Silvicultural treatments for converting loblolly pine to longleaf pine dominance: Effects on resource availability and their relationships with planted longleaf pine seedlings

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ABSTRACT

Throughout the southeastern United States, land managers are currently interested in converting loblolly pine (Pinus taeda L.) plantations to species rich longleaf pine (Pinus palustris Mill.) ecosystems. In a 3-year study on moderately well- to well-drained soils of the Lower Coastal Plain in North Carolina, we examined the effects of four canopy and three cultural treatments on plant resources and quantified relationships between plant resources and longleaf pine seedling survival and growth. Canopy treatments consisted of four levels of timber harvest applied to loblolly pine stands: Control (uncut, mean basal area of 16.2 m^2/ha), MedBA (single-tree selection to a mean residual basal area of 9.0 m^2/ha), LowBA (single-tree selection to a mean residual basal area of 6.4 m^2/ha), and Clearcut (complete canopy removal). Within each canopy treatment, we applied three cultural treatments designed to benefit the early growth of planted seedlings: no treatment (NT), herbicide (H), and herbicide plus fertilization (H + F). Gap light index (GLI) significantly differed among canopy treatments and nonlinearly increased with decreasing basal area. The H treatment resulted in higher temperatures at 10 cm in the soil. Canopy thinning increased foliar calcium (Ca) concentration. The annual root collar diameter (RCD) increment of planted longleaf pine seedlings was positively correlated with GLI, and foliar phosphorus (P) and Ca concentrations but was negatively correlated with soil moisture. Our results confirm that light is an important factor controlling the growth of longleaf pine seedlings.

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1. Introduction

Forest canopy cover, a stand condition that is often subjected to silvicultural manipulation, significantly affects forest succession and ecosystem function (Kohn and Franklin, 1997; Gray et al., 2002; Wagner et al., 2011). By manipulating the degree of canopy cover, silvicultural treatments can change the partitioning of solar energy between understory and overstory, affect the vertical distribution of soil moisture, and control the regeneration environment (Kohn and Franklin, 1997; Gray et al., 2002; Ma et al., 2010). Understory light availability is directly controlled by the amount and spatial distribution of the forest canopy (e.g., Lieffers et al., 1999), and the reduction in canopy cover by thinning can greatly increase light levels in the understory (e.g., Drever and Lertzman, 2003). Consistently lower daytime air and soil temperatures, higher humidity, and lower diurnal fluctuations in both temperature and humidity have been observed beneath intact forests when compared to thinned forests or large openings (e.g., Chen et al.,

1993; Carlson and Groot, 1997; Ma et al., 2010). Previous research in longleaf pine (Pinus palustris Mill.) forests of the southeastern United States has shown that understory light availability (Palik et al., 1997; Battaglia et al., 2003), soil nitrogen availability (Palik et al., 1997, 2003), and surface soil temperature (Palik et al., 2003) increased with decreasing canopy cover. Within loblolly pine (Pinus taeda L.) forests, previous studies have reported that thinning increased volumetric soil moisture content and seasonal soil temperature fluctuation (Selig et al., 2008). Given the importance of canopy cover in regulating micro-site conditions, historical and current management actions can have important implications for forest development.

Due to logging, land-use changes, and fire exclusion and suppression, the extent of the longleaf pine ecosystem has declined to approximately 2.2% (or 1 million hectares) of the acreage prior to European settlement (Wahlenburg, 1946; Frost, 2006). Currently, about 11 million hectares of pine plantations, predominately loblolly and slash pine (Pinus elliottii Engelm.), occupy the former longleaf pine range (Frost, 2006). In recent decades, much effort has been invested in restoring the longleaf pine ecosystem to its native range, in large part to conserve biodiversity and to

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provide habitat for federally-protected, endangered species such as the red-cockaded woodpecker (RCW; *Picoides borealis*) and gopher tortoise (*Gopherus polyphemus*) (e.g., U.S. Fish and Wildlife Service, 2003). Many stands targeted for restoration are currently dominated by other pine species, requiring conversion of the canopy to longleaf pine. Traditional management practices for longleaf pine establishment in such situations typically include clearcutting existing canopy trees and planting longleaf pine seedlings. However, overstory retention is increasingly used in forests traditionally managed for even-aged structure (e.g., Palik et al., 2003). It is believed that the residual stand structure associated with canopy retention better resembles the complex structure of forests after natural disturbances and therefore helps to maintain biodiversity and to perpetuate ecosystem functions dependent on that structure (Hansen et al., 1995; Franklin et al., 1997; Seymour and Hunter, 1999; Schliemann and Bockheim, 2011). In longleaf pine ecosystems, canopy retention helps to control hardwood encroachment and provides needlefall for fuels, both of which contribute to a fuel matrix that supports the characteristic frequent, low-intensity surface fire regime (Palik et al., 2002; Mitchell et al., 2006; Kirkman et al., 2007; Pecot et al., 2007). Furthermore, because the widespread loss of longleaf pine forests has resulted in existing RCW populations using loblolly pine stands for nesting and foraging habitat, clearcutting is often not desirable in loblolly pine stands that currently support RCWs (U.S. Fish and Wildlife Service, 2003).

