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Using silvicultural practices to regulate competition, resource availability, and growing conditions for *Pinus palustris* seedlings underplanted in *Pinus taeda* forests

Benjamin O. Knapp, G. Geoff Wang, Joan L. Walker, and Huifeng Hu

Abstract: In the southeastern United States, many forest managers are interested in restoring longleaf pine (*Pinus palustris* Mill.) to upland sites that currently support loblolly pine (*Pinus taeda* L.). We quantified the effects of four canopy treatments (uncut Control; MedBA, harvest to 9 m²·ha⁻¹; LowBA, harvest to 5 m²·ha⁻¹; and Clearcut) and three cultural treatments (NT, no treatment; H, herbicide release of longleaf pine seedlings; and H+F, herbicide release plus fertilization) on resource availability and growing conditions in relation to longleaf pine seedling response for 3 years. Harvesting treatments reduced competition from canopy trees but resulted in greater abundance of understory vegetation. Harvesting shifted the interception of light from the canopy to the subcanopy vegetation layer; however, total light availability at the forest floor increased with the intensity of canopy removal. Soil moisture was not affected by harvesting or by the cultural treatments. Foliar nutrient concentrations (N, P, and K) of longleaf pine seedlings generally increased with the intensity of the harvest treatment. Of the plant resources measured, we found that light was most strongly correlated with longleaf pine seedling growth and that incorporating the interception of light by subcanopy vegetation improved the relationship over that of canopy light transmittance alone.

Key words: foliar nutrients, gap light index, longleaf pine restoration, resource availability, underplanting.

Résumé : Dans le sud-est des États-Unis, plusieurs aménagistes forestiers sont intéressés à restaurer le pin des marais (*Pinus palustris* Mill.) sur des stations bien drainées présentement occupées par le pin à encens (*Pinus taeda* L.). Nous avons quantifié les effets de quatre traitements d'éclaircie du couvert dominant (témoin non traité; surface terrière résiduelle de 9 m²·ha⁻¹, MedBA; surface terrière résiduelle de 5 m²·ha⁻¹, LowBA; et coupe à blanc) et de trois traitements culturaux (témoin non traité, TEM; application d'un herbicide autour des semis de pin des marais, H; et application d'un herbicide et d'une fertilisation, H+F) sur la disponibilité des ressources et sur les conditions de croissance en relation avec la réaction des semis de pin des marais pendant trois ans. Les traitements de coupe ont réduit la compétition des arbres du couvert dominant, mais ont entraîné une plus grande abondance de la végétation sous couvert. La coupe a fait passer l'interception de la lumière du couvert dominant à la strate de végétation sous le couvert, mais la disponibilité totale de la lumière au sol a augmenté avec l'intensité de l'éclaircie du couvert dominant. L'humidité du sol n'a pas été influencée par la coupe ou par les traitements culturaux. La concentration foliaire en nutriments (N, P et K) des semis de pin des marais a généralement augmenté avec l'intensité des traitements de coupe. Parmi les ressources nécessaires à la croissance des plantes que nous avons mesurées, la lumière était la plus étroitement corrélée à la croissance des semis de pin des marais et cette relation était améliorée en tenant compte de l'interception de la lumière par la strate de végétation sous le couvert dominant en plus de la transmission de la lumière par le couvert dominant. [Traduit par la Rédaction]

Mots-clés : nutriments foliaires, coefficient de trouées lumineuses, restauration du pin des marais, disponibilité des ressources, plantation sous couvert.

Introduction

In forested ecosystems, the combination of abiotic conditions and biotic interactions at the growing site largely controls the establishment success (i.e., growth and survival rates) of individual tree seedlings (Grubb 1977). Forest managers interested in promoting the establishment of specific species often modify these factors to favor the success of the target species. Such practices are common during restoration, because site conditions associated with degradation must often be overcome to reach restoration objectives (Hobbs and Harris 2001; Martin and Kirkman 2009). In the southeastern United States, restoring longleaf pine (*Pinus palustris* Mill.) ecosystems on upland sites is an important objective of many forest managers, particularly on public lands that support federally endangered red-cockaded woodpeckers (RCW; *Picoides borealis* (Vieillot)). Historical land use and management practices have resulted in the current dominance of loblolly pine (*Pinus taeda* L.) in many such forests (Frost 2006; Schultz 1999), and therefore, restoration requires artificial regeneration for the establishment

B.O. Knapp,* G.G. Wang, and H. Hu.† Department of Forestry and Environmental Conservation, Clemson University, 261 Lehotsky Hall, Clemson, SC 29634, USA.
J.L. Walker. USDA Forest Service, Southern Research Station, Clemson University, 233 Lehotsky Hall, Clemson, SC 29634, USA.
Corresponding authors: Benjamin O. Knapp (email: knappb@missouri.edu) and G. Geoff Wang (email: gwang@clemson.edu).
*Present address: Department of Forestry, University of Missouri, 203-S ABNR Building, Columbia, MO 62511, USA.
†Present address: State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing 100093, China.

of longleaf pine seedlings. Because longleaf pine seedlings are considered to be intolerant to competition for resources (Boyer 1990), successful seedling establishment often requires a reduction in competitive pressures to improve the suitability of the growing site (Palik et al. 1997, 2002; Pecot et al. 2007).

Previous studies have generally established inverse relationships between longleaf pine seedling growth and the abundance of canopy trees. For example, Palik et al. (1997) reported a negative, exponential relationship between longleaf pine seedling biomass growth increment and overstory basal area of longleaf pine canopy trees, with substantial increases in seedling growth at basal areas <6 m²·ha⁻¹. To account for the spatial distribution of canopy trees, other studies have used competitive indices that integrate the size and distance of canopy trees from individual seedlings and report similar relationships between overstory competition and seedling growth (Palik et al. 2003; Pecot et al. 2007). Thus, some degree of canopy removal is typically prescribed for longleaf pine regeneration.

Canopy removal increases the amount of growing space and the availability of light, nutrients, and water for planted seedlings and other vegetation. In longleaf pine forests, which characteristically do not have a well-developed midstory vegetation layer, light availability in the understory is closely related to canopy density because canopy trees are the primary source of light interception (Battaglia et al. 2002). However, an increase in the abundance of understory or midstory vegetation following canopy removal may shift the interception of incident solar radiation from canopy plants to subcanopy plants and result in reduced light available to longleaf pine seedlings at the forest floor.

