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Restoring longleaf pine (*Pinus palustris* Mill.) in loblolly pine (*Pinus taeda* L.) stands: Effects of restoration treatments on natural loblolly pine regeneration

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ABSTRACT

Historical land use and management practices in the southeastern United States have resulted in the dominance of loblolly pine (*Pinus taeda* L.) on many upland sites that historically were occupied by longleaf pine (*Pinus palustris* Mill.). There is currently much interest in restoring high quality longleaf pine habitats to such areas, but managers may also desire the retention of some existing canopy trees to meet current conservation objectives. However, fast-growing natural loblolly pine regeneration may threaten the success of artificially regenerated longleaf pine seedlings. We evaluated the establishment and growth of natural loblolly pine regeneration following different levels of timber harvest using single-tree selection (Control (uncut, residual basal area ∼16 m^2/ha), MedBA (residual basal area of ∼9 m^2/ha), LowBA (residual basal area of ∼6 m^2/ha), and Clearcut (complete canopy removal)) and to different positions within canopy gaps (approximately 2800 m^2) created by patch cutting at two ecologically distinct sites within the longleaf pine range: Fort Benning, GA in the Middle Coastal Plain and Camp Lejeune, NC in the Lower Coastal Plain. The density of loblolly pine seedlings was much higher at Camp Lejeune than at Fort Benning at the end of the first growing season after harvesting. Following two growing seasons, there were no significant effects of canopy density or gap position on the density of loblolly pine seedlings at either site, but loblolly pine seedlings were taller on treatments with greater canopy removal. Prescribed fires applied following the second growing season killed 70.6% of loblolly pine seedlings at Fort Benning and 64.3% of seedlings at Camp Lejeune. Loblolly pine seedlings were generally less than 2 m tall, and completeness of the prescribed burns appeared more important for determining seedling survival than seedling size. Silvicultural treatments that include canopy removal, such as patch cutting or clearcuts, will increase loblolly pine seedling growth and shorten the window of opportunity for control with prescribed fire. Therefore, application of prescribed fire every 2–3 years will be critical for control of loblolly pine regeneration during restoration of longleaf pine in existing loblolly pine stands.

1. Introduction

Throughout the southeastern US, many sites dominated by longleaf pine (*Pinus palustris* Mill.) prior to European settlement have been converted to loblolly pine (*Pinus taeda* L.) through historical land use and past management practices (Frost, 1993; Schultz, 1999). The ecological significance of the longleaf pine ecosystem has been widely documented (e.g. Van Lear et al., 2005; Jose et al., 2006), with characteristically high levels of floral diversity (Walker and Peet, 1983; Kirkman et al., 2001) and many faunal species dependent on specific habitat conditions provided by the ecosystem (Engstrom, 1993; Guyer and Bailey, 1993; Means, 2006). For example, the federally endangered red-cockaded woodpecker (RCW; *Picoides borealis*) prefers longleaf pine stands for nesting and foraging habitat but will utilize other southern pines in the absence of longleaf pine (USFWS, 2003). Managers interested in providing high quality habitat for RCW populations, or meeting other ecological objectives, require information for converting existing loblolly pine stands to longleaf pine forests.

Longleaf pine regeneration grows more slowly than that of other southern pine species, with the majority of seedling growth allocated to the root system during the species' characteristic grass stage. Seedlings have a low tolerance of competition, and longleaf pine seedling growth has been shown to increase exponentially following canopy removal (Palik et al., 1997, 2003). Although stand conversion can be achieved by clearcutting the existing stand and artificially regenerating longleaf pine (Boyer, 1988; Brockway et al., 2006; Knapp et al., 2006), the retention of existing canopy pines may provide desirable ecosystem services during the regeneration period (Mitchell et al., 2006; Kirkman et al., 2007). Needlefall from canopy pines is an important fuel source for the frequent surface fire regime that is considered to be the most important ecological process for sustaining the longleaf pine ecosystem (Peet and Allard,

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1993; Mitchell et al., 2006). Additionally, in pine stands that currently provide habitat for target species such as the RCW, retaining canopy trees may be necessary for providing continuous habitat until longleaf pine regeneration reaches critical habitat size. As a result, there has been increased interest in group selection silvicultural systems, where harvesting is used to create a patchwork of canopy gaps that are surrounded by a matrix of existing trees (Brockway and Outcalt, 1998; McGuire et al., 2001; Palik et al., 2002; Gagnon et al., 2003), or in single-tree selection techniques that reduce canopy basal area uniformly throughout the stand (McGuire et al., 2001; Pecot et al., 2007). The choice of silvicultural options for longleaf pine regeneration depends not only on the characteristics of longleaf pine seedlings but also on site conditions, current stand structure, and overall management objectives.

Restoring longleaf pine to loblolly pine stands presents unique challenges that have not been addressed by previous research focused on regeneration dynamics within existing longleaf pine stands. The silvical characteristics of loblolly pine make it an easier species to regenerate than longleaf pine, a fact that has contributed to the current dominance of loblolly pine throughout the southeastern US (Schultz, 1999). Natural loblolly pine regeneration can be successfully achieved using various even-aged silvicultural methods, including shelterwood, seed-tree, and clearcut techniques (Langdon, 1981). Good seed crops are typically produced every 3–6 years (Baker and Langdon, 1990; Shelton and Cain, 2000), and the large trees likely to be retained for ecological value are also the most prolific seed producers (Schultz, 1997). Large seed crops can range from 200,000 seeds/ha to over 2000,000 seeds/ha, while marginal to poor seed crops are generally considered to be less than 100,000 seeds/ha (Baker and Langdon, 1990; Shelton and Cain, 2000). Seed-to-seedling ratios depend on site and climatic conditions but have been reported to be as low as 5:1 (Cain, 1986), suggesting that even a 'poor' seed crop can result in abundant loblolly pine regeneration during longleaf pine restoration.

In addition to partial or whole canopy removal, longleaf pine restoration in stands with significant midstory or undesirable understory species often requires chemical or mechanical site preparation (Boyer, 1988; Knapp et al., 2006), and prescribed burning is a standard practice prior to planting container grown longleaf pine seedlings. Natural loblolly pine seedling establishment increases following soil disturbances caused by logging, and prescribed fire further improves the seedbed by increasing exposure of mineral soil (Cain, 1987; Schultz, 1997). Additional treatments designed to benefit longleaf pine through competition reduction are likewise expected to increase growth of loblolly pine volunteers (Haywood, 1986; Wittwer et al., 1986; Bacon and Zedaker, 1987; Miller et al., 1991) and may heighten the risk of site dominance by fast-growing loblolly pine regeneration before longleaf pine seedlings can emerge from the grass stage. Therefore, effective control of loblolly pine regeneration is critical to the success of restoring longleaf pine in loblolly pine stands.

Prescribed fire is the primary tool land managers can use to control loblolly pine regeneration during the first few years after planting longleaf pine. Loblolly pines less than 2.5 m tall with ground line diameters less than 5 cm experience high levels of mortality when exposed to surface fires (Cain, 1985, 1993), while longleaf pine seedlings are considered tolerant of fire throughout the majority of the grass stage (Boyer, 1990). However, the effectiveness of prescribed fire for controlling loblolly pine seedlings may be quite variable, depending on the continuity of fire behavior. Artificially regenerated longleaf pine stands are typically burned within two or three years after planting, and it is critical that early prescribed fires effectively minimize loblolly pine competition.