Studies from longleaf pine forests have shown that canopy retention significantly affects natural or artificial longleaf pine regeneration and that decreasing canopy cover improves longleaf pine seedling growth associated with increases in the availability of limiting resources (Palik et al., 1997, 2003; McGuire et al., 2001; Pecot et al., 2007). However, the effect of canopy density on understory resource availability may be species dependent. For example, in a study aimed to convert slash pine plantations to longleaf pine forests, Kirkman et al. (2007) found higher canopy light transmittance in longleaf pine stands than in slash pine stands across a range of basal areas. Given the large-scale historical conversion of natural longleaf pine ecosystems to loblolly pine plantations throughout the southeastern United States (Kirkman and Mitchell, 2006), future longleaf pine restoration projects will likely occur in existing loblolly pine stands. Differences in rooting habits between loblolly and longleaf pines may affect the availability of soil moisture and nutrients for underplanted longleaf pine seedlings (Baker and Langdon, 1990); therefore, it is important to understand how different degrees of loblolly pine canopy retention affect understory environmental conditions and resource availability in relation to longleaf pine seedling establishment. In addition, other management actions are often used to improve growing conditions for planted longleaf pine seedlings by reducing competition from understory vegetation, which could also indirectly affect understory environmental conditions and the availability of resources for planted longleaf pine seedlings (e.g., Haywood, 2000, 2005, 2007; Harrington et al., 2003; Ramsey and Jose, 2004; Knapp et al., 2008; Jose et al., 2010). For example, Knapp et al. (2008) found that applying herbicide could significantly increase the amount of moisture within the upper 6 cm of the soil.

Across the southeastern United States, land managers share the challenge of restoring longleaf pine forests to stands currently occupied by loblolly pine. This study is part of a large project designed to find the optimal silvicultural practices for restoring longleaf pine forests in loblolly pine stands. The objectives of our study are to: (1) quantify light availability, soil surface moisture, soil surface temperature, and longleaf pine seedling foliar nutrients following canopy and cultural treatments; and (2) determine relationships between seedling mortality/growth and the measured resource variables.

2. Methods and materials

2.1. Study site

This study was conducted at the United States Marine Corps Base Camp Lejeune, in Onslow County, NC (~34.68°N, 77.33°W). The study area is located within the Atlantic Coastal Flatlands Section of the Outer Coastal Plains Mixed Forest Province (Bailey, 1995) and falls within the White Oak watershed in Onslow County as defined by the North Carolina Department of Water Quality (USMCB Camp Lejeune, 2006). The climate is classified as warm humid temperate with hot, humid summers and mild winters. Mean annual temperature is 16 °C, and annual precipitation averages 1420 mm and is evenly distributed throughout the year, with a slight increase from June–September (National Climatic Data Center, Asheville, NC). The study sites are on moderately well- to well-drained soils with low to moderate water holding capacity and low nutrient holding capacity (Barnhill, 1992). Soil series in the study sites include the Baymeade-Urban land complex (BmB; loamy, siliceous, thermic Arenic Hapludults), Goldsboro fine sandy loam (GoA; fine-loamy, siliceous, thermic Aquic Paleudults), Norfolk loamy fine sand (NoB; fine-loamy kaolinitic, thermic Typic Kandiudults), Onslow loamy fine sand (On; fine-loamy, siliceous, thermic Spodic Paleudults), and Wando fine sand (WaB; thermic coated Typic Quartzipsamments) (Soil Survey Staff, NRCS 2012).

2.2. Experimental design

The study design was a randomized complete block split-plot, with location (loblolly pine stand) used as the blocking factor. Each block consisted of four main treatment plots, and we randomly assigned a canopy treatment to each plot. Canopy treatments included four levels of timber harvest in which residual canopy trees were distributed uniformly within each plot: Control (uncut, mean basal area of 16.2 m²/ha), MedBA (single-tree selection to a mean residual basal area of 9.0 m²/ha), LowBA (single-tree selection to a mean residual basal area of 6.4 m²/ha), and Clearcut (complete canopy removal). Base forestry personnel marked the timber for harvest using thinning from below to favor large, vigorous trees. Treatment plots were 100 × 100 m (1 ha) with the exception of Clearcut plots (141 × 141 m; 2 ha). We selected seven mature loblolly stands as replicated blocks. Four blocks (Blocks 1–4) were located in 35 year-old loblolly pine plantations, with the mean DBH (diameter at breast height) ranging from 26.4 to 33.9 cm (with 162, 82, and 60 trees per hectare for Control, MedBA, and LowBA treatments, respectively). The remaining blocks (Blocks 5–7) were located in 60 year-old loblolly pine stands, and the mean DBH for Blocks 5–7 ranged from 38.7 to 44.3 cm (with 154, 66, and 41 trees per hectare for Control, MedBA, and LowBA treatments, respectively). Harvesting was completed in all blocks between February and May 2007. We measured residual basal area (BA) following harvest and found that the LowBA and MedBA treatments in two blocks (Blocks 3 and 4) were cut to similar levels of residual BA, so both were considered to be the same canopy treatment (LowBA). We abandoned one canopy treatment plot (LowBA in Block 4) in 2010 due to conflicts with military training. As a result, we used data from seven blocks and 27 canopy treatment plots for the study.

Prior to planting longleaf pine seedlings, the study sites were mechanically prepared by mowing all standing sub-canopy vegetation with a Fecon Bull Hog® rotary mower in the late summer of 2007 and by prescribed burning in fall 2007. Container-grown longleaf pine seedlings were planted by hand in December 2007 at a spacing of 1.8 × 3.0 m (approximate 1800 seedlings/ha). Each canopy plot was divided into four equal sections and three of the

sections were randomly selected for cultural treatment application. Within each section, cultural treatments were applied to a 30 × 30 m area centered on a 20 × 20 m subplot measurement area. The three cultural treatments included: NT (no cultural treatment applied), H (a direct spray of 1% imazapyr with 1/4% non-ionic surfactant to target woody vegetation in October 2008), and H + F (the H treatment plus 10-10-10 NPK fertilizer that was broadcast at a rate of 280 kg/ha in early May 2009). To meet fire management objectives for longleaf pine restoration, prescribed fires were applied to all experimental plots between January and March 2010.

2.3. Data collection

2.3.1. Residual basal area

In the summer of 2007, we marked all overstory trees ⩾10 cm DBH with aluminum tags and recorded species and DBH. DBH measurements were converted to basal area (m²/ha) at the plot level. After harvest, residual BA significantly differed between each canopy treatment ($p < 0.001$). Mean post-harvest BAs were 16.2 (Control), 9.0 (MedBA), 6.4 (LowBA), and 0 m²/ha (Clearcut), respectively.