The effects of canopy tree removal on nutrient availability are complex; canopy trees provide nutrient inputs through litterfall, uptake nutrients for their own use, and affect microbial activity, litter decomposition, and nutrient release through the moderation of soil moisture and temperature (Covington 1981; Marshall 2000; Prescott 2002). Several studies have reported increases in nitrogen following forest harvesting, in part due to changes in the soil temperatures and moisture levels (Attiwill and Adams 1993; Matson and Vitousek 1981; Titus et al. 2006). However, previous studies reported inconsistent results regarding effects of canopy tree removal on soil moisture, with increases in soil moisture caused by a reduction in the uptake and transpiration by canopy trees (Elliott et al. 1998; Harrington and Edwards 1999) and decreases in soil moisture associated with drying effects from increased exposure to solar radiation (Redding et al. 2003). Increased exposure to solar radiation also commonly results in increased soil temperatures following timber harvest (Londo et al. 1999; Moroni et al. 2007; Redding et al. 2003).

In addition to modifying the canopy structure, forest managers commonly use subcanopy vegetation control treatments and (or) fertilization to improve the growing conditions for target species. Following the removal of longleaf pine trees from the canopy, understory vegetation can quickly fill root gaps and reduce the availability of belowground resources for planted seedlings (Jones et al. 2003; Pecot et al. 2007). Herbicides are prescribed to reduce the competitive pressure of surrounding vegetation and reportedly result in increased growth of planted seedlings (Haywood 2005; Jose et al. 2010; Ramsey et al. 2003). In pine forests, controlling the understory vegetation with herbicides has been associated with increased soil moisture availability (Knapp et al. 2008; Zutter et al. 1986) and increased nutrient availability (Nambiar and Sands 1993). However, the mechanisms by which vegetation control results in greater longleaf pine seedling growth are not fully understood. Finally, fertilizers are commonly used to alleviate nutrient limitations to seedling establishment and have been found to increase the growth of loblolly and slash (*Pinus elliottii* Engelm.) pines (e.g., Colbert et al. 1990; Jokela et al. 2004). Several studies have tested the effects of fertilization on longleaf pine seedling growth response (Gagnon et al. 2003; Hu et al. 2012*b*;

Ramsey et al. 2003), but few have directly determined the effects of fertilizer treatments on foliar nutrients.

Developing silvicultural prescriptions for longleaf pine restoration on sites dominated by loblolly pine requires an understanding of how management actions affect resource availability and how, in turn, resource availability affects longleaf pine seedling establishment. Previous research that focused on longleaf pine seedling response to resource availability and (or) growing conditions primarily occurred within existing longleaf pine forests (McGuire et al. 2001; Palik et al. 1997; Pecot et al. 2007), in the absence of canopy trees (Knapp et al. 2008), or in a greenhouse setting (Jose et al. 2003). It is not clear if species differences will result in different patterns of resource availability following similar management actions in loblolly pine stands. The overall goal of this study was to understand the effects of canopy density and cultural treatments on the abundance of competition and resource availability in relation to longleaf pine seedling establishment in upland loblolly pine forests on the border of Georgia and Alabama, United States. Our specific objectives were to (*i*) test the effects of harvesting and cultural treatments on the growing conditions (vegetation abundance, light, nutrients, soil water, soil temperature) for planted longleaf pine seedlings; (*ii*) determine relationships between canopy and subcanopy vegetation structure and light transmittance to the forest floor; and (*iii*) relate the growth response of planted longleaf pine seedlings to growing conditions modified by harvesting and cultural treatments.

Materials and methods

Study site

This study was conducted at Fort Benning Military Installation (~32.38°N, 84.88°W) in Muscogee and Chattahoochee counties, Georgia, and Russell County, Alabama. Prior to establishment as a U.S. military installation in 1918, much of the land base was used for cotton production but then was reforested with loblolly pine following the abandonment of agriculture (Fort Benning 2001). Fort Benning falls within two ecoregions, with the northeastern two-thirds in the Sand Hills Subsection of the Lower Coastal Plains and Flatwoods Section and the southwestern one-third of the installation within the Upper Loam Hills Subsection of the Middle Coastal Plain Section (Bailey 1995). The terrain of Fort Benning is predominately rolling and is highest in the Sand Hills of the northeast (225 m above sea level) and lowest near the Chattahoochee River in the southwest (58 m above sea level). Soils are generally low in organic matter and nutrient-holding capacity, although those of the Upper Loam Hills have higher silt and clay contents than the coarse-textured, sandy soils of the Sand Hills. Common soil series in the Sand Hills include Troup sandy loam, Wagram loamy sand, and Vaucluse loamy sand; those of the Upper Loam Hills include Maxton loamy sand and Wickham sandy loam. The 50 year mean annual precipitation at Fort Benning (1971–2011) was 1225 mm, with a 50 year mean annual temperature of 18.4 °C.

This study was established on upland sites that were dominated by second-growth loblolly pines and were targeted for restoration by land managers at Fort Benning. Many such sites have been managed to improve RCW habitat during the past few decades, and recent management activities include the use of prescribed fire on frequent fire return intervals (3 to 4 years) that are associated with longleaf pine ecosystem management. Common understory species included bunchgrasses (e.g., *Andropogon* spp., *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum* spp.) and herbaceous species such as legumes (e.g., *Desmodium* spp., *Lespedeza* spp.) and composites (e.g., *Eupatorium* spp., *Solidago* spp.). Woody species, including sweetgum (*Liquidambar styraciflua* L.), persimmon (*Diospyros virginiana* L.), oaks (*Quercus* spp.), and hickories (*Carya* spp.), were common in the understory and midstory.

Table 1. Summary of silvicultural practices (experimental and standard), timing of application, and purpose. Additional description is provided in the text.