This study was designed to test how loblolly pine regeneration is affected by silvicultural treatments prescribed to restore longleaf pine to existing loblolly pine stands while retaining canopy trees for ecological benefit. Prescribed fires were applied to the study sites following the second growing season after planting longleaf pine seedlings, and loblolly pine mortality was monitored. We hypothesize that: H1) loblolly pine seedling density in the first year following management (logging and site preparation) would be highest on treatments with light harvest because many seed trees would remain and the logging disturbance would expose mineral soil; H2) harvesting treatments that reduce competition from overstory trees would result in increased growth of loblolly pine seedlings; and H3) loblolly pine mortality following the prescribed fires would be related positively to canopy density because fallen needles would increase fine fuels and mortality is expected to be higher for small seedlings (expected under denser canopies in H2) than for large seedlings. This study was replicated at two ecologically distinct locations within the longleaf pine range that may differ in loblolly pine seed production and site quality.

2. Materials and methods

2.1. Study sites

This study was replicated at Fort Benning Military Installation (~32.38° N, 84.88° W) in Chattahoochee and Muscogee Counties, GA and Russell County, AL and Marine Corps Base Camp Lejeune in Onslow County, NC (~34.68° N, 77.33° W). Fort Benning falls within two ecological land units: the northeastern two thirds of the installation are within the Sand Hills Subsection of the Lower Coastal Plains and Flatwoods Section and the southwestern one third of the installation is classified as the Upper Loam Hills Subsection within the Middle Coastal Plain Section (Bailey, 1995). Soils of the Sand Hills have sandy surface horizons and loamy subsoil, and those of the Upper Loam Hills tend to be finer textured and more productive although they share the characteristics of being low in organic matter and natural fertility. Common soil series of the Sand Hills include Troup sandy loam (loamy, kaolinitic, thermic Grossarenic Kandiudults), Wagram loamy sand (loamy, kaolinitic, thermic Arenic Kandiudults) and Vaucluse loamy sand (fine-loamy, kaolinitic, thermic Fragic Kanhapludults), and those of the Upper Loam Hills include Maxton loamy sand (fine-loamy over sandy or sandy-skeletal, siliceous, subactive, thermic Typic Hapludults) and Wickham sandy loam (fine-loamy, mixed, semiactive, thermic Typic Hapludults). The terrain at Fort Benning is predominately rolling with elevation ranging from 58 to 225 m above sea level. Mean annual precipitation at Fort Benning is 1230 mm with a mean temperature of 18.4 °C.

Camp Lejeune is located in the Atlantic Coastal Flatlands Section of the Outer Coastal Plains Mixed Forest Province (Bailey, 1995), and the topography is primarily flat, ranging from 7 to 21 m above sea level. Soils in study areas at Camp Lejeune were primarily Norfolk loamy fine sand (fine-loamy, kaolinitic, thermic Typic Kandiudults) and Baymeade fine sand (loamy, siliceous, semiactive, thermic Arenic Hapludults) and are characterized by low to moderate water holding capacity and low nutrient holding capacity. The climate of Camp Lejeune is classified as warm humid temperate, with average annual precipitation of 1420 mm and mean annual temperature of 13 °C (MCBCL, 2006).

At both sites, study areas were selected from upland loblolly pine stands that managers were interested in converting to longleaf pine, and stand characteristics are summarized in Table 1. In all cases, stands were dominated almost exclusively by loblolly pine. All Fort Benning sites had been burned within the last three years, but prescribed fire had not been recently applied to the Camp Lejeune study areas. As a result, Fort Benning study areas had a relatively minor midstory component, with ground layer

Table 1
Characteristics of study sites at Fort Benning and Camp Lejeune.

Site	Block	Stand			Soil texture			Soil moisture (%)
		Age	DBH (cm)	Site index$_{50}$ (m)	Sand (%)	Silt (%)	Clay (%)	
Fort Benning	1	40	27.6	24.9	71.8	13.9	14.3	14.7
	2	47	32.8	23.5	73.2	11.9	14.9	14.6
	3	49	33.5	21.0	88.1	6.6	5.3	12.8
	4	52	32.3	24.3	88.9	5.8	5.3	4.8
	5	45	31.6	27.4	68.0	13.0	19.0	19.6
	6	48	25.8		88.5	6.4	5.1	8.3
	Mean	47	30.6	24.2	79.7	9.6	10.7	12.5
Camp Lejeune	1	35	33.9	27.4	75.2	19.0	5.8	19.0
	2	35	28.7	27.4	71.2	22.0	6.8	18.0
	3	61	38.7	27.4	92.4	4.1	3.5	14.0
	Mean	44	33.8	27.4	79.6	15.0	5.4	17.0

Note: Volumetric soil moisture at 6 cm depth was determined three times during the 2008 growing season (July, August, September) to provide general comparison of soil conditions among blocks and sites.

vegetation dominated by graminoids (e.g. *Andropogon* spp. and *Schizachyrium scoparium* (Michx.) Nash) and herbaceous species such as legumes (e.g. *Desmodium* spp., *Lespedeza* spp.) and composites (e.g. *Eupatorium* spp., *Solidago* spp.). Study areas at Camp Lejeune had a developed midstory layer that included species such as sweetgum (*Liquidambar styraciflua* L.), horse sugar (*Symplocos tinctoria* (L.) L'Hér), and redbay (*Persea borbonia* (L.) Spreng).

2.2. Experimental design and treatments

At each location, we used a randomized complete block design with location (loblolly pine stand) as the block factor to test the effect of longleaf pine restoration management on natural loblolly pine regeneration. Treatments included four levels of timber harvest in which residual canopy trees were distributed approximately uniformly within each plot: Control (uncut, residual basal area ~16 m^2/ha), MedBA (single-tree selection to residual basal area of ~9 m^2/ha), LowBA (single-tree selection to residual basal area of ~6 m^2/ha), and Clearcut (complete canopy removal). Timber marking was completed by base forestry personnel using thinning from below to favor the larger, vigorous trees. An additional harvesting treatment used patch cutting to create a 2827 m^2 canopy gap (60 m diameter), with at least 30 m of intact residual canopy surrounding each gap. Treatment plots were 100×100 m (1 ha) with the exception of Clearcuts (141×141 m; 2 ha), and harvesting treatments were replicated in six study blocks at Fort Benning and three study blocks at Camp Lejeune. One Clearcut plot was not measured at Camp Lejeune because site access was limited by military training activities.

Harvesting was completed throughout 2007 and was followed by site preparation prescribed for longleaf pine restoration by land managers at each installation. At Fort Benning, a chemical application of 2.34 l/ha imazapyr mixed with 2.24 kg/ha glyphosate was broadcast in September to control competition from hardwood species such as sweetgum and oaks (*Quercus* spp.), and the herbicide treatment was followed by prescribed fire in November 2007. At Camp Lejeune, standing midstory and ground layer vegetation was mechanically removed with a Fecon® Bull Hog rotary mower in July/August 2007, followed by prescribed burns in November. Container-grown longleaf pine seedlings were hand planted in January 2008. In the dormant season between the 2009 and 2010 growing seasons, corresponding to the winter between the second and third growing seasons for the planted longleaf pine seedlings, a prescribed burn was conducted in each study block. Weather conditions during the prescribed burns are summarized in Table 2.