2.3.2. Plant resource measurements

To measure canopy openness and calculate light availability, hemispherical photographs were systematically taken at all subplots (two per subplot and six per main plot) during August 2008 in mornings before sunrise, evenings prior sunset, or uniformly cloudy days. Photographs were taken with a Nikon® Coolpix 4500 digital camera, using a Nikon® FC-E8 fisheye lens (Nikon Corporation, Tokyo, Japan). The top of the camera was oriented toward north on a tripod, and the camera lens was positioned at a height of 1.5 m above the ground.

Surface soil moisture (in the entire top 6 cm) and soil temperature at a depth of 10 cm were measured adjacent to five systematically selected longleaf pine seedlings (seedlings closest to each of the four corners and the center of the subplot) in each subplot (15 seedlings per main plot). We used a ML2 Theta Probe moisture meter (Delta-T Devices, Cambridge, England) to measure volumetric soil moisture and a Traceable® Thermometer (Control Company, Friendswood, TX) to measure soil temperature. Both measurements were taken in June and October 2009, and June, July, and September 2010.

In late October 2009 (i.e., the end of the second growing season after planting) and January 2011 (i.e., after the third growing season after planting), a composite sample of current year needles was systematically collected from the five longleaf pine seedlings (5–10 needles per seedling) selected for soil moisture/temperature measurements in each subplot (three samples per main plot). We collected needles after the growing season, when nutrient reallocation fluxes are at a minimum (Dickson, 1989). Needles were dried at 70 °C and prepared for foliar nutrient analyses following protocols of Clemson Agricultural Services Laboratory. Foliar nitrogen (N) concentrations were determined using LECO FP528 Nitrogen Combustion Analyzer (LECO Corporation, St. Joseph, MI). Foliar phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) concentrations were analyzed using a Jobin Yvon Contained Inductively Coupled Plasma Emission Spectrometer (ICP-ES, Horiba Ltd., Edison, NJ).

2.3.3. Longleaf pine seedling survival and growth

In the beginning of the 2008 growing season, we randomly selected and marked 30 seedlings per subplot, for a total of 90 seedlings in each main plot. Survival of each seedling was monitored, and the growth of each seedling was measured at the end of each growing season (late September to early October of 2008–2010).

Growth was quantified by measuring the root collar diameter (RCD) using digital calipers and annual RCD increment was calculated as the differences between the RCD of the current year and the RCD of the previous year.

2.4. Data analysis

Each hemispherical photograph was analyzed using the image analysis program HemiView version 2.1 (Delta-T Devices Ltd., Cambridge, UK) following a standard procedure (Rich et al., 1993; Gendron et al., 1998; Battaglia et al., 2003) to estimate direct and diffuse beam radiation above each location on a daily basis over a 12-mo period. It was assumed that canopy openings in coniferous forests do not change significantly throughout the year (Rich, 1990; Battaglia et al., 2003). For each location, we calculated gap light index (GLI; Canham, 1988) using the following equation:

$$GLI = [(T_{diffuse} * P_{diffuse}) + (T_{beam} * P_{beam})] * 100$$

where $P_{diffuse}$ and P_{beam} are proportions of incident seasonal photosynthetically active radiation (PAR) reaching the top of the canopy as diffuse and direct radiation, respectively, and $T_{diffuse}$ and T_{beam} are proportions of diffuse and direct radiation reaching the hemispherical photograph. We assume that $P_{diffuse}$ and P_{beam} are equal to 0.5 (Battaglia et al., 2002).

GLIs were averaged at the plot level for statistical analyses. Other resource variables including soil moisture, soil temperature, and foliar nutrients were averaged across sampling months at the subplot level for each year for statistical analyses.

One-way analysis of variance (ANOVA) was used to test the effect of canopy treatment on GLI. Split-plot ANOVA was used to test the effects of canopy and cultural treatments on soil moisture, soil temperature, and foliar nutrients in each year. Repeated measures ANOVA was used to examine the changes in foliar nutrients over time. Soil moisture data were log-transformed to improve normality (Krebs, 1999). All analyses were performed using PROC MIXED in SAS 9.1 (SAS Institute, 2004) with mixed-models and a random block effect. In the case of a significant interaction between main-plot and subplot effects, we used the SLICE statement to determine significant effects of one treatment (i.e., canopy or cultural) within each level of the other treatment. Tukey's honestly significant difference (HSD) test was used to determine differences in pairwise comparison among the canopy and cultural treatments for each variable. The level of statistical significance was set as α = 0.05.

At the main plot level, we used regression analysis to determine relationships between residual BA and resources variables measured in each year (GLI, soil moisture, soil temperature, and foliar nutrients). At the subplot level, we used Pearson correlation analysis to determine relationships between longleaf pine seedling response (annual mortality and annual RCD increment) and resources variables measured in 2009 and 2010 (GLI, soil moisture, soil temperature, and foliar nutrients). Assuming that GLI did not significantly change during the three growing seasons, we related GLI measured in 2008 to mortality and growth rates of the 2009 and 2010 growing seasons. We related foliar nutrients measured in October 2009 and January 2011 to mortality and growth rates of the 2009 and 2010 growing seasons, respectively. Scatterplots and the best fit regression models were developed and processed in SigmaPlot 9.0 (SYSTAT Software Inc., 2004).

3. Results

3.1. Light, soil moisture and soil temperature

GLI significantly differed between each canopy treatment ($p ⩽ 0.040$) with Clearcut (94.3%) > LowBA (69.4%) > MedBA

(61.4%) > Control (47.8%). Regression analysis indicated that GLI increased nonlinearly with decreasing BA ($R^2 = 0.973$; $p < 0.001$) (Fig. 1).