Activity	Type	Month	Year	Purpose
Timber harvest	Study treatment (main plot)	January–July	2007	Reduce canopy density
Broadcast herbicide	Standard practice (site preparation)	September	2007	Reduce competition from hardwoods
Prescribed burn	Standard practice (site preparation)	November	2007	Reduce competition from hardwoods, aid planting, and maintain frequent fire regime
Plant seedlings	Standard practice (regeneration)	November–January	2007–2008	Establish longleaf pine seedlings
Herbicide release	Study treatment (split plot)	October	2008	Targeted control of hardwoods (release longleaf pine)
Herbicide release	Study treatment (split plot)	March	2009	Band application to control herbaceous competition (release longleaf pine)
Fertilization	Study treatment (split plot)	April	2009	Broadcast application of 10–10–10 at 280 kg·ha^{-1}
Prescribed burn	Standard practice (fire management)	January–April	2010	Maintain frequent fire regime

Note: The "Type" describes activity as either a study treatment (part of experimental design) or a standard management practice applied to all experimental units. Additional information on the treatment is provided parenthetically.

Experimental design and study treatments

The experiment used a randomized, complete block, split-plot design, with the location of individual loblolly pine stands as the block factor ($n = 6$). Given the number of management practices used in the study, including both experimental treatments and "standard" management practices applied to all experimental units, we summarize management activities in Table 1. Each block was divided into four main treatment plots and each main plot received an overstory treatment. Main plots were 100 m × 100 m (1 ha), with the exception of the Clearcut plots, which were 141 m × 141 m (2 ha) to create clearcut conditions in the plot center. The overstory treatments were designed to manipulate the density of canopy pines: Control (uncut; residual basal area ~16 m²·ha^{-1}); MedBA (harvesting to a target basal area of 9 m²·ha^{-1}); LowBA (harvesting to a target basal area of 5 m²·ha^{-1}); and Clearcut (all trees removed to basal area of 0 m²·ha^{-1}). The harvesting prescription removed small trees of poor form and left dominant, vigorous trees in the stand in summer 2007, using a modified cut-to-length system in which a feller buncher cut the trees, a processor topped and bucked the trees, and a forwarder transported the logs to the landing.

Following timber harvest, study sites were prepared in accordance with standard management procedures used for longleaf pine establishment at Fort Benning, with the objectives of reducing the abundance of woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 L·ha^{-1} imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid) mixed with 2.24 kg·ha^{-1} glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) that was applied in September 2007, followed by prescribed fire in November 2007. Study sites were planted with container-grown longleaf pine seedlings at 1.8 m × 3.7 m spacing, for a total of 1500 seedlings·ha^{-1}. Longleaf pine seedlings were grown from seed collected in Escambia County, Alabama, in 12.7 cm depth and 98.3 cm³ volume containers by the International Forest Co. (Moultrie, Georgia). Root collar diameter (RCD) averaged 7.9 mm (standard deviation, 1.9 mm) at the time of planting. Planting began in mid-November 2007 and was completed by January 2008. All study areas were burned with dormant season prescribed fires between the second and third growing seasons (January–April 2010), which were applied to all experimental units and were intended to be operational burns rather than study treatments (Table 1).

Split-plot treatments were additional cultural practices designed to improve growing conditions to favor planted longleaf pine seedlings. The split-plot treatments included an untreated control (NT), competition control with herbicide (H), and competition control with herbicide combined with fertilizer (H+F). Main-plot treatments were each divided into four equal sections, and three of the sections were each randomly assigned one split-plot treatment. Within each selected split plot, the cultural treatment was applied to a 30 m × 30 m area centered on a 20 m × 20 m measurement plot. The H treatment included an October 2008 application of 4.8 g acid equivalent·L^{-1} of imazapyr applied in a 1% solution with 0.25% non-ionic surfactant sprayed directly to the foliage of understory and mid-story woody vegetation. To achieve complete subcanopy vegetation control in the local growing environment for planted seedlings, we applied an additional granular mix of 63.2% hexazinone [3-cyclohexyl–6-(dimethylamino)-1-methyl–1,3, 5-triazine-2,4(1H,3H)-dione] and 11.8% sulfometuron methyl (Methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl] benzoate) at a rate of 0.84 kg·ha^{-1}, sprayed in approximately 1 m wide bands over longleaf pine seedlings in March 2009. The H+F treatment included the herbicide treatments described above, as well as an application of 280 kg·ha^{-1} 10–10–10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009, with care taken to distribute the fertilizer evenly throughout the split-plot treatment areas.

Data collection

Longleaf pine seedlings

In each split plot, we randomly selected 30 longleaf pine seedlings in 2008 and tagged them for repeated growth and survival measurements. We monitored seedling survival among the subsample of seedlings at the end of the first (October 2008), second (October 2009), and third (October 2010) growing seasons. At the time of survival surveys, we measured RCD of each seedling with digital calipers. Measurements were taken at two perpendicular directions to account for irregularity in root collar form, and the average of the two measurements was used for analyses. In each split plot, the seedling nearest to each corner and the seedling nearest to the center of the measurement unit (referred to hereafter as "target seedlings"; $n = 5$ per split plot) were selected as locations to quantify growing conditions for longleaf pine seedlings (vegetation abundance, light, foliar nutrient concentrations, soil water content, and soil temperature).

Abundance of canopy and understory vegetation

The abundance of canopy pine trees (≥10 cm diameter at breast height (DBH), 1.37 m) was quantified using two metrics: basal area (m²·ha^{-1}), the traditional metric to describe forest stand density, and the overstory abundance index (OAI), a unitless measure that integrates the distance and size of canopy trees surrounding target individuals into a distance-dependent measure of competition. Because OAI incorporates both the size and distance of the competing canopy trees, it has been reported to capture the competitive effects of canopy trees better than traditional density measures such as basal area (Pecot et al. 2007; Stoll et al. 1994). We calculated OAI with the following equation:

$$OAI = \sum_{i=0}^{n} \frac{A}{d}$$

where A = the cross-sectional area of tree$_i$ at 1.37 m height (cm^2) and d = the distance of tree$_i$ from the target seedling (cm). Trees closer than 1 m were given a value of d = 100 to limit excessive weight placed on trees in close proximity to target seedlings, and we measured all trees within a 15 m radius of each target seedling (Palik et al. 2003; Pecot et al. 2007). We also determined the basal area of trees within a 15 m radius of each target seedling.