2.3. Data collection

We randomly located twenty 1-m^2 sampling quadrats in uniform treatment plots (Control, MedBA, LowBA, Clearcut) to quantify initial establishment of loblolly pine seedlings following timber harvest and site preparation. In each quadrat, we counted the number of loblolly pine seedlings in May and September 2008, representing the start and the end of the first growing season after treatment. Throughout this paper, the term "seedling" is used to refer to any loblolly pine regeneration that established following site preparation, regardless of size.

Loblolly seedling density and size were quantified again in May 2010, following the dormant season prescribed fires. In each uniform plot, we established one 20×20 m measurement area with 15 m sampling transects running from plot center to each corner ($n = 4$ transects per plot). At the 4, 8, and 12 m distances along each transect, we established one 1-m^2 sampling quadrat and measured the height of all loblolly pine seedlings >10 cm tall whose pith at the groundline was within the quadrat. We chose the height threshold of 10 cm because we were interested in assessing seedlings that had become established in previous years (prior to the 2010 prescribed burns), and field observation indicated that a height of 10 cm effectively separated new germinants from established seedlings. Each seedling was classified as living or dead, and observed mortality was assumed to be fire-induced. At Fort Benning, many quadrats contained no loblolly pine seedlings, so to increase the number of individuals sampled per plot, the sampling area was expanded to a 2-m wide belt that was centered on, and ran the length of, each transect. Additionally, we tallied the number of newly established seedlings (germinants) in each sampling area.

In each gap plot, we established one transect extending from gap center to 10 m into the forest (40 m total transect length) along each cardinal direction (azimuths of 0°, 90°, 180°, and 270°). We sampled loblolly pine regeneration at 10 m intervals along each transect (positions are described by distance from the forest edge to gap center: −10, 0, 10, 20, and 30 m). At each interval position, three 1-m^2 sampling quadrats (subsamples) were established along the transect, with 30 cm between each quadrat (i.e. quadrats centered at 8.7, 10, and 11.3 m were used to sample the 10 m position along each transect). The height and mortality status of each seedling >10 cm tall within each quadrat was recorded, as well as the number of new germinants present. At Fort Benning, a 2-m belt centered on each transect was sampled to supplement low numbers of seedlings measured in each quadrat.

We quantified the area burned (%) in each uniform treatment plot immediately following the prescribed burns. Evidence of

Table 2
Weather conditions from the 2010 dormant season prescribed fires at Fort Benning and Camp Lejeune. Data at Fort Benning were collected with a Kestrel 3000 Pocket Weather Meter at the time of ignition; data from Camp Lejeune were acquired from the North Carolina Division of Forest Resources, Remote Automated Weather Station at the Sandy Run station (34.61° N, 77.49° W).

Site	Block	Treatment	Burn date	Temperature (°C)	Relative Humidity (%)	Average wind speed (km/h)	Maximum gust wind speed (km/h)	Wind direction
Fort Benning	1	All	7-Mar-2010	16.7	15	7.9	17.6	West
	2	All	5-Apr-2010	26.9	44	3.2	4.7	Southwest
	3	Clearcut	17-Feb-2010	7.8	49	14.4	28.8	West
	3	LowBA, MedBA, Control, Gap	25-Feb-2010	7.2	26	4.7	10.1	Northwest
	4	Clearcut, LowBA, Gap	18-Feb-2010	12.0	28	4.7	11.2	West
	4	MedBA, Control	25-Feb-2010	6.1	27	17.6	30.6	Northwest
	5	All	8-Mar-2010	24.0	26	2.9	4.7	North
	6	All	18-Feb-2010	14.4	26	6.5	13.0	Northwest
Camp Lejeune	1	All	5-Jan-2010	2.2	45	14.4	27.7	Northwest
	2	All	5-Jan-2010	2.2	45	14.4	27.7	Northwest
	3	All	15-Mar-2010	16.7	47	14.4	32.0	Northwest

burning (char or consumed fuels) was recorded as either present or absent at each meter point along each of the four transects ($n = 60$ points total per plot).

2.4. Data analysis

We calculated mean seedling density (number of seedlings/ha) at the plot level in May and September 2008 and used mixed model analysis of variance (ANOVA) with a random block effect to test for differences in initial density among the uniform canopy treatments. Data collected following the prescribed fires of 2010 were separated into two groups for analyses. Based on field observations of fire behavior and effects, we assume that no loblolly pine seedlings were completely consumed by the low intensity surface fires. Consequently, the combined dataset of live and dead seedlings represents regeneration demographics two growing seasons following initial management activities (i.e. harvesting and site preparation). For both the pre-fire dataset and the live seedlings remaining after the fires, we calculated mean seedling height and density at the plot level (using quadrat data at Camp Lejeune and transect data at Fort Benning). The distribution of loblolly pine seedlings was quantified as the percentage of quadrats sampled that contained at least one loblolly pine seedling (frequency, $n = 12$ quadrats per plot at each location). We tested effects of uniform canopy treatments on response variables (seedling height, density, and frequency) using plot level means with mixed model ANOVA and a random block effect.

Data from the gap plots were analyzed to determine effects of distance from canopy trees on loblolly pine seedling height and density. At Fort Benning, seedling data collected along each 2-m wide belt transect were grouped into the nearest 10 m interval position, and at Camp Lejeune the mean of the three sampled quadrats was calculated for each position. Initial analyses indicated no effect of transect direction on any response variable, so data from all four transects were pooled and effects of gap position on seedling height and density were analyzed using mixed model ANOVA with a random block effect.

We calculated the mortality rate from the prescribed fires as the percentage of dead seedlings out of the total number of seedlings counted at the plot level. The percent of the study area that burned was calculated as the percentage of points with evidence of fire out of the total number of points observed at the plot level. Relationships between loblolly pine mortality and percent area burned were tested with linear regression models. Uniform harvesting treatment effects on area burned and on the number of germinants established following prescribed fires (May 2010) were analyzed using mixed model ANOVA with a random block effect. We tested for differences between study sites for all response variables using *t*-tests and site-level means, with data from uniform plots and data from gap plots tested separately. All statistical analyses were conducted with SAS statistical software (version 9.1; SAS Institute, Inc., Cary, NC). Transformations were used when necessary to satisfy assumptions of normality and constant variance, and we used $\alpha = 0.05$ to determine significant treatment effects.

3. Results

3.1. Initial seedling establishment following management

At Fort Benning, there was a significant effect of canopy treatment on loblolly pine seedling density at the start of the first growing season after treatment (May 2008), and the Control plots had more seedlings present than the Clearcut plots (Table 3). By the end of the first growing season, however, seedling density had dropped on all plots and there was no longer a treatment effect. At Camp Lejeune, variability within treatments was high, and there were no treatment effects on seedling density in May or September 2008. Seedling density was higher at Camp Lejeune than Fort Benning in May ($t = 2.76$, $p = 0.0200$), with mean densities of 94,489 seedlings/ha and 7784 seedlings/ha, respectively. Seedling densities remained different between the study sites in September ($t = 3.88$, $p = 0.0031$), with a mean density of 66,054 seedlings/ha at Camp Lejeune and a mean density of 3901 seedlings/ha at Fort Benning.

