons. Clearcutting resulted in the greatest seedling growth and the greatest percentage of seedlings that had emerged from the grass stage, although mean seedling size within canopy gaps did not differ from that within clearcut plots. Within canopy gaps, seedling root collar diameter did not significantly increase beyond 10 m from the forest edge. Canopy trees provided an apparent facilitation effect on longleaf pine seedling survival, with the highest mortality in clearcut plots and on the northern half of canopy gaps. Releasing planted longleaf pine seedlings with herbicides resulted in a moderate increase in the percentage of seedlings in height growth but had no effect on root collar diameter. Our results demonstrate trade-offs between longleaf pine seedling survival and growth associated with canopy retention but also suggest that managers have some degree of flexibility in prescribing harvesting treatments to meet restoration objectives on sites currently dominated by loblolly pines.

1. Introduction

A widespread shift in stand structure and composition, from historically dominant longleaf pine (*Pinus palustris* Mill.) forests to second-growth loblolly pine (*Pinus taeda* L.) stands, has greatly changed the landscape of upland forests in the southeastern United States. Longleaf pine ecosystems are generally characterized by relatively open canopies, frequent surface fires that reduce or eliminate mid-story vegetation, and diverse communities of herbaceous vegetation in the ground layer (Mitchell et al., 2006; Peet, 2006; Sorrie and Weakley, 2001; Van Lear et al., 2005; Walker and Peet, 1984). Longleaf pine forests are valued for both economic and ecological services; longleaf pine produces higher-quality timber products than other southern pines, and longleaf pine ecosystems provide habitat for threatened or endangered species such as the gopher tortoise (*Gopherus polyphemus*) and the red-cockaded woodpecker (RCW; *Picoides borealis*). Red-cockaded woodpeckers prefer large, old longleaf pine trees for nesting habitat (U.S. Fish and Wildlife Service, 2003) but commonly use other southern pines for nesting or foraging habitat if longleaf pines are not available. The high levels of floristic biodiversity and endemism associated with longleaf pine ecosystems have resulted in a growing list of threatened and endangered plant species that occur in these ecosystems (Glitzenstein et al., 2001; Walker, 1993). As a result, public and private land managers throughout the southeast are interested in restoring longleaf pine to upland sites,

Abbreviations: H, herbicide treatment; H+F, herbicide plus fertilizer treatment; LG, large gap treatment; LowBA, low basal area treatment; MedBA, medium basal area treatment; MG, medium gap treatment; NT, no treatment; RCD, root collar diameter; RCW, red-cockaded woodpecker; SG, small gap treatment.

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with a large emphasis on restoring conservation values (Lavoie et al., 2011; Mitchell et al., 2006). Establishing longleaf pine as a canopy dominant is required on sites occupied by other species.

Longleaf pine seedlings are considered intolerant of competition for resources (Boyer, 1990), and therefore traditional silvicultural practices for stand conversion to longleaf pine typically include clearcutting the existing canopy followed by artificial regeneration (e.g., Boyer, 1988; Brockway et al., 2006; Freeman and Jose, 2009; Knapp et al., 2006). However, this approach is less desirable in stands that currently provide habitat for existing RCW populations or provide other ecological services associated with canopy trees. Recently, the importance of canopy retention has been recognized for maintaining ecological function in a variety of forest systems (e.g., Attiwill, 1994; Franklin et al., 2002; Palik et al., 2002), and consequently, variable canopy retention has been increasingly incorporated into forest management. In southeastern pine forests, retaining canopy pines provides habitat for existing RCW populations but also regulates the structure of the ground layer vegetation and provides important fine fuel inputs from the needlefall of canopy pines (Jack et al., 2006; Kirkman and Mitchell, 2006; Mitchell et al., 2006). Kirkman et al. (2007) discussed the concept of gradually converting slash pine (*Pinus elliottii* Engelm.) stands to longleaf pine forests by retaining slash pine in the canopy to sustain ecological function during restoration. Such an approach may be feasible for establishing underplanted longleaf pine during the restoration of loblolly pine stands (e.g., Hu et al., 2012a, 2012b), provided that longleaf pine seedlings are able to successfully establish and recruit into the canopy over time.

Previous studies that have tested silvicultural methods for regenerating longleaf pine report that seedling growth is reduced by the presence of canopy trees. Natural longleaf pine regeneration is commonly aggregated in canopy openings (Gagnon et al., 2004; Grace and Platt, 1995a; Platt et al., 1988) created by lightning strikes or other disturbance events (Outcalt, 2008; Palik and Pederson, 1996). Several studies have explored regeneration dynamics within artificially or naturally created canopy openings in longleaf pine forests (e.g., Brockway and Outcalt, 1998; Gagnon et al., 2003; McGuire et al., 2001; Palik et al., 2003; Rodríguez-Trejo et al., 2003). These studies report that the influence of canopy pines on longleaf pine seedlings ranges from distances of 10 to 18 m from canopy trees, and they generally recommend that gap sizes of 0.1–0.2 ha are needed to increase seedling growth in the center of canopy openings (Brockway and Outcalt, 1998; McGuire et al., 2001). However, it may be acceptable to meet the objectives of ecological restoration over longer timeframes than that traditionally considered in plantation forestry; therefore, single-tree selection may be an option for reducing competitive pressure from canopy trees while retaining canopy pines in the stand (Kirkman and Mitchell, 2006; Pecot et al., 2007). Palik et al. (1997) reported a negative, exponential relationship between overstory density and the size of planted longleaf pine seedlings, in which seedling size increased substantially with less than 8 m^2/ha of overstory basal area. Habitat guidelines for RCW recovery recommend maintaining at least 9 m^2/ha basal area of trees $\geq$25 cm for foraging habitat (U.S. Fish and Wildlife Service, 2003), which suggests that balancing RCW habitat management with longleaf pine restoration requires a better understanding of longleaf pine seedling responses to variable canopy densities.

Longleaf pine seedling establishment can be additionally limited by competition from ground layer or mid-story vegetation, especially following the removal of canopy trees that compete with sub-canopy vegetation (Pecot et al., 2007). Herbicides may be used to improve longleaf pine seedling establishment by controlling competition from woody (Freeman and Jose, 2009; Jose et al., 2010; Knapp et al., 2006) and/or herbaceous (Haywood, 2000, 2005; Ramsey et al., 2003) vegetation. Herbicides are commonly used during artificial regeneration of cut-over forests or abandoned agricultural sites that have abundant competing vegetation (e.g., Ramsey et al., 2003; Knapp et al., 2006) and have the potential for meeting longleaf pine restoration objectives by improving seedling establishment and shifting the ground layer vegetation from woody to herbaceous species (Addington et al., 2012; Freeman and Jose, 2009). Additionally, fertilization has been suggested as a cultural treatment for increasing initial seedling growth on the nutrient-poor sites that support longleaf pine (Gagnon et al., 2003). However, the efficiency of herbicide application or fertilizers for improving underplanted longleaf pine seedling establishment in loblolly pine stands is not clear.