Canopy treatments did not affect soil moisture or soil temperature in 2009 or 2010 ($p \geqslant 0.372$). Cultural treatments did not affect surface soil moisture ($p \geqslant 0.214$) but affected soil temperatures in both measurement years (2009: $p < 0.001$; 2010: $p = 0.027$). In 2009, H and H + F subplots had higher soil temperatures than the NT subplots ($p < 0.001$). In 2010, only H subplots had higher soil temperatures than the NT subplots ($p = 0.021$; Table 1). Neither soil moisture nor soil temperature was significantly correlated with residual BA either in 2009 or in 2010 ($p \geqslant 0.304$).

3.2. Foliar nutrients

In 2009, significant interactions between canopy and cultural treatments were detected for foliar P concentration ($p = 0.007$; Table 2). For foliar P, no differences among cultural treatments were found in Clearcut plots. In Control and LowBA plots, H + F subplots had higher foliar P than NT subplots; in MedBA plots, H + F subplots resulted in higher foliar P than both H and NT subplots. Among the four canopy treatments, no significant differences were detected in foliar N, K, and Mg centrations ($p \geqslant 0.105$), but significant differences were detected in foliar Ca concentration ($p < 0.001$; Table 3). The Clearcut treatment had higher foliar Ca than other treatments ($p \leqslant 0.009$). Among the three cultural treatments, no significant differences were detected in foliar N, K, Ca, and Mg concentrations ($p \geqslant 0.197$).

In 2011, no significant differences among the four canopy treatments were detected in foliar N, K, and Mg concentrations ($p \geqslant 0.275$), but significant differences were detected for foliar P and Ca concentrations ($p \leqslant 0.045$; Table 3). The Clearcut plots had higher foliar P than the Control plots ($p = 0.041$) and higher foliar Ca than the Control and LowBA plots ($p \leqslant 0.035$). No significant differences were detected for foliar nutrient concentrations among the three cultural treatments ($p \geqslant 0.106$).

Compared to 2009, foliar Ca and Mg concentrations significantly increased in 2011 ($p < 0.001$), but foliar N concentration significantly decreased in 2011 ($p < 0.001$). Foliar P concentration did not change from 2009 to 2011 ($p = 0.205$) but the change in foliar K concentration depended on canopy treatments ($p = 0.013$). Compared to 2009, foliar K significantly decreased on Clearcut, LowBA and MedBA plots ($p \leqslant 0.033$), but not on Control plots ($p = 0.659$) in 2011. Regression analysis showed that foliar Ca was negatively related to residual BA in both 2009 and 2011 (Fig. 2A and B).
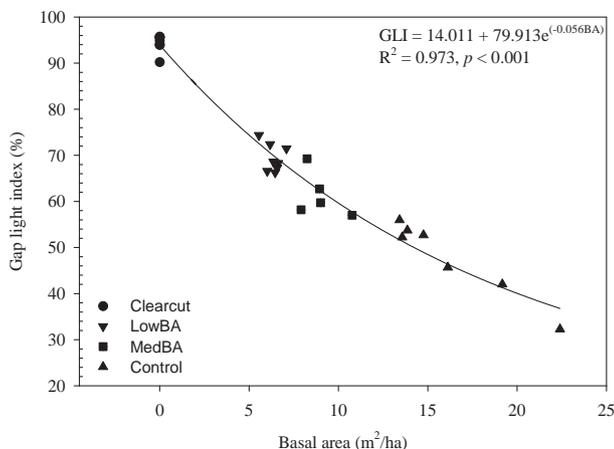
Table 1
Soil temperature (°C) at a depth of 10 cm in 2009 and 2010 by cultural treatment. Means are followed by standard error in parenthesis. The same letter within a measurement period indicates no significant difference ($\alpha = 0.05$).

Cultural treatment	2009	2010
NT	22.2 b (0.3)	26.2 b (0.2)
H	22.7 a (0.3)	26.7 a (0.2)
H + F	22.6 a (0.3)	26.5 ab (0.2)
p	<0.001	0.027

Notes: NT: no cultural treatment; H: herbicide cultural treatment; H + F: herbicide plus fertilization cultural treatment.

Table 2
Foliar phosphorus (P;%) stratified by canopy and cultural treatments in 2009. Means are followed by standard deviation in parenthesis. The same letter within each canopy treatment indicates no significant difference ($\alpha = 0.05$).

Treatment	Control	MedBA	LowBA	Clearcut
NT	0.07 b (0.02)	0.08 b (0.02)	0.07 b (0.02)	0.09 a (0.02)
H	0.07 ab (0.02)	0.07 b (0.01)	0.07 ab (0.03)	0.08 a (0.02)
H + F	0.08 a (0.01)	0.10 a (0.02)	0.08 a (0.02)	0.09 a (0.02)

3.3. Longleaf pine seedling response to plant resources

A few variables were significantly correlated with the annual mortality of planted longleaf pine seedlings, but none indicated significantly consistent correlations over the 2 years (Table 4). The annual mortality rate in 2009 was correlated negatively with GLI ($p = 0.018$), but positively with foliar K ($p = 0.009$).

Several variables were found to be significantly correlated with annual RCD increment of planted longleaf pine seedlings, and these correlations were consistent over years (Table 4). GLI, foliar P, and Ca concentrations were positively correlated with seedling annual RCD increment ($p \leqslant 0.007$), while soil moisture was negatively correlated with seedling annual RCD increment ($p \leqslant 0.008$). In 2009, soil moisture accounted for 40.7% of the variability in seedling RCD increment, followed by foliar Ca (22.4%), foliar P (17.3%), and GLI (11.5%) (Fig. 3); in 2010, GLI accounted for 27.5% of the variability in seedling RCD increment, followed by foliar Ca (9.5%), foliar P (8.8%), and soil moisture (8.6%) (Fig. 4). In addition, the annual RCD increment in 2009 was positively correlated with foliar N concentration ($p = 0.037$; Table 4).