We measured the abundance of understory vegetation (≤1 m tall) by recording vegetation cover in circular 1 m^2 sampling areas centered on each target seedling (n = 5 per split plot) in July 2009 and July 2010. Cover estimates were made as the percentage of the ground covered by vegetation biomass when viewed from directly overhead. We recorded cover by functional group (ferns, forbs, graminoids, woody shrubs and trees, and woody vines) using cover classes (1, trace; 2, 0%–1%; 3, 1%–2%; 4, 2%–5%; 5, 5%–10%; 6, 10%–25%; 7, 25%–50%; 8, 50%–75%; 9, 75%–95%; and 10, 95%–100%), and total cover for a sampling area could sum to greater than 100% if vegetation overlapped.

Light

In July–August 2009, we used hemispherical photographs to quantify the transmittance of light through the overstory. Within each split plot, we took hemispherical photographs directly above two of the target seedlings (the seedling located near the corner closest to main-plot center and the seedling located diagonally across the split plot). We mounted a Nikon Coolpix 4500 digital camera (Nikon Corporation, Tokyo, Japan) that was equipped with a 180° fisheye lens on a self-leveling mount at a height of 1.4 m above each selected seedling. The lens was adjusted to be level with the horizon, and an image of the canopy above each sampling point was captured. To prevent problems with sunflecks and glare, all hemispherical photographs were taken at dawn, dusk, or on uniformly cloudy days when the sun was not directly in the image.

We quantified the transmittance of light through the subcanopy vegetation by measuring photosynthetically active radiation (PAR) using an AccuPAR model LP-80 ceptometer (Decagon Devices, Inc., Pullman, Washington) in August 2010. At each target seedling per split plot (n = 5), we measured PAR at 15 cm above the ground, directly adjacent to each selected seedling, with care taken to avoid shade from the target seedlings. We recorded two PAR measurements at each seedling (PAR$_{below}$), with readings taken along perpendicular sides of each seedling. Immediately following seedling-level readings, we repeated PAR measurements above each target seedling to determine PAR above the subcanopy vegetation but below the canopy vegetation (PAR$_{above}$). Measurements were taken on uniformly cloudless days, and all measurements within a block were taken within a 3 hour period between 1100 and 1600 to reduce variability from the diurnal pattern of the sun.

Soil moisture and temperature

We measured soil moisture and soil temperature adjacent to each seedling in each split plot in May and September 2009 and in June, July, and August 2010. Volumetric soil moisture was measured in the upper 6 cm of the soil using a ML2 ThetaProbe moisture meter (Delta-T Devices, Ltd., Cambridge, England). The ThetaProbe generates a 100 MHz signal between stainless steel rods extended into the soil, and the impedance of the signal between the rods is related to the water content of the soil. We took readings of soil moisture directly east and directly west of each target seedling. Soil temperature was taken at a depth of 10 cm using a digital thermometer. All soil moisture and temperature measurements within a single block were taken within 3 h to minimize the effects of diurnal fluctuations in weather or site

conditions, and no measurements were taken within 24 h of a precipitation event.

Longleaf pine foliar nutrients

To quantify the concentration of foliar nutrients in longleaf pine seedlings, we collected three fascicles of needles from each of the five target seedlings per split plot following the 2009 and 2010 growing seasons. Foliar samples were collected between November and February, because nutrient levels are the most stable during the dormant season (van den Driessche 1974). Foliar samples were composited for each split plot, placed into paper bags, and stored in a cooler until they were processed in the lab. On return to the laboratory, foliar samples were oven-dried at 70 °C to a constant mass and analyzed for concentrations of N, P, and K by the Agricultural Services Laboratory at Clemson University. Foliar N was determined using LECO FP–528 Nitrogen Combustion Analyzer (LECO Corporation, St. Joseph, Michigan) and P and K concentrations were determined using a Jobin Yvon Contained Inductively Coupled Plasma Emission Spectrometer (ICP-ES, Horiba Ltd., Edison, New Jersey).

Data analysis

We used HemiView version 2.1 Canopy Analysis Software (Delta-T Devices, Ltd.) to calculate light availability in each hemispherical photograph. HemiView uses the longitude and latitude for the study site to determine the diurnal and annual sunpath in each image. A user-defined threshold of light intensity classifies each pixel as open sky or obstructed sky, allowing HemiView to calculate gap fraction and the diffuse and direct solar radiation that reaches the photograph location. For each image, we then calculated the gap light index (GLI) as a representation of the percentage of incident PAR transmitted through the canopy to a point in the understory during the course of a growing season (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 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). We used the PAR values measured with the ceptometer to calculate the transmittance of light through the subcanopy vegetation at each sampling position, using the following equation:

$$SCT = \left(\frac{PAR_{below}}{PAR_{above}}\right)100$$

where SCT = subcanopy transmittance, PAR$_{below}$ = mean of PAR measurements at 15 cm above the ground, and PAR$_{above}$ = mean of PAR measurements above the subcanopy vegetation. To integrate the effects of canopy and subcanopy vegetation on light transmittance to the forest floor, we multiplied the calculated canopy light transmittance (GLI) by the calculated SCT as a measure of total light transmittance (TLT) at the seedling level.

We calculated the annual mortality rate of longleaf pine seedlings for each split-plot and split-plot level mean values of longleaf pine seedling growth response (RCD and annual RCD increment), overstory competition (OAI and basal area), understory vegetation cover, light availability (GLI, SCT, and TLT), soil moisture, soil temperature, and longleaf pine seedling foliar nutrients (N, P, K) for each measurement year. We used split-plot analysis of variance (ANOVA) with a random block effect to test for effects of canopy density and cultural treatments on the abundance of competition and plant resources. In the case of a significant treatment effect, we evaluated pair-wise comparisons using Tukey's honest

Table 2. Treatment effects on canopy and subcanopy competition measures.