Much of our understanding of longleaf pine regeneration has come from research conducted within longleaf pine stands, on cut-over forestland, or on abandoned agricultural sites. The factors affecting longleaf pine seedling survival and growth may differ among sites with different histories and stand conditions, suggesting that outcomes of artificial regeneration in loblolly pine stands may differ from those previously reported. This study provides a comparison of three silvicultural systems used with artificial regeneration of longleaf pine: (1) clearcutting (the traditional conversion method); (2) group selection (applied to simulate natural regeneration patterns; e.g., Brockway and Outcalt, 1998; Palik et al., 2002); and (3) single-tree selection (recommended to retain ecological services of canopy pines during regeneration; e.g., Kirkman and Mitchell, 2006; Pecot et al., 2007). In addition, we tested the effects of cultural treatments on seedling survival and growth. This study and a parallel study applied in a different ecoregion in the longleaf pine range (Hu et al., 2012a) are the first to evaluate the effects of canopy retention on longleaf pine artificial regeneration in loblolly pine stands. Our specific objectives were to: (1) determine the effects of harvesting treatments that vary the distribution and density of residual canopy trees on planted longleaf pine seedling survival and growth; (2) determine the effects of herbicides and fertilizer on longleaf pine seedling survival and growth; and (3) determine the effects of within-gap position on planted longleaf pine seedling survival and growth.

2. Materials and methods

2.1. Study site

This study was conducted at Fort Benning Military Installation (~32.38°N, 84.88°W) in Muscogee and Chattahoochee Counties, GA and Russell County, AL. Prior to establishment as a U.S. military installation in 1918, much of the land base was used for cotton production but then reforested with loblolly pine following the abandonment of agriculture (Fort Benning, 2001). Currently, Fort Benning occupies 74,000 ha, of which approximately one-third (22,500 ha) is dominated by loblolly pine and approximately 15,000 ha support pure or mixed longleaf pine stands (Fort Benning, 2001). Fort Benning falls within two ecoregions, with the northeastern two-thirds in the Sand Hills Subsection of the Lower Coastal Plains and Flatwoods Section and the southwestern one-third of the installation within the Upper Loam Hills Subsection of the Middle Coastal Plain Section (Bailey, 1995). Soils are generally low in organic matter and nutrient holding capacity, although those of the Upper Loam Hills have higher silt and clay content than the coarse-textured, sandy soils of the Sand Hills. Common soil series in the Sand Hills include Troup sandy loam, Wagram loamy sand, and Vaucluse loamy sand; those of the Upper Loam Hills include Maxton loamy sand and Wickham sandy loam. The terrain of Fort Benning is predominately rolling and is highest in the Sand Hills of the northeast (225 m above sea level) and lowest near the Chattahoochee River in the southwest (58 m above sea level). The 50-year mean annual precipitation at Fort Benning (through 2011) was 1252 mm, with annual precipitation of 1289, 2037, and 946 mm in 2008, 2009, and 2010, respectively; the 50-year mean temperature was 18.4 °C, with mean annual temperature of 18.2, 18.0, and 18.3 °C in 2008, 2009, and 2010, respectively (National Climatic Data Center, NOAA, Columbus Metropolitan Airport Station, GA).

For this study, we used upland sites dominated by second-growth loblolly pine that were targeted for longleaf pine restoration by land managers at Fort Benning. Many such sites have been managed to improve RCW habitat over the past few decades, and recent management activities include the use of frequent prescribed fire. Common understory species included bunchgrasses (e.g., *Andropogon* spp., *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum* spp.) and herbaceous species such as legumes (e.g., *Desmodium* spp., *Lespedeza* spp.) and composites (e.g., *Eupatorium* spp., *Solidago* spp.). Woody species, including sweetgum (*Liquidambar styraciflua* L.), persimmon (*Diospyros virginiana* L.), oaks (*Quercus* spp.), and hickories (*Carya* spp.), were common in the understory and mid-story.

2.2. Experimental design and treatments

The experiment was a randomized, complete block, split-plot design, with the location of individual loblolly pine stands used as the block factor, and the study was replicated in six blocks located across Fort Benning. Each block was divided into seven main treatment plots and each main-plot received an overstory treatment. Main-plots were 100 m × 100 m (1 ha), with the exception of the Clearcut plots, which were 141 m × 141 m (2 ha) to create clearcut conditions in the center. The overstory treatments include four treatments that resulted in the uniform distribution of canopy pines: Control (uncut; residual basal area ~16 m^2/ha); MedBA (single-tree selection with the target basal area of 9 m^2/ha); LowBA (single-tree selection with the target basal area of 5 m^2/ha); and Clearcut (all trees removed to basal area of 0 m^2/ha). In three additional treatments, referred to as "gap" treatments, we used group selection to create circular canopy gaps of different sizes: LG (large-sized gap; radius of 40 m and total area of approximately 5027 m^2); MG (medium-sized gap; radius of 30 m and total area of approximately 2827 m^2); and SG (small-sized gap; radius of 20 m and total area of approximately 1257 m^2). Each experimental gap was surrounded by a buffer of at least 20 m of undisturbed canopy, and canopy gaps were created by removing any tree for which the center of the bole was within the respective radius distance from the gap center.

Following timber harvest, study sites were prepared in accordance with standard management procedures for longleaf pine establishment at Fort Benning, with the objectives of removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-pyridinecarboxylic acid) mixed with 2.24 kg/ha glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) and broadcast throughout the entire study area in September 2007, followed by prescribed fire in November 2007. Study sites were planted with container-grown longleaf pine seedlings at 1.8 m × 3.7 m spacing, for a total of 1500 seedlings per hectare. Within each gap treatment, longleaf pine seedlings were planted in rows that were oriented north/south across the canopy openings. Planting began in mid-November 2007 and was completed by January 2008.

Sub-plot treatments include additional cultural practices designed to enhance ecosystem restoration, by either improving the growing conditions for planted longleaf pine seedlings or by reducing the abundance of woody vegetation in the understory. The sub-plot treatments include an untreated control (NT), competition control with herbicide (H), and competition control with herbicide combined with fertilizer (H+F). Main-plot treatments Control, MedBA, LowBA, and Clearcut were each divided into four equal sections for cultural treatment application. Within each section, sub-plot treatments were applied to a 30 m × 30 m treatment area centered on a 20 m × 20 m measurement plot. In gap plots, we systematically selected three rows near the center of each gap, and sub-plot treatments were applied to a 6-m wide band centered on each seedling row, extending 10 m into the forest on either end.