3.2. Loblolly pine regeneration density and height two years after management (pre-fire)

After two growing seasons, the density of loblolly pine seedlings >10 cm tall was not significantly affected by canopy density in uniform plots at Fort Benning or at Camp Lejeune (Table 4). Similar to initial seedling establishment, mean seedling density at Camp Lejeune (27,500 seedlings/ha) remained much higher than that at Fort Benning (2010 seedlings/ha) ($t = 3.05$, $p = 0.0122$). Seedling frequency was also higher at Camp Lejeune (mean of 58.0%) than at Fort Benning (mean of 14.9%) ($t = 5.55$, $p < 0.0001$), with no effect of canopy treatment at either site (Table 4). Seedling size following two growing seasons was significantly affected by the canopy treatments at Fort Benning ($F = 12.24$, $p = 0.0003$) and Camp Lejeune ($F = 8.8$, $p = 0.0193$), with loblolly pine seedlings largest on Clearcut plots (mean of 54.0 cm tall at Fort Benning and mean of 82.4 cm at Camp Lejeune) and smallest on the Control plots (mean of 18.9 cm at Fort Benning and mean of 29.5 cm at Camp Lejeune; Fig. 1A). Seedling size did not differ between the study sites ($t = 1.08$, $p = 0.2862$).

In gap plots, the density of loblolly pine seedlings did not differ with distance from forest edge at either location, although the

Table 3
Density of loblolly pine seedlings in May and September 2008, the first year following harvesting and site preparation, and the density of new germinants in May 2010, following the dormant season prescribed fire. Different letters within a study location indicate statistically different least square means at $\alpha = 0.05$.

Site	Treatment	May 2008		September 2008		May 2010	
		Mean	St. error	Mean	St. error	Mean	St. error
Fort Benning	Control	12,166^{A}	2007	6000	1538	8208^{A}	3190
	MedBA	7973^{AB}	1130	3855	1190	10,458^{A}	5096
	LowBA	6833^{AB}	2747	3333	1564	2319^{AB}	730
	Clearcut	4166^{B}	963	2417	970	167^{B}	78
	p-value	0.0422		0.2289		0.0096	
Camp Lejeune	Control	75,278	30,123	69,483	21,409	329,167	113,604
	MedBA	165,548	123,904	97,523	58,639	259,167	42,544
	LowBA	56,798	21,731	34,035	4996	151,944	75,741
	Clearcut	80,333	37,648	63,177	8846	32,083	32,083
	p-value	0.5584		0.4325		0.0994	

Table 4
Density and frequency of occurrence of loblolly pine seedlings >10 cm (mean and standard error) by uniform harvesting treatment before and after the 2010 prescribed fires at Fort Benning and Camp Lejeune. Prescribed fire mortality values were calculated at the plot level for analysis and may differ slightly from that calculated at the treatment level with data in the table. *P*-values are from ANOVA tests of treatment effects for each site.

Site	Treatment	Total seedlings (pre-fire)				Live seedlings (post-fire)				Prescribed fire mortality (%)	
		Density (number/ha)		Frequency (%)		Density (number/ha)		Frequency (%)			
		Mean	St. error	Mean	St. error	Mean	St. error	Mean	St. error	Mean	St. error
Fort Benning	Control	722	249	11.1	5.1	222	109	5.6	3.5	69.2	14.1
	MedBA	2264	1203	19.4	9.8	181	119	4.2	4.2	94.0	3.6
	LowBA	3583	2448	22.2	7.0	1125	738	9.7	3.4	66.2	8.5
	Clearcut	1472	488	6.9	5.4	333	195	1.4	1.4	64.8	18.4
	p-value	0.5225		0.3931		0.2739		0.3301		0.3069	
Camp Lejeune	Control	8056	3737	38.9	16.9	4167	3005	25.0	21.0	60.3	30.7
	MedBA	42,778	26,581	66.7	12.7	7222	2650	30.6	7.3	66.3	17.4
	LowBA	23,333	11,345	47.2	14.7	6111	4547	19.4	10.0	70.3	26.2
	Clearcut	35,833	6667	79.2	12.5	16,250	14,583	41.7	25.0	60.5	30.6
	p-value	0.3240		0.3248		0.5148		0.6552		0.9853	

distance effect was nearly significant at Fort Benning (Table 5). Seedling size gradually increased from 10 m in the forest interior to the gap center (30 m from the forest edge) at Fort Benning, with the size of seedlings in the gap significantly larger than those in the forest ($F = 4.29$, $p = 0.0036$). A distance effect was present at Camp Lejeune as well ($F = 6.89$, $p = 0.0009$), where seedlings 10 m in the forest interior were smaller than those in the center of gaps (Fig. 1B). Mean seedling size in gaps was greater at Camp Lejeune than at Fort Benning ($t = 2.85$, $p = 0.0072$).

3.3. Fire effects on loblolly pine regeneration

The uniform harvesting treatments did not affect the percentage of loblolly pine seedlings killed by the prescribed fires at either study location (Table 4). At Fort Benning, the fires killed 70.6% of the loblolly pine regeneration in uniform plots compared to 64.3% mortality at Camp Lejeune, although the difference was not significant ($t = 0.47$, $p = 0.6426$). For gaps, a slight trend of reduced mortality with distance from the forest edge was evident at both study locations, although mortality was not significantly affected by gap position at either site (Table 5). Average loblolly pine mortality in forest gaps was lower at Camp Lejeune (38.1%) than at Fort Benning (74.4%) ($t = 2.89$, $p = 0.0112$).

For the range of loblolly pine seedling sizes observed in this study, there is little evidence that seedling size affected the likelihood of mortality from the prescribed fires at either location (Figs. 2 and 3). Mortality occurred for seedlings of virtually all sizes up to 2 m tall. Few seedlings were killed that were taller than 1.5 m, but the number of seedlings that were in that size class was low; at Fort Benning there were only two seedlings and no mortality, and at Camp Lejeune only six out of 22 seedlings in that size class were killed by fire. The area burned was significantly affected by harvesting treatment at Fort Benning ($F = 7.34$, $p = 0.003$), with nearly 100% of the Control and MedBA plots burned, compared to 78% burned on Clearcut plots (Fig. 4). A similar pattern among the treatments was evident at Camp Lejeune, although no treatment effect was detected ($F = 1.97$, $p = 0.2197$). The percent area burned was significantly related to loblolly pine mortality at each study site (Fig. 5). The relationship was much stronger at Camp Lejeune than Fort Benning, because Fort Benning had some plots with high percent area burned but relatively low loblolly pine mortality.

3.4. Post-fire loblolly pine regeneration density and height

After the prescribed fires of 2010, there were no significant treatment effects on the number of live seedlings or the frequency of loblolly pine seedlings in the uniform plots at either study location (Table 4). Fort Benning averaged 465 remaining loblolly pine seedlings per hectare, with only around 5% frequency, and Camp Lejeune averaged 8438 seedlings per hectare and 29.2% frequency. Both measures of seedling abundance were greater at Camp Lejeune than at Fort Benning (density: $t = 2.62$; $p = 0.0252$, frequency: $t = 3.14$; $p = 0.0093$). We found no significant treatment effects on seedling size at Fort Benning ($F = 2.11$, $p = 0.1744$), despite an increase from 15.2 cm on Control plots to 41.6 cm on Clearcut plots (Fig. 6A). Size of the live seedlings at Camp Lejeune was significantly affected by harvesting treatment ($F = 5.76$, $p = 0.0213$), with seedlings in Clearcut plots averaging 79.6 cm, compared to an average of 25.8 among the other three treatments. In gap plots,