| | Basal area (m²·ha⁻¹) | | OAI | | Understory cover (%) | | | |
| | | | | | 2009 | | 2010 | |
Level	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Main-plot treatment								
Control	17.50a	0.67	16.39a	0.81	20.89b	3.60	34.16c	3.83
MedBA	10.06b	0.76	9.13b	0.63	36.03a	1.30	52.45b	5.71
LowBA	5.51c	0.76	5.22c	0.64	38.22a	5.75	59.67ab	5.95
Clearcut	0.00d	0.00	0.00d	0.00	49.42a	4.90	62.43a	2.45
p value	<0.0001		<0.0001		0.0003		<0.0001	
Split-plot treatment								
NT	8.25	0.49	7.72	0.42	44.54a	2.23	52.34	4.48
H	8.48	0.80	8.02	0.71	27.53b	2.26	49.66	4.57
H+F	8.08	0.36	7.32	0.39	36.35a	4.45	54.22	4.83
p value	0.8453		0.7621		<0.0001		0.5385	

Note: The same lowercase letter within a treatment effect indicates no significant difference at $\alpha = 0.05$. OAI, overstory abundance index; SE, one standard error of the mean.

significant difference (HSD) test. To meet assumptions of constant variance and normality, the OAI and understory vegetation cover data were transformed by taking the square root of the original data; other variables required no transformation. All results are presented using untransformed data. We conducted ANOVAs for each year separately to maintain consistency for response variables (GLI, OAI, SCT, and TLT were measured in only 1 year) and due to different months of sampling between years for soil moisture and soil temperature. Analyses were conducted using PROC MIXED in SAS statistical software (SAS Institute, Inc., Cary, North Carolina).

For data from each year, we used Pearson's correlation analysis to determine correlations between the split-plot level means for seedling response variables (annual RCD increment and annual mortality rate) and the measures of competition (overstory basal area and understory vegetation cover), measures of resource availability (GLI, SCT, TLT, soil moisture, and foliar concentrations of N, P, and K), and soil temperature. Correlations with SCT and TLT were reported in only 2010 because SCT was measured in only 2010. We assumed that the overstory basal area and GLI measured in 2008 did not change over the course of the study. Otherwise, each correlation included data from only the growing season for which was reported; for example, soil moisture measured in 2009 was correlated with annual mortality from 2009. Scatterplots and linear or nonlinear regression analyses were used to further explore relationships among variables of interest. For all analyses, we used $\alpha = 0.05$ to determine statistical significance.

Results

Canopy and understory vegetation

The main-plot treatments applied in this study resulted in significantly different levels of residual basal area and OAI, but canopy abundance was not affected by the split-plot treatments (Table 2). Although previous research suggests that OAI is a better metric for describing overstory competition than basal area, we found that basal area explained 98% of the variation in OAI in a nearly one-to-one, linear relationship. Therefore, we present only basal area for the remaining results of this study, because basal area is commonly used and widely understood by forest managers. The abundance of understory vegetation was significantly affected by the harvesting treatments in 2009 and 2010, and total cover surrounding target seedlings was significantly greater on plots that had been cut than on the Control plots (Table 2). The split-plot treatments also significantly affected understory vegetation cover in 2009, with significantly less cover on H than on the NT or H+F split plots. There was no effect of the split-plot treatments on the vegetation cover surrounding seedlings in 2010.

Light

GLI and SCT were significantly affected by canopy density but displayed inverse patterns in response to canopy removal (Fig. 1A). GLI increased with canopy removal, from less than 40% on Control plots to almost 100% on Clearcut plots, and the percentage of PAR penetrating the subcanopy vegetation decreased from 85% on the Control plots to 63% on the Clearcut plots. We calculated TLT as an integrated measure of canopy and SCT and found that TLT increased with harvesting intensity but was moderated by the increase in subcanopy vegetation following release by canopy removal. We found no effects of split-plot treatments on GLI, SCT, or TLT (Fig. 1B). Canopy transmittance was strongly related to stand basal area, and a negative exponential relationship accounted for 95% of the variability in GLI (Fig. 2A). The understory vegetation cover explained 60% of the variability in SCT, and less than 50% SCT was found only on plots with greater than 60% vegetation cover (Fig. 2B).
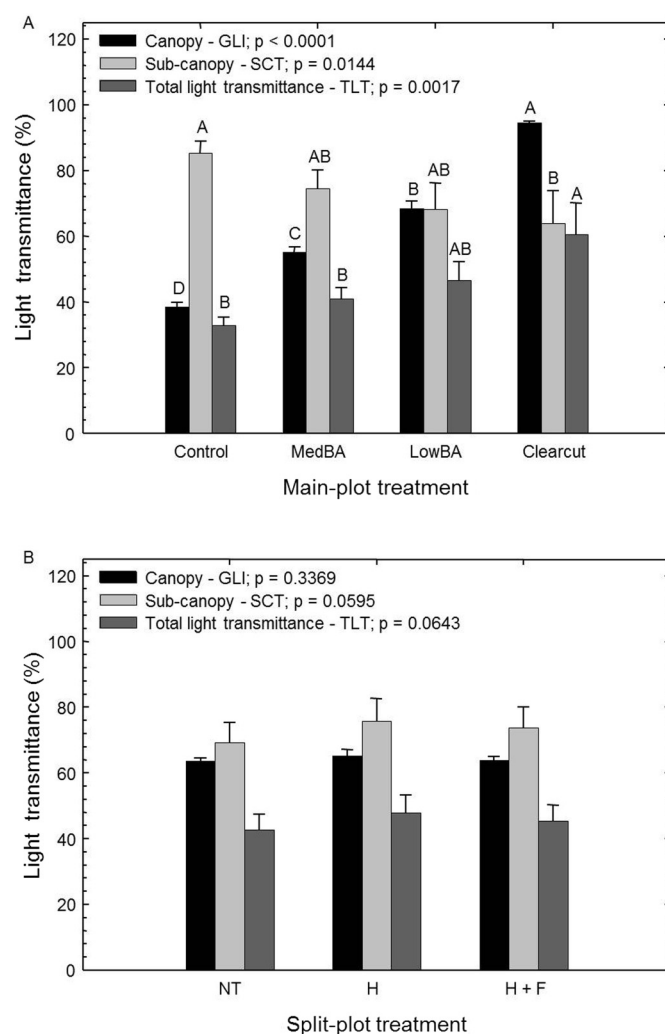
Soil moisture and soil temperature

We found no interactions between main-plot and split-plot treatments for soil moisture in 2009 ($p = 0.5418$) or 2010 ($p = 0.9575$) or for soil temperature in 2009 ($p = 0.5677$) or 2010 ($p = 0.2908$). Neither main-plot nor split-plot treatments significantly affected soil moisture in either year, despite patterns of increasing soil moisture with increasing basal area in each year (Table 3). Mean soil moisture across study plots was 15.6% in 2009 and 6.1% in 2010. Soil temperature was significantly affected by canopy density in both years, with soil temperature highest on Clearcut plots and generally lowest on Control plots (Table 3). The split-plot treatments significantly affected soil temperature only in 2009, when the NT plots had lower soil temperatures than the H and H+F plots.