The herbicide treatment was designed to reduce the abundance of competing vegetation around planted longleaf pine seedlings and to reduce the abundance of hardwoods in the ground layer and mid-story. We prescribed an application of 1% imazapyr plus 0.25% non-ionic surfactant that was applied directly to hardwood vegetation, with care taken to avoid longleaf pine seedlings, in October 2008. Because herbaceous vegetation dominated most of the study sites, we applied an additional mix of 63.2% hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] and 11.8% sulfometuron methyl {methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl]benzoate} at a rate of 0.84 kg/ha, sprayed in approximately 1-m wide bands over top of longleaf pine seedlings in March 2009. The H+F treatment included the herbicide treatments described above as well as an application of 280 kg/ha 10-10-10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009, with care taken to evenly distribute the fertilizer throughout each treatment area. All study areas were burned with prescribed fire between the second and third growing seasons (January–April 2010). This burn was applied to meet the management objective of maintaining frequent fire on these sites and was not applied as a study treatment.

2.3. Data collection

In June 2008, we selected a sub-sample of longleaf pine seedlings in each sub-plot and permanently marked each seedling with an aluminum tag. In uniform canopy plots (Control, MedBA, LowBA, and Clearcut), we randomly selected a sample of 30 seedlings (approximately half of the trees planted in each 20 × 20 m measurement area), and in gap plots we tagged every seedling that occurred on each north/south sub-plot measurement row, extending 10 m into the forest on either end. Therefore, the total number of seedlings marked in each gap varied with gap size (average of 42, 34, and 23 seedlings/row in LG, MG, and SG, respectively). We monitored seedling survival shortly after planting (May 2008), shortly after the 2010 prescribed fire (May 2010), and at the end of each of the first three growing seasons (October 2008, October 2009, and October 2010). At the end of each growing season, root collar diameter (RCD) of each seedling was measured with digital calipers along two perpendicular axes of the root collar, and the average of the two measurements was calculated to account for irregularity in root collar shape. Seedling height was measured as the distance from the root collar to the tip of the terminal bud. Because all seedlings were in the grass stage in 2008, seedling height was measured only in 2009 and 2010.

2.4. Data analysis

2.4.1. Effects of study treatments on seedling response

We tested the effects of management treatments on the plot-level means of longleaf pine response variables during each year.

Mean mortality and growth variables (RCD and the percentage of seedlings in height growth) were calculated at the main-plot level in 2008 (only RCD) and at the sub-plot level in 2009 and 2010. Incremental mortality was calculated as the percentage of seedlings that died between measurement periods: $((N_1 - N_2)/N_1) \times 100$, where N_1 is the number of seedlings alive at the start of the measurement period and N_2 is the number of seedlings alive at the end of the measurement period. Seedlings were determined to be in height growth when the terminal bud was $\geq$15 cm from the root collar, and we calculated the percentage of seedlings in height growth based on the number of surviving seedlings in each plot in 2009 and 2010.

We used mixed-model Analysis of Variance (ANOVA) with a random block effect to determine significant treatment effects in each year, using a split-plot model for October 2009 and 2010 data. We also conducted repeated measures ANOVA to determine the effect of time (measurement period) on longleaf pine mortality and root collar diameter. Because sub-plot treatments were applied after the first growing season, we used only the control sub-plot (NT) data for the repeated measures analyses and included only seedlings that remained alive in 2010 for the repeated measures analysis of root collar diameter.

2.4.2. Effects of gap position on seedling response

In gap plots, we tested the effects of gap position on longleaf pine mortality and root collar diameter in two ways: (1) we compared seedling responses in the north vs. the south half of gaps, and (2) we tested the effects of gap position (in 10 m intervals) on seedling response along the north/south gradients. We calculated mean values for each direction (north vs. south) and each 10 m interval position by grouping data into bins for analyses. Sub-plot data were grouped together for the analyses because we found no interactions between the sub-plot effects and gap position or direction effects.

We used split-plot ANOVA with gap size as the main-plot effect and direction as the sub-plot effect to test for interactions between gap size and direction. In the absence of an interaction, we tested the effects of gap direction on response variables with data from all gaps combined. We used ANOVA to test effects of gap position in 10 m intervals for each gap separately because gap size differed (and therefore the number of positions per gap differed). For the analyses, we used a repeated measures model with a first order autoregressive covariance structure to account for spatial correlation in gap position. For all analyses, treatment differences were determined using Tukey's honestly significant difference test, and degrees of freedom were calculated using the Satterthwaite approximation. When necessary, transformations were used to meet assumptions of normality and constant variance. Treatment effects were determined to be significant when $\alpha < 0.05$.

3. Results

3.1. Seedling response to treatment effects

3.1.1. Seedling mortality

The repeated measures analysis indicated that there was no significant interaction between measurement period and canopy treatment on seedling mortality ($F_{24,\,140} = 1.57$; $p = 0.0559$). There was a significant effect of measurement period on cumulative seedling mortality ($F_{4,\,140} = 147.08$; $p < 0.0001$), and cumulative mortality increased each measurement period with exception of from October 2009 to May 2010 (Table 1). By the end of the third growing season, over half of the planted seedlings had died, but the majority of the mortality occurred in the first year. The canopy treatments also affected seedling mortality ($F_{6,\,30} = 6.22$; $p = 0.0003$), with the highest mortality on the Clearcut plots and the lowest mortality on Control and MedBA plots (Table 1).

Table 1
Longleaf pine seedling cumulative mortality (%) by measurement period and canopy treatment; the same superscript letter within an effect indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.

Effect	Level	Mortality	
		Mean	SE
Measurement period	May 2008	6.77[d]	(2.97)
	October 2008	29.05[c]	(4.76)
	October 2009	36.25[b]	(5.16)
	May 2010	41.21[b]	(6.08)
	October 2010	55.00[a]	(7.32)
Canopy treatment	Control	20.82[b]	(4.20)
	MedBA	19.77[b]	(3.15)
	LowBA	39.51[a]	(7.51)
	Clearcut	47.02[a]	(8.35)
	LG	38.00[ab]	(5.03)
	MG	39.20[a]	(5.98)
	SG	31.27[ab]	(7.70)

There were no significant interactions between the main-plot and sub-plot treatment effects on cumulative or incremental mortality in 2009 or 2010 (Table 2). We found significant treatment effects on cumulative mortality at the end of each growing season (Table 2 and Fig. 1A), with general patterns similar to those found in the repeated measures analysis. After the first growing season, there was close to 50% mortality of the planted seedlings on the Clearcut plots, which was significantly greater than the mortality on the Control and MedBA plots. Cumulative mortality was similar after the second growing season, but by the end of the third growing season (2010) mortality on only the Control plots was significantly lower than that on the Clearcut and LG plots. There was no significant sub-plot effect in 2009 or 2010 (Table 2 and Fig. 1B). The incremental mortality was not significantly affected by the main-plot treatments between October 2008 and October 2009 or between October 2009 and October 2010. However, incremental mortality was higher on NT sub-plots than on H sub-plots between the second and third growing seasons (Fig. 2).