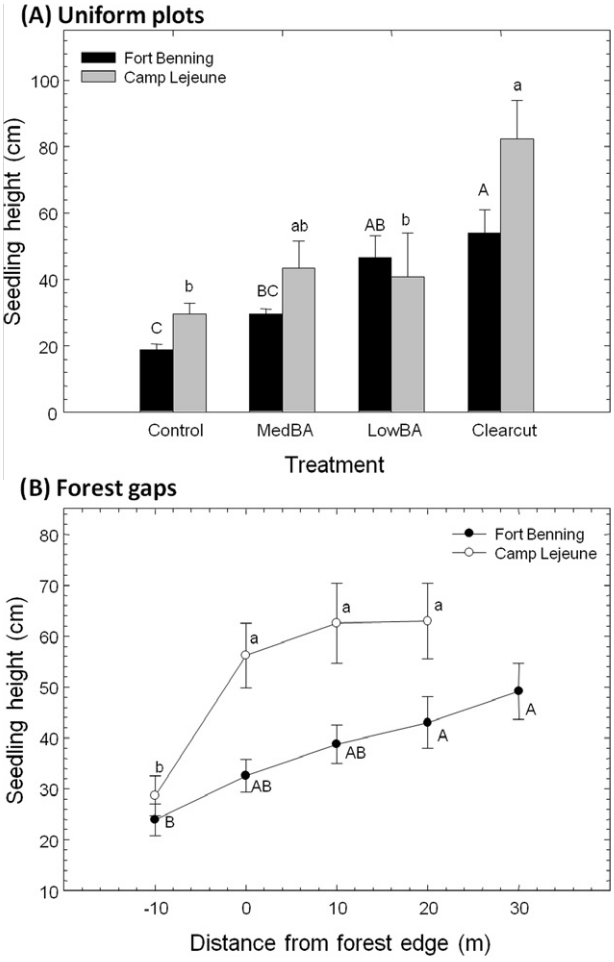

Fig. 1. Height of loblolly pine natural regeneration (mean ± standard error) two growing seasons after harvest and site preparation at Fort Benning and Camp Lejeune by (A) harvesting treatment in uniform plots and (B) distance from forest edge in gap plots. Data was not taken in gap centers at Camp Lejeune due to concerns about the disturbance created at the intersection of four sampling transects. Different letters within a study location indicate statistically different least square means at α = 0.05.

the density of live seedlings following the prescribed fires was not affected by distance from the forest edge at Fort Benning or Camp Lejeune (Table 5). Patterns of seedling size and distance to forest edge were similar to those before the prescribed fires (Fig. 1B and Fig. 6B), with a significant position effect at both sites after the prescribed fires ($F = 4.23$, $p = 0.0063$ at Fort Benning and $F = 5.61$, $p = 0.0037$ at Camp Lejeune).

The density of new germinants following the 2010 prescribed fires in uniform plots was highest on the MedBA and Control plots, with very little recruitment in the Clearcut plots at Fort Benning. The treatment effect was only marginally significant at Camp Lejeune, despite a range from 329,167 seedlings/ha on Control plots to 32,083 seedlings per hectare on Clearcut plots (Table 3). There were significantly more new germinants at Camp Lejeune than at Fort Benning after the prescribed fires ($t = 4.26$; $p = 0.0017$).

4. Discussion

The large difference in initial loblolly pine seedling density (May 2008) between Fort Benning and Camp Lejeune, in which nearly 10 times as many seedlings were present at Camp Lejeune, may be attributed to multiple factors. Seed production is often a reliable predictor of first year pine density (Cain, 1991), and it is well understood that loblolly pines experience large annual variation in seed crops (Wenger, 1957; Cain, 1991). Cain and Shelton (2001) reported complete failure (zero sound seeds/ha) one year, followed by a bumper crop of over 2 million sound seeds per hectare the following year in a study in Arkansas. Generally, seed crops are larger and more consistent in the lower Coastal Plain than in the upper Coastal Plain or Piedmont (Wakeley, 1947; Brender and McNab, 1972; Schultz, 1997), so it is possible that differences in seedling density between the two study sites were associated with differences in seed production in 2007 (prior to the treatment). Additionally, site conditions during germination and early establishment play an important role in regeneration success. At both study locations, precipitation early in the first growing season (March–June 2008) was well below the 50-year average (Camp Lejeune: 346 vs. 430 mm, respectively; Fort Benning: 343 vs. 442 mm, respectively). Forest soils are typically drier at Fort Benning than at Camp Lejeune (Table 1), and the dry conditions during the period of early seedling establishment may have been more inhibitive for seedling establishment at Fort Benning than at Camp Lejeune. Finally, it is unclear how the different site preparations used at each location may have affected the recruitment of loblolly pine on these sites.

Generally, loblolly pine seedling establishment increases following disturbances that reduce vegetation cover and expose mineral soil (Pomeroy and Trousdell, 1948; Cain, 1991; Schultz, 1997), and therefore we expected initial loblolly pine recruitment to be highest on harvested treatments that still retain some canopy trees as a seed source (Hypothesis 1). However, we did not see evidence that disturbance from logging improved the seedbed over that provided by site preparation (mechanical or chemical vegetation control plus fire) at either site. The importance of seedbed preparation is reduced during years of high seed production because abundant seed rain increases the likelihood that all suitable microsites are utilized (Trousdell, 1963). Although seed production was not directly measured, the high density of seedlings at Camp Lejeune suggests that seed production was high the previous year. On the other hand, lower seed production at Fort Benning may have increased the importance of canopy trees as a seed source, resulting in a higher number of established seedlings on uncut plots than those in which canopy trees had been removed. Additionally, the shade of canopy trees may have facilitated seedling establishment at Fort Benning by improving microsite conditions for seedling establishment during the dry summer of 2008.

Interestingly, we found a high number of loblolly pine seedlings in Clearcut plots at Camp Lejeune, despite complete removal of the seed source. Loblolly pine seed dispersal is reported to occur 60 m from seed trees, with diminishing recruitment out to 100 m (Pomeroy, 1949; Wenger and Trousdell, 1958; Schultz, 1997). Because our Clearcut plots were 2 ha in size (141 × 141 m), the centers of the plots were only 70 m from the nearest forest edge and were not out of range of seed dispersal. Very few loblolly pine seeds remain viable from one year to the next (Little and Somes, 1959; Baker and Langdon, 1990; Cain and Shelton, 1997), so it is not likely that residual seeds contributed to initial seedling density. However, it is possible that loblolly pine regeneration came from seedlings that had not been killed during logging or site preparation. Although we did not measure loblolly pine seedling density before timber harvest, field observations following site preparation indicated that loblolly pine regeneration was not abundant at the start of 2008, and contributions from previously established seedlings were not likely significant.