4. Discussion

4.1. Plant resources response to canopy and cultural treatments

Variable retention silvicultural systems have been proposed as one approach for rapidly restoring micro-climate factors associated with structurally complex forests (Kohn and Franklin, 1997). The application of these systems requires decisions on the type, density, and spatial pattern of the residual trees, which must be based on an understanding of how the understory environment is affected by different degrees of canopy retention (Van Pelt and Franklin, 1999; Battaglia et al., 2002).

As expected, our canopy treatments significantly affected understory light availability. Our results are consistent with previous studies conducted in loblolly pine forests (e.g., Tang et al., 1999), longleaf pine forests (e.g., Boyer, 1993; Palik et al., 1997) and other forest types (e.g., Lieffers et al., 1999; Drever and Lertzman, 2003). Our study found that the relationship between GLI and residual loblolly pine BA followed an exponential decay function (Fig. 1). Similarly, Palik et al. (1997) found that the relationship between GLI and residual longleaf pine BA followed a curvilinear function (GLI = 85.51/(1 + 0.068*BA), $R^2 = 0.71$, $p < 0.001$)

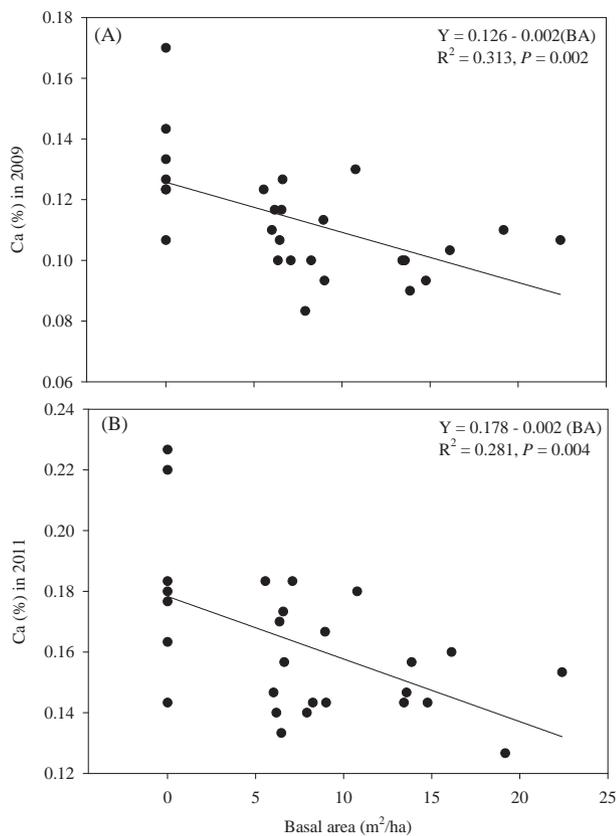**Fig. 1.** The relationship between gap light index (GLI;%) and residual basal area (BA;m²/ha).

Table 3
Foliar nutrients by canopy treatment in 2009 and 2011. Means are followed by standard deviation in parenthesis. The same letter within a measurement period indicates no significant difference ($\alpha = 0.05$).

Canopy	Control	MedBA	LowBA	Clearcut	p
N (%)					
2009	1.03 (0.08)	1.13 (0.14)	1.11 (0.17)	1.10 (0.16)	0.399
2011	1.02 (0.11)	0.99 (0.11)	1.05 (0.19)	0.98 (0.09)	0.275
P (%)[a]					
2011	0.07 b (0.02)	0.08 ab (0.02)	0.08 ab (0.02)	0.09 a (0.02)	**0.045**
K (%)					
2009	0.66 (0.10)	0.71 (0.09)	0.69 (0.07)	0.72 (0.07)	0.243
2011	0.65 (0.10)	0.63 (0.08)	0.64 (0.08)	0.60 (0.07)	0.358
Ca (%)					
2009	0.10 b (0.02)	0.11 b (0.02)	0.11 b (0.02)	0.13 a (0.02)	**<0.001**
2011	0.15 b (0.02)	0.17 ab (0.03)	0.15 b (0.03)	0.18 a (0.04)	**0.011**
Mg (%)					
2009	0.08 (0.01)	0.09 (0.01)	0.09 (0.01)	0.09 (0.01)	0.105
2011	0.11 (0.01)	0.11 (0.02)	0.12 (0.02)	0.12 (0.02)	0.378

Notes: N: Nitrogen; P: Phosphorus; K: Potassium; Ca: Calcium; Mg: Magnesium.
[a] The interactions between canopy and cultural treatments were detected in foliar P concentration in 2009.