3.1.2. Seedling growth

The repeated measures analysis (using data from only NT sub-plots) showed a significant interaction between year and canopy treatment effects on root collar diameter ($F_{12,\,68} = 3.86$; $p = 0.0002$). Root collar diameter increased over time on all treatments except the Control plots ($F_{2,\,68} = 1.48$; $p = 0.2351$). In the split-plot ANOVA using the entire dataset, there were no significant interactions between main-plot and sub-plot effects on root collar diameter in 2009 or 2010 (Table 3). The main-plot treatment effect was significant in each year, and seedlings in the Control plots were significantly smaller than those in the Clearcut, LowBA, and SG plots in each year (Fig. 3). After three growing seasons, seedlings in the Control plots were significantly smaller than those in each of the gap treatments, and there was a general pattern of increased seedling size associated with the amount of canopy removal. The sub-plot treatments had no effect on seedling root collar diameter (Table 3).

There were no interactions between main-plot and sub-plot effects on the percentage of seedlings in height growth (Table 3). The canopy treatments significantly affected the percentage of seedlings in height growth in 2009 and 2010, with differences among treatments similar to those observed for root collar diameter (Table 4). The Control and MedBA plots generally had

Table 2
Results of ANOVA to determine main-plot and sub-plot treatment effects on longleaf pine cumulative and incremental mortality in October 2008, 2009, and 2010.

Variable	Period	Effect	Num DF	Den DF	*F*-Value	*p*-Value
Cumulative mortality	October 2008	main	6	30	8.59	<0.0001
	October 2009	main	6	30	7.02	<0.0001
		sub	2	70	0.37	0.6944
		main × sub	12	70	0.73	0.7134
	October 2010	main	6	30	3.97	0.0048
		sub	2	70	0.40	0.6714
		main × sub	12	70	0.83	0.6180
Incremental mortality	October 2008–October 2009	main	6	30	1.22	0.3236
		sub	2	70	0.94	0.3966
		main × sub	12	70	0.69	0.7530
	October 2009–October 2010	main	6	30	0.64	0.7004
		sub	2	70	5.19	0.0079
		main × sub	12	70	1.00	0.4562

Table 3
Results of ANOVA to determine main-plot and split-plot treatment effects on longleaf pine seedling root collar diameter and the percentage of seedlings in height growth in October 2008, 2009, and 2010.

Variable	Year	Effect	Num DF	Den DF	*F*-Value	*p*-Value
Root collar diameter	2008	main	6	30	3.86	0.0057
	2009	main	6	30	8.94	<0.0001
		sub	2	70	1.65	0.2004
		main × sub	12	70	1.27	0.2576
	2010	main	6	30	8.75	<0.0001
		sub	2	67	1.25	0.2935
		main × sub	12	67	1.87	0.0540
Percentage of seedlings in height growth	2009	main	6	30.2	3.59	0.0083
		sub	2	69.4	0.09	0.9127
		main × sub	12	69.4	0.83	0.6172
	2010	main	6	30.2	3.44	0.0104
		sub	2	69.4	0.12	0.8835
		main × sub	12	69.4	0.73	0.7160

significantly fewer seedlings in height growth than the Clearcut and SG plots. After three growing seasons, almost no seedlings had emerged from the grass stage on the Control treatments, but 35% of the seedlings remaining alive on Clearcut plots were in height growth. The sub-plot treatments had no effect on seedling emergence from the grass stage in 2009, but significantly more seedlings had emerged from the grass stage on the H than on the NT sub-plots in 2010.

Table 4
The percentage of longleaf pine seedlings in height growth by main-plot and sub-plot treatments in 2009 and 2010. The same superscript letter within a column indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$ for each effect.

Effect	Treatment	Height growth (%)			
		2009		2010	
		Mean	SE	Mean	SE
Main-plot	Control	0.00^{b}	0	0.23^{c}	0.23
	MedBA	0.76^{b}	0.76	$3.38b^{c}$	1.63
	LowBA	3.31^{ab}	1.8	16.04^{ab}	3.9
	Clearcut	8.17^{a}	3.54	34.59^{a}	9.18
	LG	1.78^{ab}	1.24	11.94^{abc}	5.33
	MG	3.54^{ab}	1.98	12.48^{abc}	5.9
	SG	5.53^{a}	2.3	23.31^{a}	8.59
	p-Value	0.0081		<0.0001	
Sub-plot	NT	3.21	0.8	10.25^{b}	3.48
	H	3.28	1.49	18.14^{a}	5.78
	H+F	3.47	1.58	15.31^{ab}	4.4
	p-Value	0.9487		0.0224	

3.2. Seedling response to canopy gap position

3.2.1. Seedling mortality

We found no significant interactions between gap size and direction on seedling mortality in 2008 ($F_{2,\,86.8} = 0.83$; $p = 0.4391$), 2009 ($F_{2,\,86.8} = 0.27$; $p = 0.7611$), or 2010 ($F_{2,\,85.8} = 1.81$; $p = 0.1704$). In each year, cumulative seedling mortality was significantly greater in the northern half of gaps than in the southern half of gaps (Fig. 4A). Cumulative mortality generally increased from the forest edge to the gap center within each gap size and at each measurement period (Fig. 5A, C, and E). By the end of the third growing season, however, few significant differences in mortality by gap position were detected. In LG plots, for example, the only differences in seedling mortality rates were between seedlings located 10 m into the forest on the north side of the gaps and seedlings located at both 10 and 20 m into the gap interior on the north side of the gaps (Fig. 5A). Mortality ranged from 40 to 70% in LG plots, from 31 to 61% in MG plots, and from 40 to 64% in SG plots at the end of the third growing season, with the lowest mortality rates consistently located within the forest interior.

3.2.2. Seedling growth

We found no significant interactions between gap size and direction on seedling root collar diameter in 2008 ($F_{2,\,87} = 0.10$; $p = 0.9055$), 2009 ($F_{2,\,87} = 2.39$; $p = 0.0975$), or 2010 ($F_{2,\,83.5} = 2.98$; $p = 0.0565$). Root collar diameter was not affected by gap direction in any measurement year (Fig. 4B) but generally increased from the forest edge to the gap center (Fig. 5B, D, and F). There were no significant effects of gap position on seedling size after one growing