Longleaf pine seedling foliar nutrients

There were no significant interactions between the main-plot and split-plot treatments for N, P, or K in either 2009 or 2010 ($p \geq 0.1226$). In both years, foliar N was significantly greater in Clearcut plots when compared with the treatments with residual canopy density (Fig. 3A). In 2009, the Control plots had the lowest foliar N concentration, but Control plots were not different from the MedBA and LowBA plots in 2010. Although P concentrations were not significantly affected by canopy density in 2009, Clearcut plots had the greatest P concentration in 2010, and canopy treatments with residual pines had similar levels of P (Fig. 3C). Foliar K was greater on the Clearcut plots than on the Control plots in 2009, but the differences were no longer significant in 2010 (Fig. 3E). The split-plot treatments only affected foliar nutrients in 2009. Foliar N was greater on the H and H+F plots than on the

Fig. 1. Transmittance of light (mean + one SE) through the canopy (gap light index, GLI), through the subcanopy (SCT), and total light transmittance (TLT) to the forest floor by (A) main-plot treatment and (B) split-plot treatment. The same letter within a light variable indicates no significant difference at $\alpha = 0.05$.
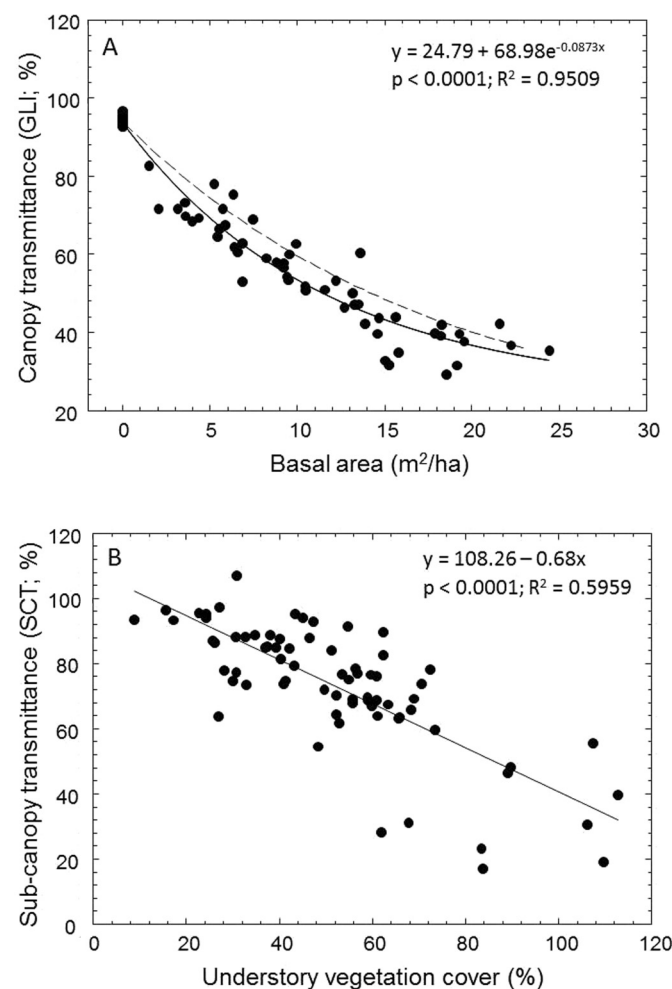

Fig. 2. Scatterplots and relationships between (A) overstory basal area ($m^2 \cdot ha^{-1}$) and canopy light transmittance (gap light index, GLI; %) and (B) understory vegetation cover (%) and subcanopy light transmittance (photosynthetically active radiation, PAR; %). The dashed line in panel A is the relationship (GLI = 14.011 + $e^{(-0.056x)}$; $R^2 = 0.973$; $p < 0.0001$) between overstory basal area and GLI in loblolly pine forests in North Carolina (Hu et al. 2012a).

untreated NT plots, but there was no difference between the H and H+F plots (Fig. 3B). The H+F plots had greater levels of foliar P than the NT plots, and foliar P on the H plots was not different from either NT or H+F plots (Fig. 3D). There were no effects of the split-plot treatments on foliar concentrations of K.

Relationships between growing conditions and longleaf pine seedling response

Overstory basal area exerted a strong influence on the RCD of longleaf pine seedlings at the end of the first, second, and third growing seasons, with the relationship becoming stronger through time (Fig. 4). After one growing season, the range in RCD was small, and the basal area of canopy trees accounted for 33% of the observed variability in the RCD. By the end of the third growing season, seedling RCD had increased at low basal areas but remained low at high basal areas. A negative, exponential relationship with overstory basal area accounted for 62% of the variability in RCD at the end of 2009 and 2010. Root collar diameters in Clearcut plots (overstory basal area = 0 $m^2 \cdot ha^{-1}$) ranged from 14.4 to 30.0 mm at the end of the third growing season, suggesting that additional factors were affecting seedling growth following canopy removal. Generally, the Clearcut plots treated with herbicides

tended to have greater RCD (23.1 mm) than those that were not treated with herbicide (20.5 mm), but the difference was not found to be significant in a t test ($p = 0.2867$).

The annual mortality rates in 2009 and in 2010 were not strongly correlated (all r values between –0.5 and 0.5) with any of the measures of plant resources or growing conditions (Table 4). In 2009, the only two significant correlations were with foliar P and the cover of surrounding vegetation. In 2010, significant correlations were with SCT, TLT, understory vegetation cover, soil moisture, soil temperature, and the foliar concentration of P.