Fig. 2. Scatterplots with regression lines for foliar calcium (Ca;%) in 2009 (A) and in 2011 (B) vs. residual basal area (BA;m²/ha).
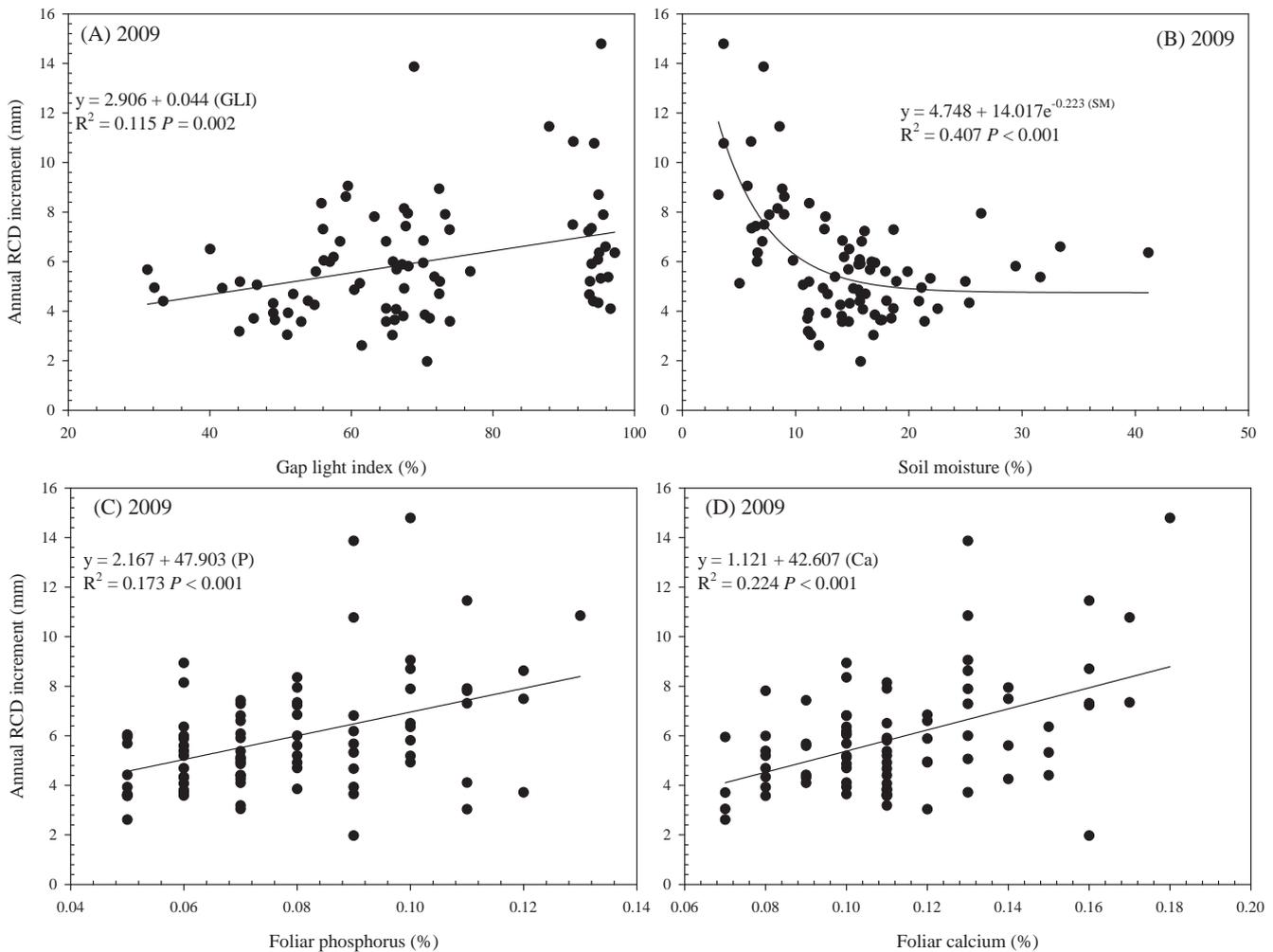
Table 4
Results of Pearson correlation analysis (Pearson's r; p-values in bold) between longleaf pine annual mortality (%) and annul RCD increment (mm) and plant resources.

Plant resources[a]	Annual mortality		Annual RCD increment	
	2009	2010	2009	2010
GLI	−0.262	−0.178	0.339	0.525
	0.018	**0.112**	**0.002**	**<0.001**
Moisture	−0.039	0.070	−0.394	−0.294
	0.727	**0.536**	**<0.001**	**0.008**
Temperature	−0.189	−0.106	−0.091	−0.101
	0.091	**0.347**	**0.420**	**0.369**
N	−0.040	0.740	0.233	0.004
	0.721	**0.511**	**0.037**	**0.973**
P	−0.065	−0.170	0.415	0.296
	0.566	**0.129**	**<0.001**	**0.007**
K	0.291	0.126	0.056	−0.164
	0.009	**0.261**	**0.622**	**0.143**
Ca	−0.145	−0.141	0.473	0.308
	0.196	**0.21**	**<0.001**	**0.005**
Mg	0.045	−0.039	0.052	0.085
	0.690	**0.732**	**0.647**	**0.448**

[a] GLI: Gap light index; N: Nitrogen; P: Phosphorus; K: Potassium; Ca: Calcium; Mg: Magnesium.

2003; Ma et al., 2010) and soil moisture (Tang et al., 2005; Ma et al., 2010) with decreasing BA. The lack of differences in surface soil moisture and soil temperature in our study may be attributed to the rapid recovery of understory vegetation. Reducing competition from canopy trees by thinning increases the abundance of ground layer vegetation and releases understory hardwoods (Harrington et al., 2003; Pecot et al., 2007; Outcalt and Brockway, 2010; Knapp et al., 2011). We found that understory vegetation control with herbicide application resulted in higher soil temperatures. The effects of removing vegetation competition on soil resource availability have been frequently reported. For example, within longleaf pine plantations, herbicides increased surface soil water content on well-drained soils in the sandhills of South Carolina (Harrington and Edwards, 1999) and on poorly-drained soils in lower coastal plain of North Carolina (Knapp et al., 2008). However, our herbicide plus fertilization treatment increased soil temperature only in 2009, suggesting that rapid recovery of understory plants following fertilization made the initial effects of the herbicide application on soil temperature short-lived.

Foliar analyses provide a way to determine the nutritional status, needs, and likely response of target trees to fertilization, and

in southwestern Georgia. Direct comparison of our equation with the equation of Palik et al. (1997) may be difficult because many factors, including stand age, stand density, tree size, and site index, could affect the canopy structure and therefore result different light transmittance. Nevertheless, such a comparison was made by Kirkman et al. (2007), and their result suggested that longleaf pine canopy did allow more light transmittance than slash pine canopy.