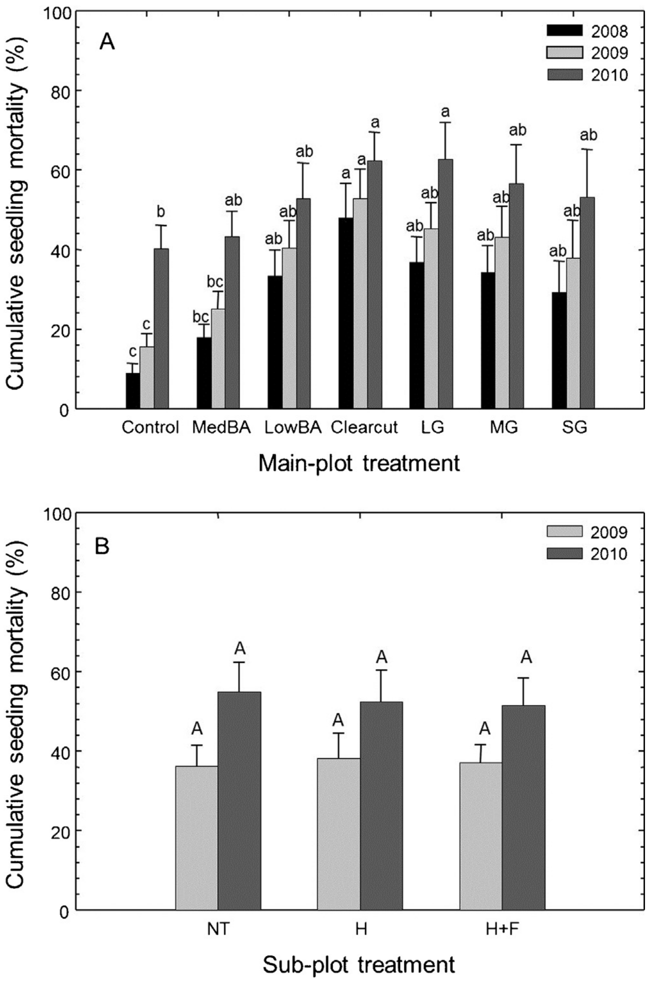

Fig. 1. Cumulative seedling mortality (mean + 1 SE) by (A) main-plot canopy treatment in October 2008, 2009, and 2010 and (B) sub-plot cultural treatment in October 2009 and 2010. The same letter within a year indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.

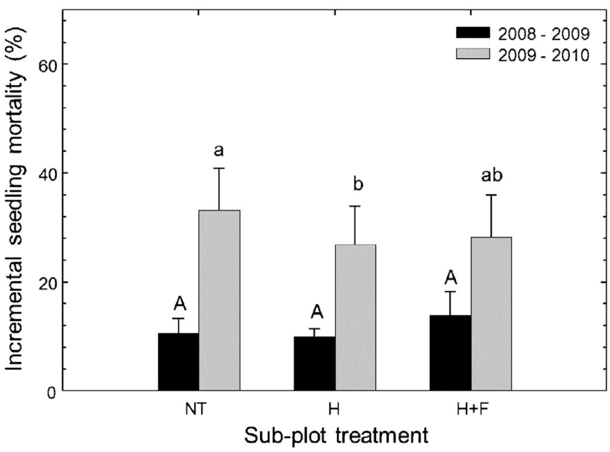

Fig. 2. Incremental seedling mortality (mean + 1 SE) by sub-plot treatment from October 2008 to October 2009 and from October 2009 to October 2010. The same letter within a period indicates pair-wise comparisons are not significantly different at $\alpha = 0.05$.

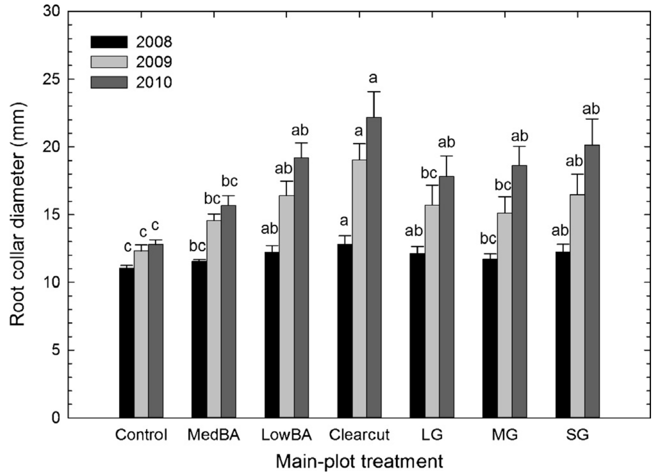

Fig. 3. Root collar diameter (mean + 1 SE) by main-plot canopy treatment in October 2008, 2009, and 2010. The same letter within a year indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.

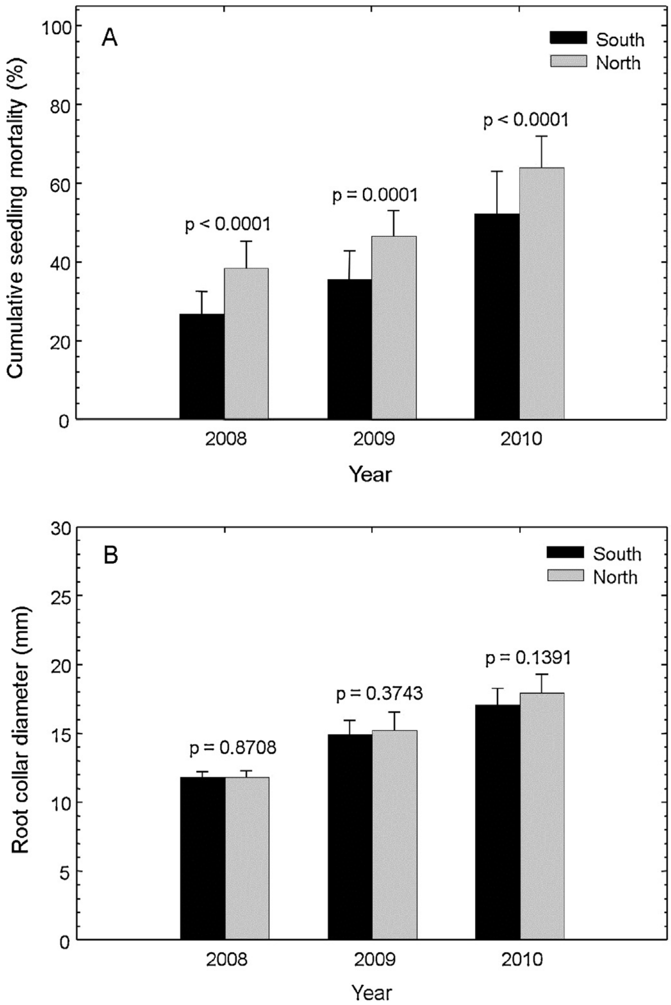

Fig. 4. Effects of gap direction (north vs. south) on (A) cumulative seedling mortality (mean + 1 SE) and (B) root collar diameter (mean + 1 SE) at the end of the first (2008), second (2009), and third (2010) growing seasons; p-values indicate differences in gap direction for each year.