As expected, we found that canopy thinning and gap harvesting, both used to reduce overstory competition with planted longleaf pine seedlings, increased the growth of natural loblolly pine regeneration (Hypothesis 2). Hu (1983) compared growth of natural

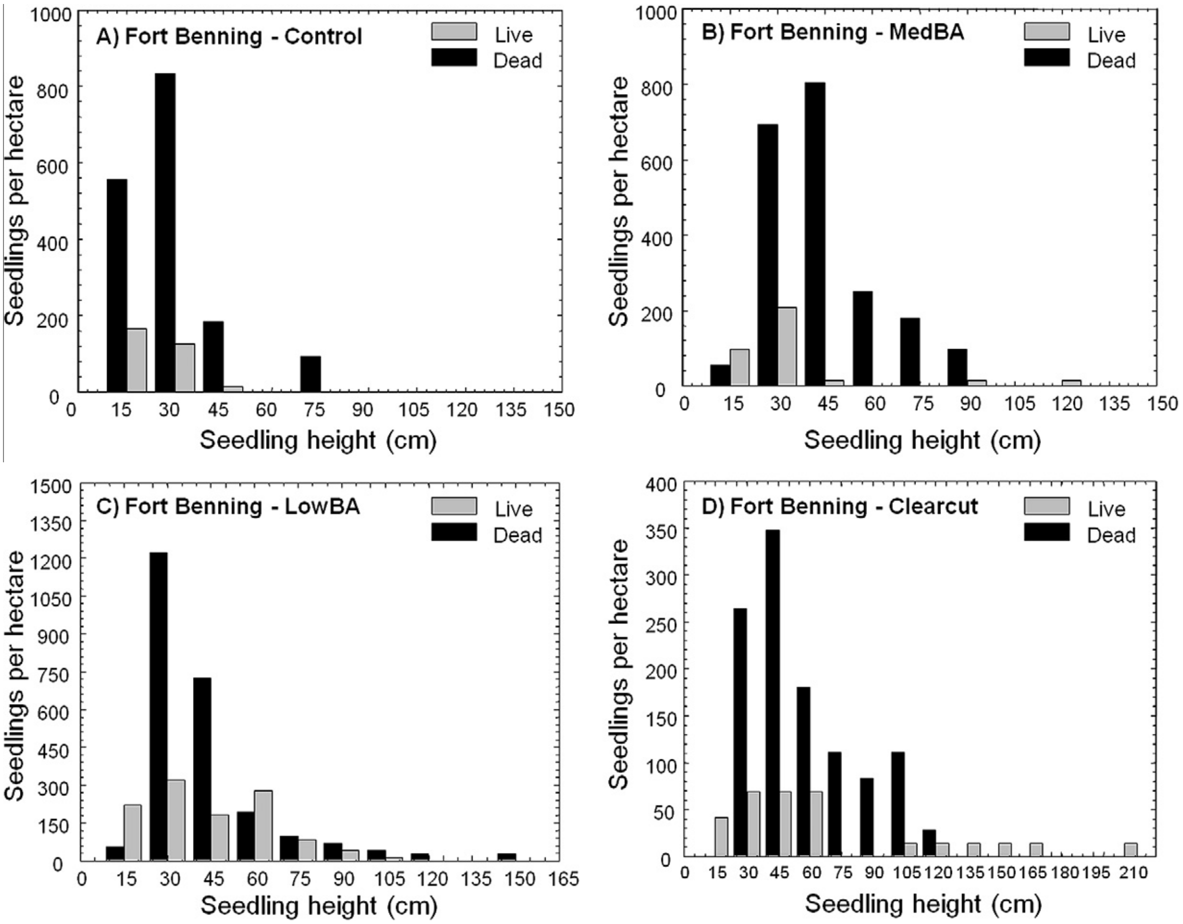

Fig. 2. Density (seedlings per hectare) of live and dead loblolly pine seedlings by size following 2010 prescribed fires for (A) Control, (B) MedBA, (C) LowBA, and (D) Clearcut plots at Fort Benning. Note: scales of *y*-axes are not consistent for each treatment.

loblolly pine regeneration following various regeneration techniques (clearcut, shelterwood, seed tree, selection cutting) and reported results similar to ours, with the greatest growth on clearcuts and reduced growth associated with canopy competition. Results from the gap plots show that seedling size increases from within the forest to the gap center, although the rate of increase differed between the study sites. At Fort Benning, we noted a gradual increase in seedling size associated with the distance from the forest edge, but at Camp Lejeune seedling size increased rapidly from 10 m into the forest to the forest edge and remained constant toward the gap center. The ability of a species to respond to increased resource availability is often controlled by limitations of other resources (Teskey et al., 1987), and differences in site quality (nutrients and moisture) between the study sites are likely responsible for the observed growth patterns.

The susceptibility of loblolly pine seedlings to fire-induced mortality decreases with seedling size, and previous research suggests that once loblolly pine seedlings reach 2.5 m in height they become resistant to fire (Cain, 1985; Cain and Shelton, 2002). By the end of two growing seasons, no measured seedlings had reached the size threshold suggested by previous research, and we found little evidence that seedling size affected the likelihood of survival following our prescribed fires because fire-induced mortality was observed for nearly all size classes. We did observe low mortality levels for the largest seedlings in Clearcut plots (typically >1.5 m), but because so few seedlings of that size were observed, and we did not quantify the distribution of fire at the seedling level, it cannot be concluded that seedling size was responsible for the observed survival. These results confirm that prescribed burning during the second or perhaps even the third year after planting longleaf pine seedlings will allow managers the opportunity to control loblolly pine regeneration when it is still susceptible to fire-induced mortality.

Fires in frequently burned pine systems can be quite heterogeneous at fine scales, depending on fuel distributions and micro-site conditions (Gibson et al., 1990; Thaxton and Platt, 2006; Hiers et al., 2009), and it is unclear how interactions between seedling size and heterogeneity of prescribed burns may affect fire-induced mortality at the stand level. In Hypothesis 3, we expected loblolly pine seedling mortality to be highest on sites with more canopy trees present because inputs from needlefall would improve the continuity of the fuelbed, resulting in more uniform, complete burns. We found that prescribed fires burned more completely in treatments with intact canopies, with evidence of burning in nearly 100% of the observation points in the Control plots at both sites, compared to 78% and 69% on Clearcut plots at Fort Benning and Camp Lejeune, respectively. We attribute the lack of a treatment effect on loblolly pine mortality rates in uniform plots to fine scale heterogeneity in prescribed fire intensity, which was not accounted for in the measurement of area burned. However, the relationships between the percent area burned and loblolly pine mortality (Fig. 5) demonstrate the importance of complete burns for loblolly pine control, as mortality tended to decrease sharply with slight decreases in the area burned.

We found a general pattern of higher loblolly pine mortality under the forest canopy than in the center of canopy gaps at both study sites, although this trend was not statistically significant in either case. Previous research has suggested that canopy gaps

Table 5

Density of loblolly pine seedlings >10 cm (mean and standard error) relative to the forest edge in gap plots before and after the 2010 prescribed fires at Fort Benning and Camp Lejeune. Prescribed fire mortality values were calculated at the plot level for analyses and may differ slightly from that calculated at the treatment level with data in the table. *P*-values are from ANOVA tests of treatment effects for each site.

Site	Distance from forest edge (m)	Total seedlings (pre-fire)		Live seedlings (post-fire)		Prescribed fire mortality (%)	
		Density (number/ha)		Density (number/ha)			
		Mean	St. error	Mean	St. error	Mean	St. error
Fort Benning	−10	2958	1218	542	255	87.0	7.5
	0	3333	892	896	429	71.3	11.7
	10	4333	1121	292	79	90.0	3.2
	20	2875	796	938	232	65.3	9.1
	30	1969	579	719	309	58.5	21.0
	p-value	0.0763		0.2017		0.1020	
Camp Lejeune	-10	38,333	19,867	12,424	5524	45.3	28.2
	0	33,611	7276	27,500	7120	36.7	24.1
	10	25,833	5367	17,500	5537	38.3	29.4
	20	29,722	5278	15,277	3110	32.0	28.0
	30[a]						
	p-value	0.4156		0.1155		0.2118	

[a] Data was not taken in gap centers at Camp Lejeune due to concerns about the disturbance created at the intersection of four sampling transects.