Root collar diameter increments in 2009 and 2010 were most strongly correlated with overstory basal area and GLI, as well as TLT and soil temperature in 2010 only. The correlation with overstory basal area was negative in both years, and the correlations with GLI and TLT were positive. A positive, exponential relationship with GLI explained 22.6% of the variability in incremental RCD in 2010 (Fig. 5A). Incorporating SCT into the TLT variable improved the relationship and accounted for 32.4% of the variability in RCD increment (Fig. 5B). In 2009, RCD increment was also positively correlated with the cover of surrounding understory vegetation and the concentrations of foliar N and K and negatively correlated with soil moisture (Table 4).

Table 3. Treatment effects on soil moisture and soil temperature in 2009 and 2010.

| | 2009 | | | | 2010 | | | |
| | Soil moisture (m³·m⁻³) | | Temperature (°C) | | Soil moisture (m³·m⁻³) | | Temperature (°C) | |
Level	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Main-plot treatment								
Control	17.84	1.84	24.26b	1.55	7.08	1.42	31.16b	0.41
MedBA	16.47	3.00	24.56ab	1.50	6.89	1.75	31.87ab	0.55
LowBA	14.10	2.85	25.81a	1.69	5.93	1.83	31.85b	0.45
Clearcut	14.01	2.67	25.62a	1.28	4.65	1.69	33.85a	0.81
p value	0.0810		0.0078		0.3867		0.0056	
Split-plot treatment								
NT	15.28	2.59	24.76b	1.44	6.20	1.59	31.98	0.33
H	16.40	2.49	25.28a	1.52	6.01	1.55	32.42	0.49
H+F	15.14	2.32	25.15a	1.53	5.49	1.35	32.28	0.50
p value	0.2452		0.0053		0.4982		0.1674	

Note: Values followed by the same lowercase letter indicate no significant difference within a treatment and for each response variable at $\alpha = 0.05$. SE, one standard error of the mean.

Fig. 3. Main-plot and split-plot treatment effects (mean + one SE) on concentrations (%) of (A and B) foliar nitrogen, (C and D) foliar phosphorus, and (E and F) foliar potassium in 2009 and 2010. The same letter indicates no significant difference within a year at $\alpha = 0.05$.
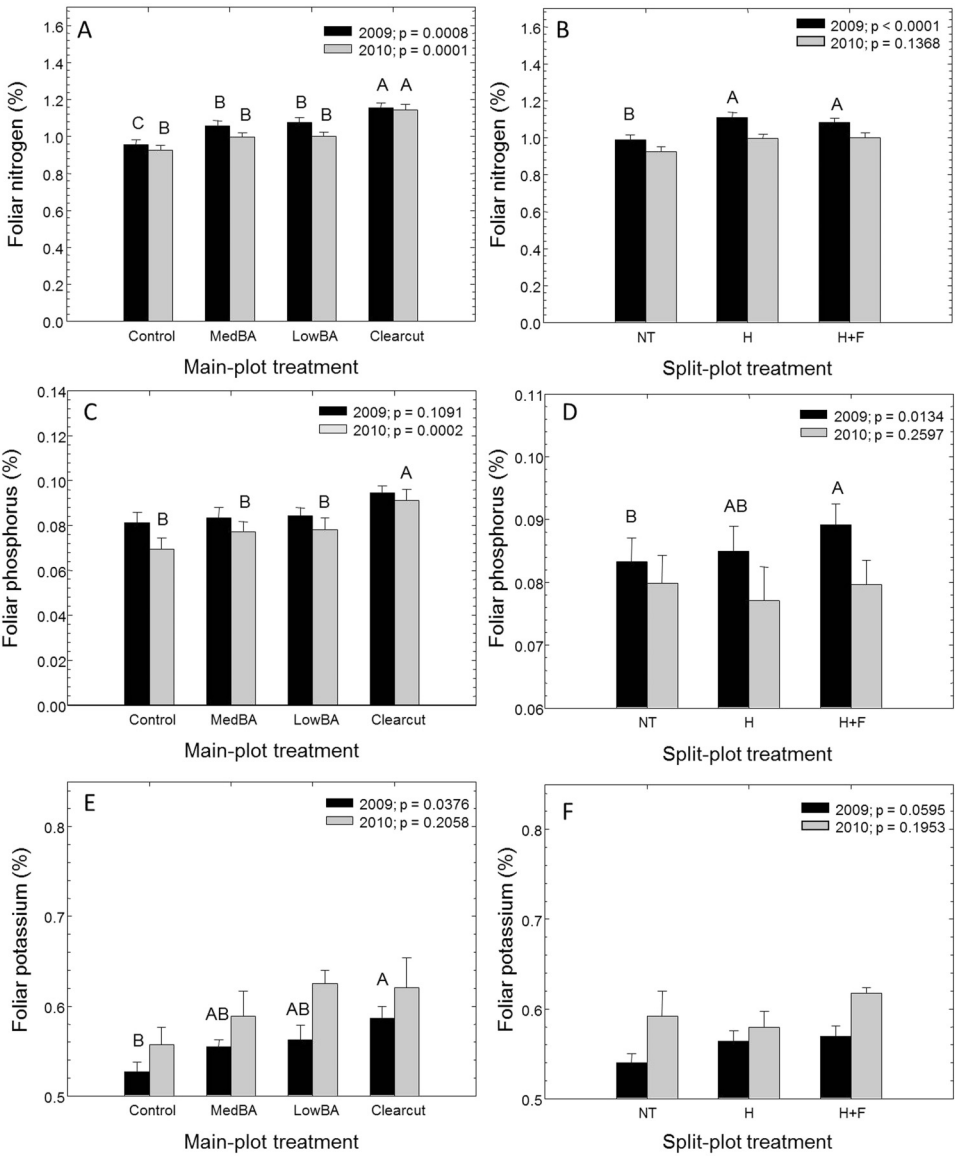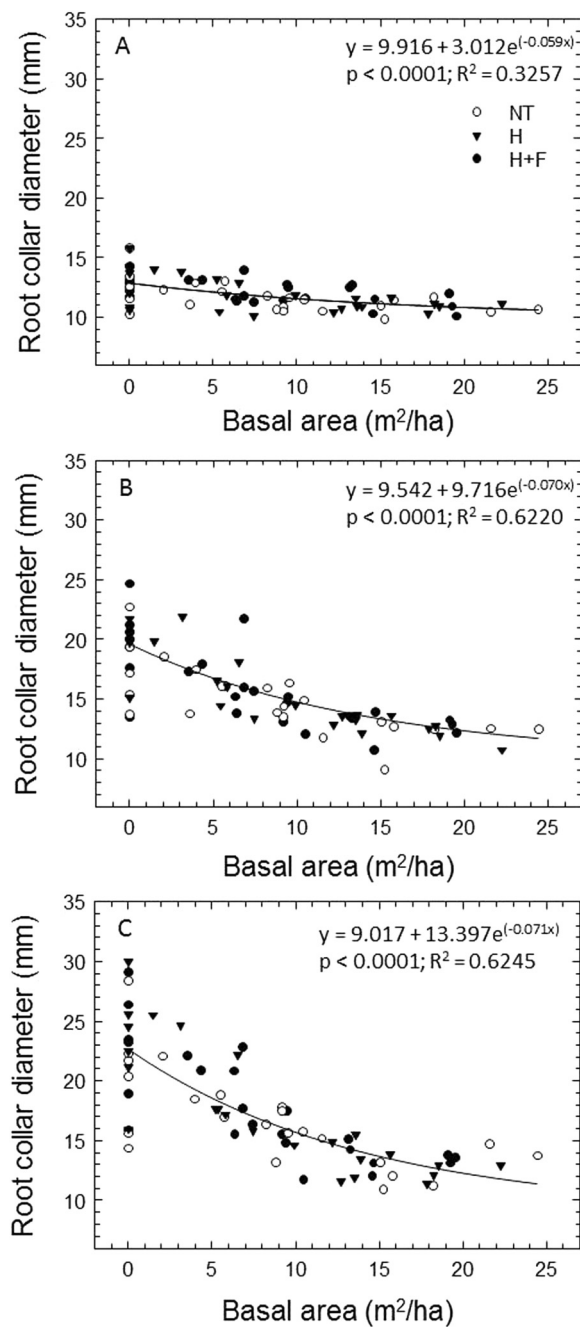
Fig. 4. Relationships between the root collar diameter of longleaf pine seedlings and the basal area of overstory trees at the end of (A) 2008, (B) 2009, and (C) 2010. Open points represent plots that were not treated with herbicide; filled points represent plots that were treated with herbicide.