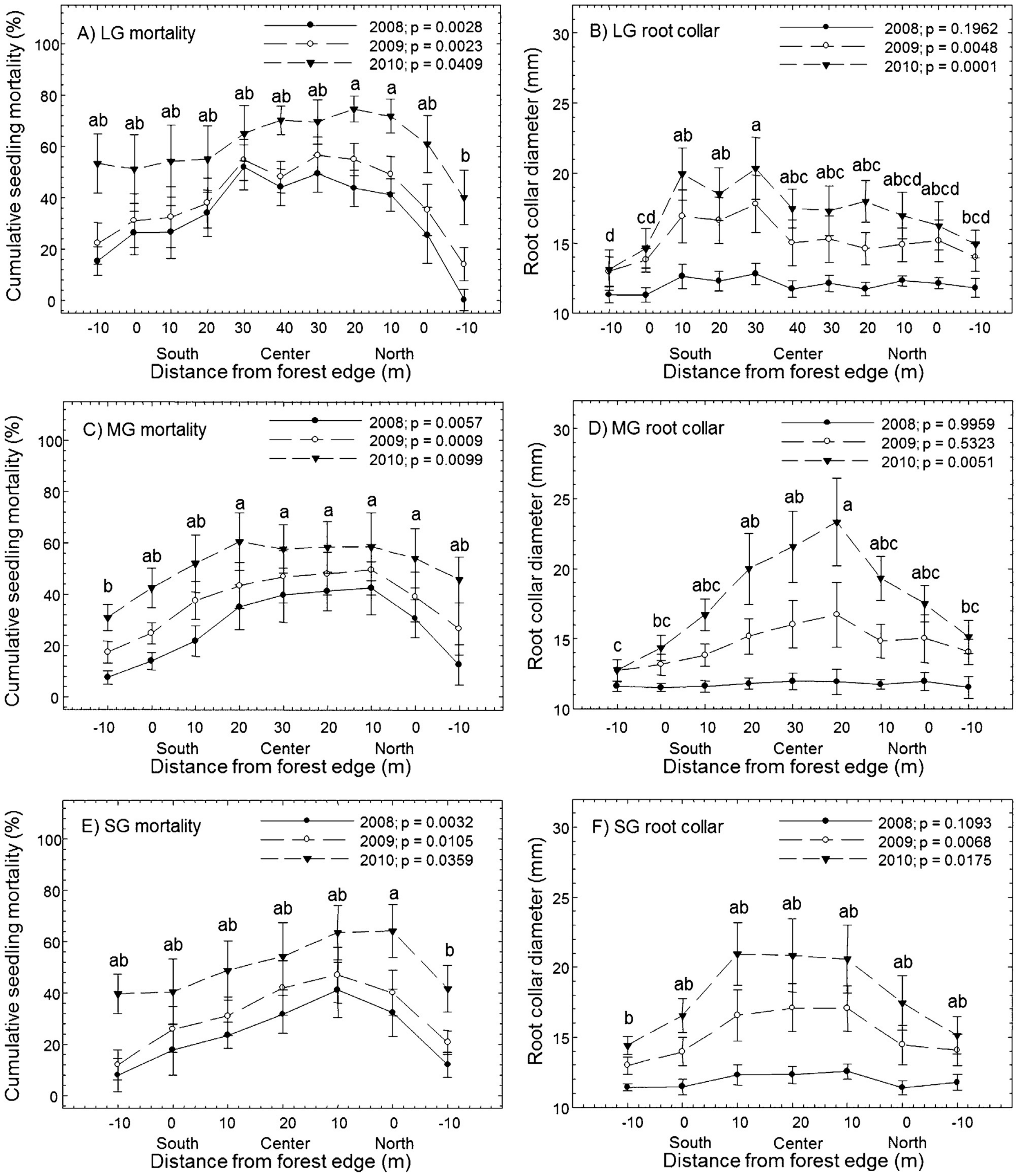

Fig. 5. Effects of gap position on cumulative seedling mortality (A, C, and E) and root collar diameter (B, D, and F) at the end of the first (2008), second (2009), and third (2010) growing seasons for each gap size. Negative values on the *x*-axis indicate distances from the gap edge into the forest interior. The same letter within a panel indicates pair-wise comparisons are not significantly different at $\alpha = 0.05$ (only shown for cumulative response in 2010).

season for any gap size, but by the end of the third growing season root collar diameter was maximized at or near the center of each gap. Seedling size did not significantly increase beyond 10 m from the forest edge in any gap.

4. Discussion

The widespread loss of longleaf pine from its natural range has made artificial regeneration necessary for converting existing forests to longleaf pine dominance, and early survival of planted seedlings is critical to the success of restoration efforts. The development of container-grown seedlings, which were used in this study, has increased the success of artificial regeneration when compared to attempts with bare-root seedlings (Barnett, 2002; Boyer, 1988; Rodríguez-Trejo et al., 2003; South et al., 2005). Generally, mortality of container-grown seedlings is highest in the first year after planting because seedlings must adjust to the new growing environment (Boyer, 1988; Haywood, 2005; Knapp et al., 2006), and mortality was highest during the first growing season (between May and October 2008) in our study. However, previous studies have reported a wide range of survival rates for container-grown longleaf pine seedlings. For example, Palik et al. (1997) reported an average of 97% seedling survival one year after planting in canopy gaps that ranged from around 0.1 to 0.2 ha in southwestern Georgia. In contrast, Rodríguez-Trejo et al. (2003) reported mean survival of only 25% for container-grown seedlings planted in canopy gaps and intact forests in another study located in southwestern Georgia. Results from previous studies suggest that the early survival of planted longleaf pine seedlings is related to climatic conditions during establishment, with increased mortality during periods of drought. Two studies in particular provide strong evidence of this pattern: the Rodríguez-Trejo et al. (2003) study planted seedlings in 1998 and reported high rates of first-year mortality following a year of drought, and McGuire et al. (2001) established a study at the same location one year earlier, with planting in 1997. First-year survival was higher (50–70% survival) in the McGuire et al. (2001) study, but by the end of the second growing season (1998) the survival had dropped to around 10%.