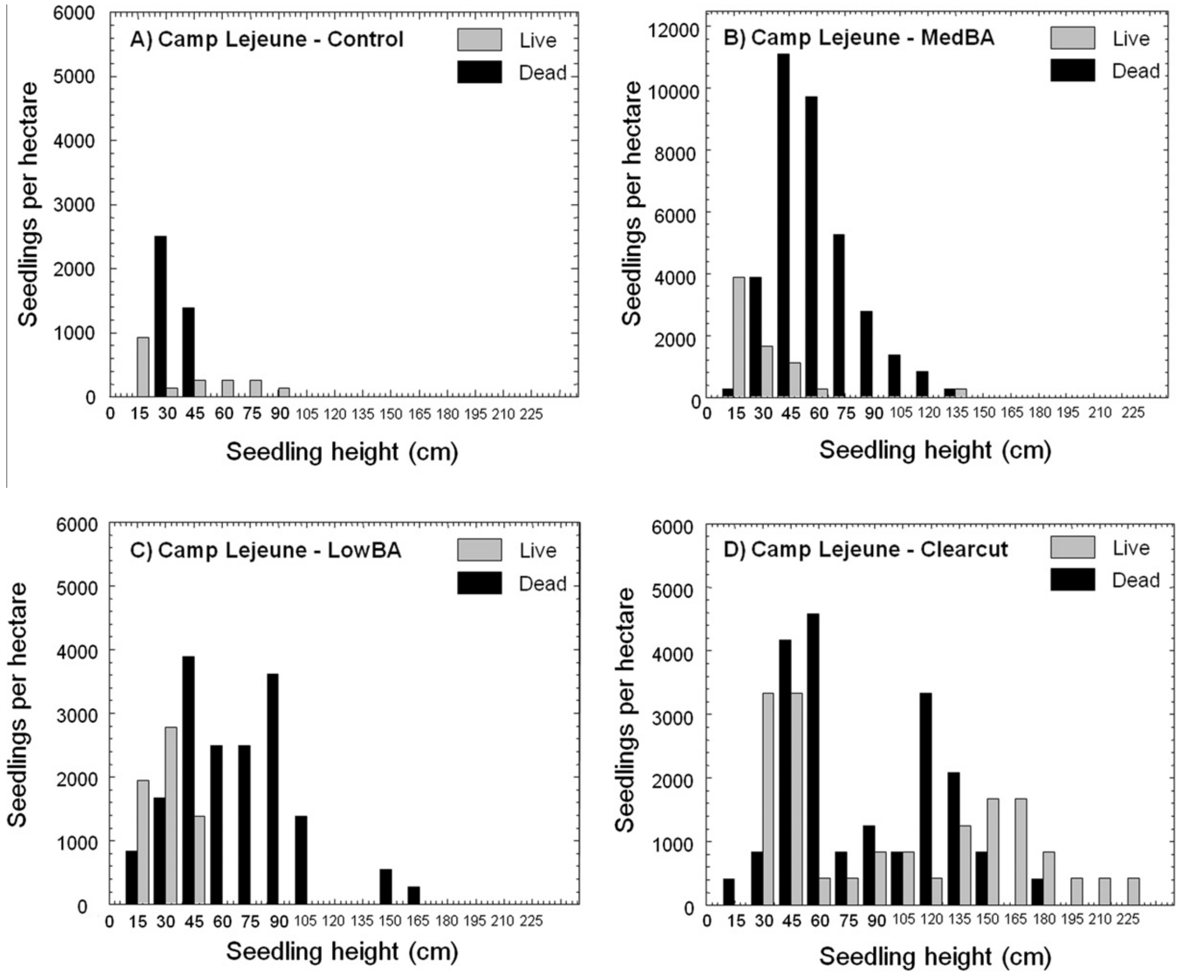

Fig. 3. Density (seedlings per hectare) of live and dead loblolly pine seedlings by size following 2010 prescribed fires for (A) Control, (B) MedBA, (C) LowBA, and (D) Clearcut plots at Camp Lejeune. Note: scales of *y*-axes are not consistent for each treatment.

may be a useful silvicultural technique for longleaf pine restoration in stands in which canopy retention is desirable (Palik et al., 1997, 2003). However, the loss of the fine fuels associated with needlefall may affect the movement of fire across canopy gaps, with potentially long-term effects on fire management (Mitchell et al., 2006). It is likely that the observed patterns of loblolly pine mortality were related to fire behavior within the gaps and that control of loblolly pine regeneration with fire will be more difficult farther from the forest edge. However, a complete analysis of the role of pine needles as a fuel source, the effects of canopy trees on fuel properties (e.g. fuel moisture), and the interactions of those factors is beyond the scope of this study.

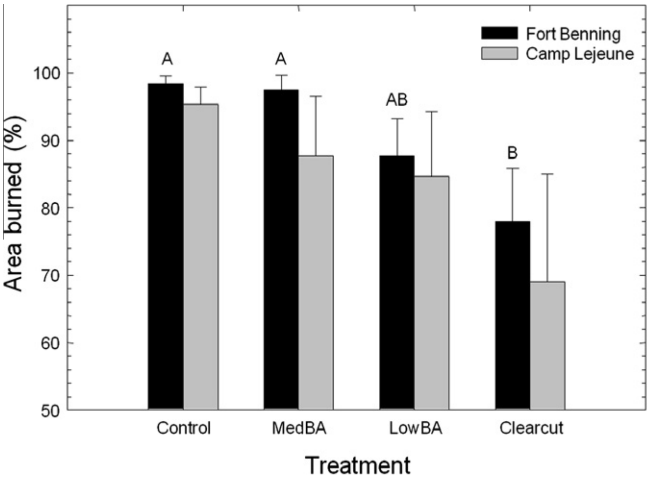

Fig. 4. Percent area burned by 2010 prescribed fires (mean ± standard error) for each uniform harvesting treatment at Fort Benning and Camp Lejeune. Different letters within a study location indicate statistically different least square means at α = 0.05.

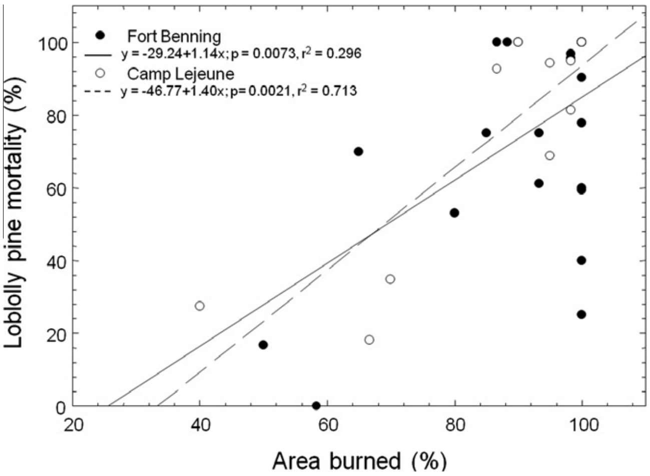

Fig. 5. Scatterplots and least square mean lines for the percent area burned and loblolly pine seedling mortality for each study plot at Fort Benning (filled circles) and Camp Lejeune (open circles).