Our canopy treatments did not affect either surface soil moisture or soil temperature. Previous studies reported increased surface soil temperatures (Carlson and Groot, 1997; Palik et al.,

Fig. 3. Scatterplots with regression lines for annual root collar diameter (RCD) increment (mm) in 2009 vs. (A) gap light index (GLI;%), (B) soil moisture (SM;%), (C) foliar phosphorus (P;%), and (D) foliar calcium (Ca;%).

the concept of a critical threshold or sufficiency level is commonly applied to foliar analyses (e.g., Blevins et al., 1996; Wang and Klin-ka, 1997). Blevins et al. (1996) suggested that the foliar sufficiency levels for N, P, K, Ca and Mg were 9.5, 0.8, 3.0, 1.0 and 0.6 g/kg, respectively, for longleaf pine. Based on these standards, foliar K and Mg concentrations were each above these standards in both years. Although 22% of the measurements of foliar Ca concentration were found below the sufficiency level in 2009, none was found below the sufficiency level in 2011. However, 51% and 48% of the measurements of foliar P concentration were found below the 0.8 g/kg level in 2009 and 2011, respectively; 12% and 28% of the measurements of foliar N concentration were below the 9.5 g/kg level in 2009 and 2011, respectively. Results from the foliar analyses indicate that both N and P were possibly limiting seedling growth. Similarly, the shortage of foliar N and P concentrations defined by Blevins et al. (1996) was also reported in a five-year-old longleaf pine stand in the west gulf region of central Louisiana (Kuehler et al., 2006) and after six growing seasons in flatwoods of central Louisiana (Haywood, 2000).

The effect of prescribed fires on foliar nutrition of longleaf pine was complicated. Kuehler et al. (2006) found that, although foliar N, P, Ca, and Mg concentrations were not different, foliar K concentration was significantly greater on the burning plots in a five-year-old longleaf pine stand of central Louisiana. Boyer and Miller (1994) found that besides foliar N, P, Ca, and Mg concentrations, re-

peated prescribed fire also had no effect on the foliar K concentration in a 30-year-old longleaf pine stand of southwest Alabama. However, prescribed fires increased soil Ca concentrations of a longleaf pine-wiregrass savanna of North Carolina (Christensen, 1977), a loblolly and longleaf pine forest of South Carolina (Binkley et al., 1992), and a shortleaf pine forest of Arkansas (Liechty et al., 2005). Our study sites were burned in spring 2010 to meet the restoration objective of a frequent fire regime, so the increase in foliar Ca concentration in 2011 may have been caused by an increased soil Ca availability following the prescribed fire in spring 2010.

Although the effect of fertilization was short-lived, the herbicide plus fertilization treatment increased foliar P concentration in 2009 among all plots except Clearcut plots, suggesting that fertilization might make up the low nutrient status of many sites that are well-suited for longleaf pine when competing plants were controlled.

4.2. Longleaf pine seedling response to plant resources

Among the few variables that were significantly correlated with seedling mortality, none showed consistent correlations over the 2 years (Table 4). We found that neither soil moisture nor soil temperature affected longleaf pine seedling survival. However, positive effects of soil moisture and negative effects of soil temperature on longleaf pine seedling survival were reported on poorly-drained
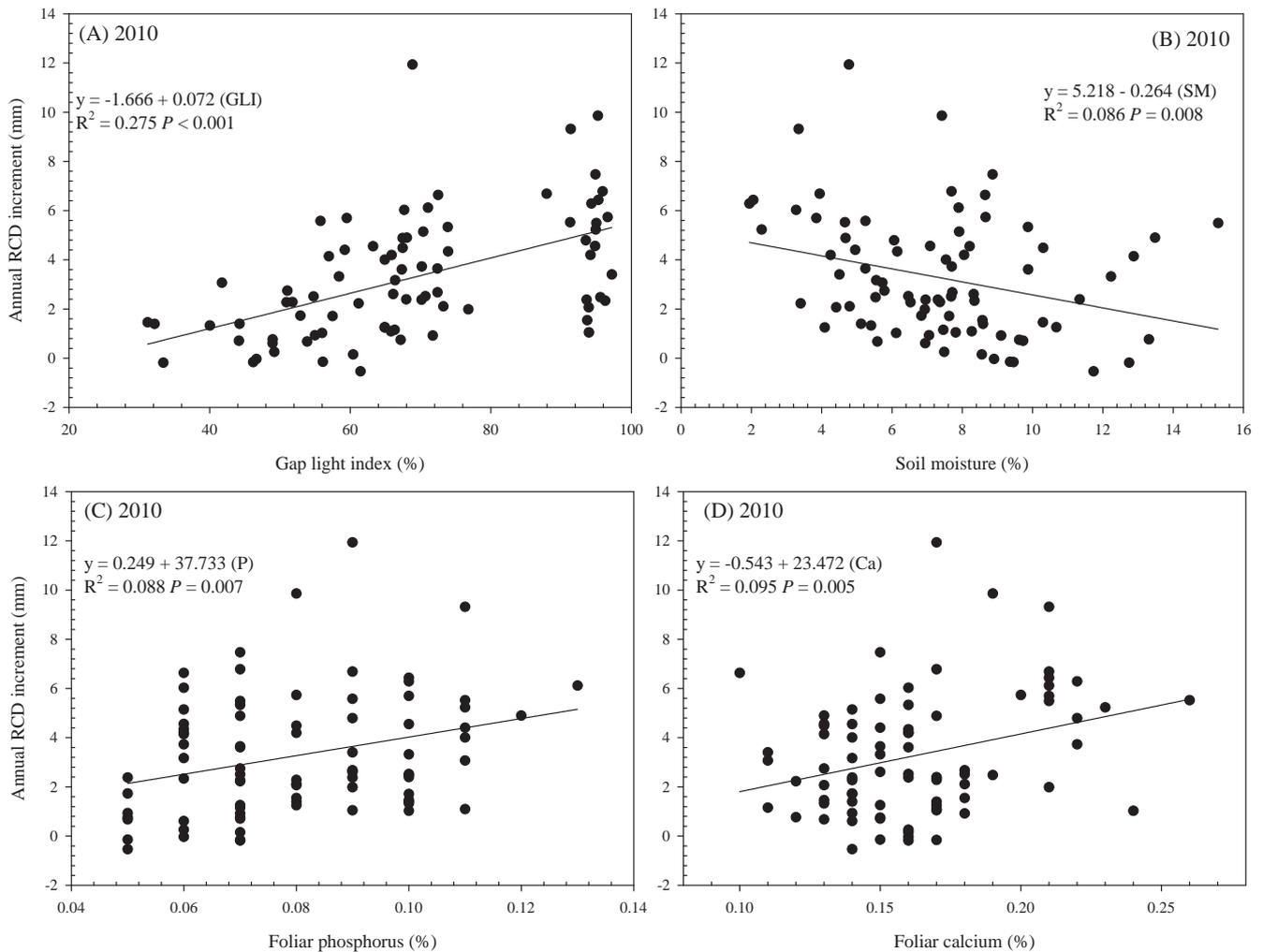
Fig. 4. Scatterplots with regression lines for annual root collar diameter (RCD) increment (mm) in 2010 vs. (A) gap light index (GLI;%), (B) soil moisture (SM;%), (C) foliar phosphorus (P;%), and (D) foliar calcium (Ca;%).