The role of drought in affecting longleaf pine seedling mortality is further supported by evidence of a facilitation effect of canopy pines on longleaf pine seedling survival (McGuire et al., 2001; Palik et al., 2003). For example, Rodríguez-Trejo et al. (2003) reported that first-year seedling survival beneath uncut forest canopies (35.1%) was over twice that within large canopy gaps (15.4%). In a study from northwest Florida, Gagnon et al. (2003) found that initial seedling survival was higher at the edge of canopy gaps (51%) than at gap centers (23%) and that survival was negatively correlated with exposure to photosynthetically active radiation (PAR). Facilitation from canopy trees has commonly been observed for regeneration in dry or extreme habitats and is attributed to the alleviation of unfavorably harsh conditions (Holmgren et al., 1997). Although longleaf pine is generally adapted to growing in dry environments, the additional stress of increased solar radiation may reduce seedling survival during drought years. Allen (1954) used palm fronds to shade longleaf pine seedlings and found that shaded seedlings had higher survival (83%) than exposed seedlings (27%) after one growing season on a dry sandy site in Mississippi. The annual precipitation in 2008 was similar to the 50-year mean for our study location, but the precipitation during the early months of the growing season (May–June; 343 mm) was 22% lower than the 50-year mean for that time period (441 mm), suggesting that dry conditions during seedling establishment may have contributed to early mortality. Several findings from our study further support that canopy pines can facilitate longleaf pine seedling survival by reducing exposure to solar radiation. First, we observed gradually increasing mortality rates as canopy removal increased from the Control to the Clearcut treatments. Second, mortality was higher in gap centers than under the uncut forest canopy at gap edges. Third, mortality was significantly higher in the northern half of gaps than in the southern half of gaps. However, in a parallel study established with the same experimental design and over the same time period at Camp Lejeune, North Carolina, Hu et al. (2012a) found that seedling survival was lowest on uncut Control plots and highest on Clearcut plots three years after planting. Moreover, there were no effects of gap position on seedling survival (Hu, 2011). These contrasting results suggest that local site conditions or weather patterns associated with different study locations may strongly affect longleaf pine seedling survival.

Longleaf pine seedlings are generally considered to be resistant to mortality from low-intensity fires when in the grass stage, but the specific interactions of fuel loads, fire intensity, and seedling response are not well understood. Grace and Platt (1995a) attributed low densities of naturally regenerated seedlings beneath canopy pines to hot fires that result from increased fuel loads from pine litter deposits, and Boyer (1974) reported post-fire mortality rates of 41% for grass stage seedlings beneath canopy pines compared to 19% for released seedlings. In a recent study from southwestern Georgia, Jack et al. (2010) experimentally manipulated fuel loads and found that high fuel loads resulted in more intense fires and higher seedling mortality than low fuel loads. Although our study was not designed to test the effects of prescribed fire on seedling mortality, we observed that mortality in the third growing season (following the 2009–2010 burns) was higher than that in the second growing season. We did not find a significant effect of canopy density on incremental seedling mortality following the fire, but mortality on Control plots, where needle litter would be high, appeared to be higher than that on other treatments between 2009 and 2010 (Fig. 1A). In addition, incremental seedling mortality was higher on the untreated sub-plots than on the H sub-plots. It is possible that the increased mortality was related to greater competition on untreated plots, but there was no difference in incremental mortality the year before, suggesting that the higher incremental mortality on NT plots may have been related to higher fuel loads and hotter fires on the untreated sub-plots. Additional research is required to understand the effects of forest management on fuels, fire behavior, and fire effects on underplanted longleaf pine seedlings, and such information is critical for integrating harvesting or cultural treatments with fire management.

In contrast to the facilitation effect of canopy pines observed for seedling survival, the canopy treatment effects on root collar diameter indicate competition between overstory and planted trees. Given the intolerant nature of longleaf pine seedlings, such growth patterns are not unexpected, and many past studies have demonstrated negative effects of canopy pines on longleaf pine seedling growth (e.g., Boyer, 1963, 1993; Kirkman and Mitchell, 2006; Mitchell et al., 2006; Palik et al., 1997; Pecot et al., 2007). The relationship between longleaf canopy trees and seedlings has been described by a negative exponential function (Mitchell et al., 2006; Palik et al., 1997), and Boyer (1993) reported drastic reductions in growth when canopy basal area exceeded 9 m^2/ha. In our study, only the uncut Control treatment (16 m^2/ha basal area) exceeded this level of stand density, and the repeated measures analysis showed no measureable increase in seedling growth over three years on the Control plots. Mean root collar diameter in all other treatments increased over time, however, suggesting the potential for early growth and eventual recruitment of longleaf pine seedlings underplanted in association with these silvicultural alternatives. In canopy gap treatments, mean seedling size was no different from that within Clearcut plots, despite significant effects of gap position on seedling root collar diameter. Generally, we found that seedling root collar diameter increased from the forest edge to 10 m within the gap, but seedling size was not significantly different among positions within the gap interiors. In canopy gaps of different sizes in southwestern Georgia, McGuire et al. (2001) reported that seedling root collar diameter increased up to 18 m from the forest edge, with no additional increases up to 72 m from the forest edge. Similarly, Grace and Platt (1995b) found that seedling growth was negatively affected by canopy trees within distances of 15 m. Our results corroborate those of previous studies that found that longleaf pine seedling growth is reduced near mature trees but increases within relatively short distance from the canopy.

We found no effect of herbicide application on seedling root collar diameter, in contrast to previous studies that report herbicides to be an effective management practice for controlling competing vegetation and increasing seedling growth when applied as site preparation (Addington et al., 2012; Knapp et al., 2006) or as over-the-top release treatments (Freeman and Jose, 2009; Haywood, 2000; Jose et al., 2010; Nelson et al., 1985; Ramsey et al., 2003). However, the effectiveness of herbicide treatments is dependent on characteristics (e.g., composition and abundance) of the dominant vegetation on the site and on the type of herbicide used. Jose et al. (2010) tested the effects of four common herbicide treatments used in longleaf pine restoration (imazapyr, hexaninone, sulfometuron methyl, and hexazinone + sulfometuron methyl) on planted seedlings and found that all treatments increased seedling root collar diameter except sulfometuron methyl alone. The imazapyr treatment resulted in the greatest seedling volume growth, a result that was associated with better control of the dominant competing species on the site. Hu et al. (2012a) reported that control of woody vegetation with imazapyr resulted in larger seedling root collar diameters in a study with a similar design to that used in our study, suggesting that differences in the vegetation composition or site characteristics between their study and ours may have been responsible for the different outcomes following herbicide application. In our study, herbaceous vegetation dominated the study sites, which was likely due to a recent history of prescribed burning and the herbicide site preparation that was applied to control woody vegetation. Competition from herbaceous vegetation has been associated with reductions in longleaf pine seedling size in other studies (Berrill and Dagley, 2010; Haywood, 2005), particularly on old-field sites with high abundances of herbaceous vegetation (Ramsey et al., 2003). It is possible that the lack of a response of root collar diameter to herbicide release in our study was related to differences in the site conditions, site/management history, or the initial abundance of vegetation on our study sites as compared to those of other studies.

Despite having no effect on seedling root collar diameter, the herbicide treatment increased the percentage of seedlings in height growth two growing seasons after application. Generally, the emergence of longleaf pine seedlings from the grass stage is believed to be related to seedling size, with emergence occurring when the root collar reaches a diameter of around 25 mm (Boyer, 1990; Knapp et al., 2006). However, Ramsey et al. (2003) reported that vegetation control treatments may affect the timing of grass stage emergence by making the resources necessary for growth more readily available. The significant effect of herbicides on the percentage of seedlings in height growth in this study also suggests that factors in addition to root collar diameter may affect seedling emergence. Additional research is required to understand the mechanisms controlling the emergence of longleaf pine seedlings from the grass stage.