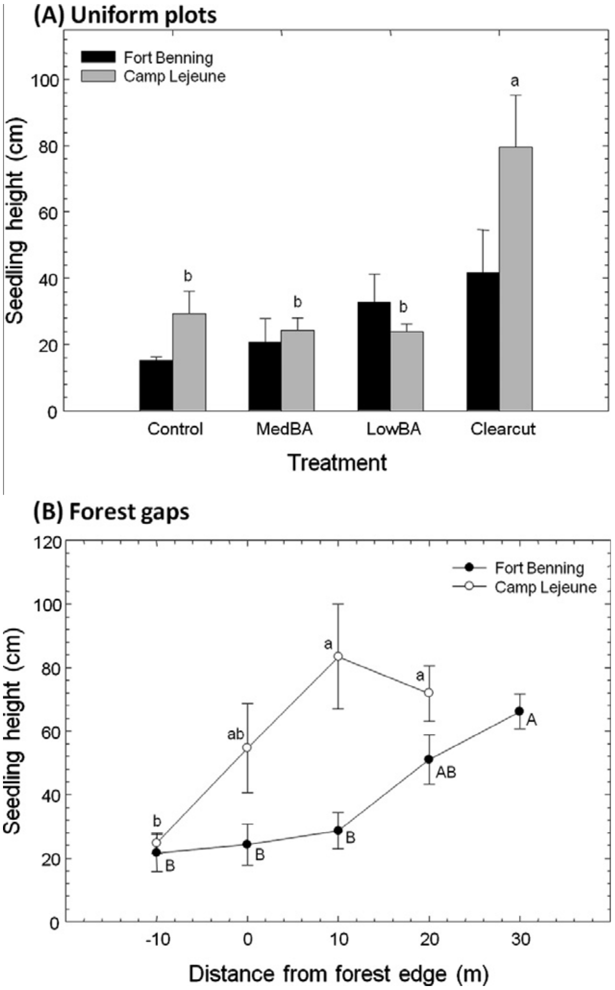

Fig. 6. Height of live loblolly pine natural regeneration (mean ± standard error) remaining after 2010 prescribed fires at Fort Benning and Camp Lejeune by (A) harvesting treatment in uniform plots and (B) distance from forest edge in gap plots. Data was not taken in gap centers at Camp Lejeune due to concerns about the disturbance created at the intersection of four sampling transects. Different letters within a study location indicate statistically different least square means at α = 0.05.

One consequence of using prescribed fire to control loblolly pine regeneration is that the seedbed is again improved for germination and seedling establishment. Additionally, loblolly pine seed production may be stimulated by release of seed trees through timber harvest (Wenger, 1954; Schultz, 1997), increasing the likelihood of a good seed crop coinciding with the first prescribed fire after planting longleaf pine seedlings in thinned stands. Following the 2010 prescribed fires, the density of newly germinated seedlings was similar to that observed during initial establishment at Fort Benning and generally higher than that observed during initial establishment at Camp Lejeune. At both study sites, our results show that additional loblolly pine seedlings will become established after each prescribed fire, and consequently managers must use prescribed fire at two to three year intervals to control each cycle of loblolly pine recruitment.

5. Management Implications

Restoring the longleaf pine ecosystem in many areas of the southeastern United States requires conversion of existing loblolly pine stands to longleaf pine forests. When silvicultural prescriptions include the retention of canopy trees for ecological benefit, managers must be prepared for natural loblolly pine regeneration and need to understand the implications of that regeneration on stand development. The comparison of two ecologically distinct study sites demonstrates that initial loblolly pine seedling establishment may be highly variable both between sites (e.g., higher seedling density at Camp Lejeune than Fort Benning) and within sites (high standard error values for seedling density for most treatments at both sites). Seed crop size and successful establishment of loblolly pine regeneration are dependent on numerous factors that include the year (e.g. seed production, weather patterns), site quality (e.g. climate, soil characteristics), stand age, and seedbed preparation. Regional differences in seed production of loblolly pines affect the likelihood of abundant regeneration, with larger and more consistent seed crops in the lower Coastal Plain (e.g. Camp Lejeune). Consequently, the feasibility of longleaf pine restoration in loblolly pine stands may depend on location, site quality, and initial loblolly pine seedling establishment. By using knowledge of site characteristics and trends in recent seed production (Wenger, 1957; Cain and Shelton, 2001), managers may be able to time longleaf pine restoration to coincide with poor seed crops to minimize initial loblolly pine establishment. Moreover, the majority of viable loblolly pine seeds are typically dispersed by the end of December (Cain, 1991), and additional control may be provided by applying a site preparation burn after seedfall has occurred. Although managers should consider ways to minimize loblolly pine regeneration during restoration, some level of recruitment is inevitable, and managers must be prepared to control it with prescribed burning.

Frequent prescribed burning is fundamental to longleaf pine ecosystem management but becomes paramount in the presence of fast-growing loblolly pine seedlings. During the early years of longleaf pine seedling development (i.e., prior to emergence from the grass stage), the ability to control loblolly pine regeneration with fire will largely determine which pine species will dominate a site. Given the heterogeneous nature of fire behavior, we expect the survival of some loblolly pine seedlings following prescribed fire. The development of mixed stands may be acceptable during ecological restoration, provided that longleaf pine makes up a significant portion of the new cohort and that subsequent thinning operations select loblolly pines for removal. However, the success of such a model is contingent on the development of competitive longleaf pine seedlings, and managers can maximize the likelihood of longleaf pine establishment with effective prescribed burning. Fire management decisions should therefore consider the control of loblolly pine regeneration as a principle objective, especially while artificially regenerated longleaf pine seedlings are in the stemless grass stage and vulnerable to competition from faster growing species.

The complex interactions among needlefall as a fine fuel, fire behavior, and loblolly pine seedling size suggest that control of loblolly pine regeneration with fire may be more difficult following removal of some canopy trees. Silvicultural treatments that include complete canopy removal (e.g. gaps or clearcuts) maximize growth of established loblolly pine seedlings and shorten the window of opportunity for control with prescribed fire. For example, in Clearcut plots at Camp Lejeune, seedlings that survived the 2010 prescribed fires averaged around 80 cm tall with mean densities in excess of 1.5 seedlings per square meter. Continued growth will make them difficult to kill with subsequent burns because seedlings will rapidly reach a size resistant to fire-induced mortality. In such cases, the fire return interval may have to be shortened or additional mechanical treatments may be required to control loblolly pine regeneration, with the potential risk of damage to planted longleaf pine seedlings.

Ultimately, developing appropriate silvicultural prescriptions for converting loblolly pine stands to longleaf pine will require information on how harvesting treatments affect ecosystem components that include longleaf pine seedling establishment, ground layer vegetation composition, stand structure, fuel complexes, and the ability for sustained management with prescribed fire. This study addresses one potential source of competition for longleaf pine seedlings that will have major implications on stand development following restoration activities. In general, our results suggest that site and stand conditions may be more important for controlling loblolly pine seedling density than the harvesting treatments used in this study. However, canopy retention is expected to increase the continuity of prescribed fire and therefore allow the manager greater flexibility in the use of prescribed fire to control loblolly pine regeneration. Overall, the challenges posed to longleaf pine restoration by natural regeneration in loblolly pine stands should not be insurmountable with the proper use of prescribed fire and adaptive management applied on a stand-specific basis.

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