soils in North Carolina (Knapp et al., 2008). On well-drained soils in southwestern Georgia, Rodríguez-Trejo et al. (2003) reported that extreme temperatures increased first year mortality by drying out and desiccating the root systems of longleaf pine seedlings during a severe drought. Although our study was conducted on moderately well- to well-drained sites, data from the National Climatic Data Center (Wilmington International Airport, 34°16′N, 77°54′W) indicated that no drought occurred during our study period (2009 = 151.7 cm; 2010 = 148.7 cm; the 50-year mean = 140.0 cm).

It is well known that longleaf pine is a shade-intolerant species (Boyer, 1990), and light becomes a limiting factor for seedling growth under intact canopies. As a result, we expected a positive relationship between seedling growth and light over the study period (Figs. 3A and 4A). The best regression model between annual RCD increment and gap light index was linear in both 2009 and 2010, suggesting that seedling growth increased as gap light index rose from 31% to 97%. Previous gap studies on resource availability within longleaf pine forests also reported that longleaf pine regeneration in gaps was limited by competition for light (Palik et al., 1997, 2003; McGuire et al., 2001). On well-drained soils in southwestern Georgia, Palik et al. (1997) found that seedling biomass increment was curvilinear with gap light index and seedling growth linearly increased as light levels rose from 30% to around 70% full sunlight; however, McGuire et al. (2001) found that total seedling biomass linearly increased as gap light index rose from

40% to around 95%. Our results confirmed that light availability limited the growth of longleaf pine seedlings not only in gaps, but also in uniformly thinned plots.

Although previous studies on resource availability have reported poor relationships between longleaf pine growth and soil moisture (Palik et al., 1997; McGuire et al., 2001) on well-drained soils, we found negative correlations between seedling growth and soil moisture. In both years, seedling growth decreased with increasing soil moisture up to 16% (Figs. 3B and 4B). A similar observation was also reported by Palik et al. (1997), who concluded that soil moisture was probably not the reason for limited growth of longleaf pine seedlings in a mature longleaf pine woodland on well-drained soils of southwestern Georgia where soil moisture rarely fell below 10%. However, Knapp et al. (2008) found that soil moisture was still negatively related to the growth of longleaf pine seedlings as soil moisture rose up to around 40% on poorly-drained soils in the coastal plain of North Carolina. These studies suggested that the effect of soil moisture on the growth of longleaf pine seedlings differed among different soil types.

We found that foliar P and Ca concentrations were positively correlated with seedling annual RCD increment in each of the two measurement years and explained higher proportions of the variability in seedling annual RCD increment in 2009 (Fig. 3C and D) than 2011 (Fig. 4C and D). The results are not surprising considering that more foliar P and Ca concentrations were below the

sufficiency levels proposed by Blevins et al. (1996) in 2009 than in 2011.

5. Conclusions and management implications

Understanding patterns of resource availability following harvesting in relation to longleaf pine seedling survival and growth is critical for determining the appropriate canopy retention system for successful longleaf pine restoration in loblolly pine stands. Our study shows that light availability under the canopy is closely related to residual basal area, and the annual RCD increment of planted longleaf pine seedlings positively responded to increasing light availability. Therefore, the need for an appropriate level of canopy retention must be balanced with the light requirement of planted longleaf pine seedlings.

Soil moisture consistently showed a negative correlation with seedling annual RCD increment, suggesting that site treatments that could improve soil drainage may increase seedling growth potential. Although soil fertility might have positive effects on seedling growth because foliar P and Ca concentrations also correlated positively with seedling annual RCD increment, the negative effect of fertility on stimulating the competition around planted longleaf pine seedlings could still reduce the growth potential of planted longleaf pine seedlings.

Conclusions from this study are based on the establishment of longleaf pine regeneration during the first three years after planting, and it is not clear how our treatments will affect long-term resource availability. Furthermore, when the management goal includes restoring other components of longleaf pine ecosystems, managers will need to consider broader effects of canopy and cultural treatments. Clearcutting could result in the largest light availability and consequently the greatest seedling RCD, but it could also result in the greatest growth of midstory or understory vegetation. In addition, changes in the fuel dynamics following canopy removal have important implications for fire management, and treatments that increase hardwood dominance may reduce the continuity of prescribed burns. Therefore, future studies are needed to test how these silvicultural treatments affect the restoration of other critical components of longleaf pine ecosystems.

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