Longleaf pine forests commonly occur on sites with low nutrient-holding capacity, and fertilization is a common practice to improve the performance of other southern pines on such sites (e.g., Haywood and Tiarks, 1990; Jokela et al., 2004). Previous studies have reported beneficial or marginally beneficial effects of fertilizers used in combination with competition control during longleaf pine regeneration (Gagnon et al., 2003; Ramsey et al., 2003), but the effects were not easily attributable to the fertilizer alone because the effects of competition removal could not be separated from those of fertilization. In fact, Ramsey et al. (2003) reported that fertilizer alone resulted in lower survival and smaller root collar diameters than untreated control plots. Other studies have also shown that fertilizers either had no effect or reduced longleaf pine seedling survival and/or growth when compared to untreated sites (Bengtson, 1976; Haywood, 2007; Loveless et al., 1989). We combined fertilizer application with competition control to increase the availability of the nutrient amendments for longleaf pine seedlings by reducing immediate uptake from competing vegetation, but we did not observe benefits of the fertilizer treatment on longleaf pine seedling response.

Our results demonstrate that longleaf pine establishment can be successfully accomplished using several silvicultural practices, suggesting a degree of flexibility for meeting different management objectives of stand conversion. The traditional practice of clearcutting resulted in the greatest seedling growth but came at the cost of seedling survival. As a result of high mortality, only 20% of the total number of seedlings planted were in height growth after three growing seasons, and only 40% of the planted seedlings remained alive on clearcut plots. Landowner objectives will largely determine the target stand density; for instance, pine straw production requires higher stand densities than are desirable for wildlife habitat or sawtimber production (South, 2006). When high-density stands are desirable, managers may have to increase planting density to compensate for mortality on clearcut sites. However, interest in maintaining ecological function, maximizing biological diversity, and providing habitat for existing wildlife species often requires the retention of canopy pines, and underplanting longleaf pine seedlings may be a viable option for meeting such restoration objectives (Kirkman et al., 2007).

Underplanting is a technique that has been used in a variety of systems to establish forest regeneration beneath an existing canopy and is typically implemented either to increase the success of regeneration or to maintain benefits from the existing canopy (Paquette et al., 2006). Underplanting has not traditionally been used for longleaf pine because of the species' intolerance to competition, but it may be a viable option to reach certain management objectives (e.g., Brockway et al., 2005). The retention of canopy pines during longleaf pine regeneration is expected to help maintain ecosystem function by providing pine needles as a fuel source for fire management (e.g., Kirkman et al., 2007; Mitchell et al., 2006, 2009), limiting the release and growth of hardwood species (e.g., Jack et al., 2006; Kirkman and Mitchell, 2006; Mitchell et al., 2006), reducing the growth potential of natural loblolly pine regeneration (Knapp et al., 2011), and improving planted seedling survival (e.g., Gagnon et al., 2003; McGuire et al., 2001; Rodríguez-Trejo et al., 2003). Moreover, retaining canopy pines can allow managers to reach multiple management objectives that may include maintaining the esthetic value of the existing forest or fulfilling habitat requirements for wildlife (including the federally endangered red cockaded woodpecker).

Similar to the results of Hu et al. (2012a), we found essentially no growth of longleaf pine seedlings underplanted in uncut loblolly pine forests with canopy basal areas of around 16 m^2/ha, suggesting that some degree of canopy removal is necessary for eventual seedling recruitment. Recent research reports discuss the potential application of single-tree selection methods for longleaf pine establishment within existing longleaf pine forests (Kirkman and Mitchell, 2006; Pecot et al., 2007), describing a three-stage model in which high levels of canopy retention (>17 m^2/ha basal area) prohibit seedling recruitment, moderate levels (9–17 m^2/ha basal area) reduce seedling growth, and low levels (<9 m^2/ha basal area) result in seedling recruitment over time (Mitchell et al., 2006). Our results indicate that single-tree selection harvests that reduce basal area to moderate levels in loblolly pine stands (5–9 m^2/ha basal area) do not preclude seedling establishment, although growth is reduced by increasing the amount of canopy retention. By focusing canopy removal within localized areas in a stand, group selection provides an alternative method for reducing canopy density and may be favored for the greater longleaf pine seedling growth potential within gap centers. Previous studies have recommended canopy gaps of 0.1–0.2 ha for longleaf pine establishment in longleaf pine forests (Brockway and Outcalt, 1998; McGuire et al., 2001), and our results indicate that similar-sized canopy gaps in loblolly pine forests result in increased growth in gap centers. To reduce the negative effects of high incident radiation on seedling survival, Rodríguez-Trejo et al. (2003) suggested that oval-shaped gaps oriented northwest to southeast may increase survival rates with minimal effects on seedling growth. Given the higher mortality rates observed on the north half of canopy gaps in our study, additional research on canopy gap shape and orientation could result in improved longleaf pine seedling establishment in loblolly pine forests as well.

5. Conclusions

Silvicultural treatments are prescribed in accordance with specific management objectives, and our results demonstrate that several silvicultural treatments may be used to establish longleaf pine seedlings in loblolly pine stands. Managers can maximize planted longleaf pine seedling growth by clearcutting the existing canopy but risk high seedling mortality, especially in drought conditions. In contrast, variable canopy retention has been recommended in longleaf pine forests that are managed to promote ecosystem function and can provide additional value from esthetics, wildlife habitat, and other ecological services. To meet such objectives in loblolly pine stands, we recommend using single-tree selection to reduce basal area to moderate levels (residual basal areas of 5–9 m^2/ha) or group selection to create small canopy openings (0.1 ha). However, these treatments do not have to be applied uniformly throughout a stand; integrating these harvesting methods into a variable retention approach provides managers with flexibility to control the spatial distribution of canopy retention and canopy openings. Such an approach may be particularly useful in stands that support red-cockaded woodpeckers; in some cases, RCW habitat requirements may restrict either the allowable density or spatial arrangement of residual trees following harvest (U.S. Fish and Wildlife Service, 2003), and variable canopy retention may be used to localize longleaf pine regeneration in areas that are compatible with stand-level management needs.

Land managers implementing canopy retention should anticipate that seedling growth will be reduced by the presence of canopy pines, but longleaf pine seedlings can become established provided that hardwood encroachment and natural loblolly pine regeneration are limited by frequent fire management. Although we found that herbicides did not improve seedling root collar growth in our study, sites with aggressive herbaceous or woody competition may require herbicide release for seedling establishment. Furthermore, it is important to consider how silvicultural practices affect other ecosystem components during restoration, including the ground layer vegetation, effects of treatments on fuel loads and fuel continuity, and the ability of land managers to effectively apply prescribed fires. Additional research is required to refine our understanding of the comprehensive effects of forest management on these ecosystem responses and to determine the long-term effects of canopy and cultural treatments on the development of artificially regenerated longleaf pine in a restoration context.

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