Table 4. Correlations between longleaf pine seedling response and growing conditions.

Independent variable	Annual mortality		Annual RCD increment	
	2009	2010	2009	2010
Overstory basal area (m²·ha⁻¹)				
r value	−0.119	0.218	−0.741	−0.469
p value	0.3180	0.0682	<0.0001	<0.0001
Understory vegetation (% cover)				
r value	0.316	0.337	0.273	0.176
p value	0.0069	0.0041	0.0203	0.1423
GLI (%)				
r value	0.064	−0.195	0.755	0.457
p value	0.5985	0.1055	<0.0001	<0.0001
SCT (%)				
r value	—	−0.331	—	−0.051
p value	—	0.0048	—	0.6746
TLT (%)				
r value	—	−0.434	—	0.476
p value	—	0.0002	—	<0.0001
Soil moisture (m³·m⁻³)				
r value	−0.206	0.260	−0.433	−0.027
p value	0.1139	0.032	0.0006	0.8297
Soil temperature (°C)				
r value	0.169	−0.287	−0.084	0.499
p value	0.1958	0.0195	0.5226	<0.0001
Foliar N (%)				
r value	0.149	0.163	0.382	0.132
p value	0.2119	0.1752	0.0009	0.2736
Foliar P (%)				
r value	0.349	0.275	0.134	0.125
p value	0.0027	0.0205	0.2627	0.2975
Foliar K (%)				
r value	0.221	0.009	0.411	0.198
p value	0.0626	0.9399	0.0003	0.0977

Note: Pearson's correlations (*r* values and *p* values) between dependent variables (annual mortality and annual root collar diameter (RCD) increment in 2009 and 2010) and independent variables that describe growing conditions and plant resources. GLI, gap light index; SCT, subcanopy transmittance; TCT, total light transmittance.

2003). Our study found that OAI and basal area, when calculated for the same competition neighborhood of 15 m radius, did not differ from each other in uniformly spaced, even-aged loblolly pine stands. These findings suggest that incorporating tree size and distance from the sampling point into the OAI measurement may be more useful for describing competition from canopy trees in stands with heterogeneous structure, but basal area is an adequate measure of canopy competition in even-aged loblolly pine stands with more uniformly distributed trees.

The effects of canopy trees on the availability of plant resources and growing conditions in the understory are dependent on canopy density and on species-specific morphological and physiological characteristics of the canopy trees. For example, crown structure, leaf angle, and crown shape influence the transmission of light through a pine forest canopy (Stenberg et al. 1994). The generally open-canopied structure of many pine species results in relatively high levels of light penetration in pine forests compared with other closed-canopy forest systems (e.g., Canham et al. 1990). Longleaf pine forests are commonly characterized by relatively open canopies and high levels of light transmittance (Battaglia et al. 2003). Canopy closure in second-growth longleaf pine stands can be around 50% (Palik and Pederson 1996), and it was reported that light transmittance was greater than 25% beneath closed canopies in longleaf pine forest in southwestern Georgia (Palik et al. 1997). Our results and those of a previous study (Hu et al. 2012a) suggest that the relationships between mature, second-growth loblolly pine canopy density and canopy light transmittance are

Discussion

Treatment effects on competitive conditions and the availability of plant resources

The OAI has been used in longleaf pine forests (Battaglia et al. 2003; Palik et al. 2003; Pecot et al. 2007) and other forest types (Stoll et al. 1994) to quantify the level of competition of canopy trees to a given point in the understory. In naturally regenerated longleaf pine stands in southwestern Georgia, it was found that stand-level OAI was lowest following large aggregate retention harvesting and greatest following single-tree selection, despite similar stand-level basal areas among the treatments (Palik et al.

Fig. 5. Relationships between the 2009–2010 incremental root collar diameter and (A) canopy transmittance (gap light index, GLI; %) and (B) total light transmittance (TLT; %).

A $y = -7.910 + 6.739e^{(0.047x)}$
$p = 0.0002; R^2 = 0.2263$

B $y = 0.541 + 0.020e^{(0.063x)}$
$p < 0.0001; R^2 = 0.3240$
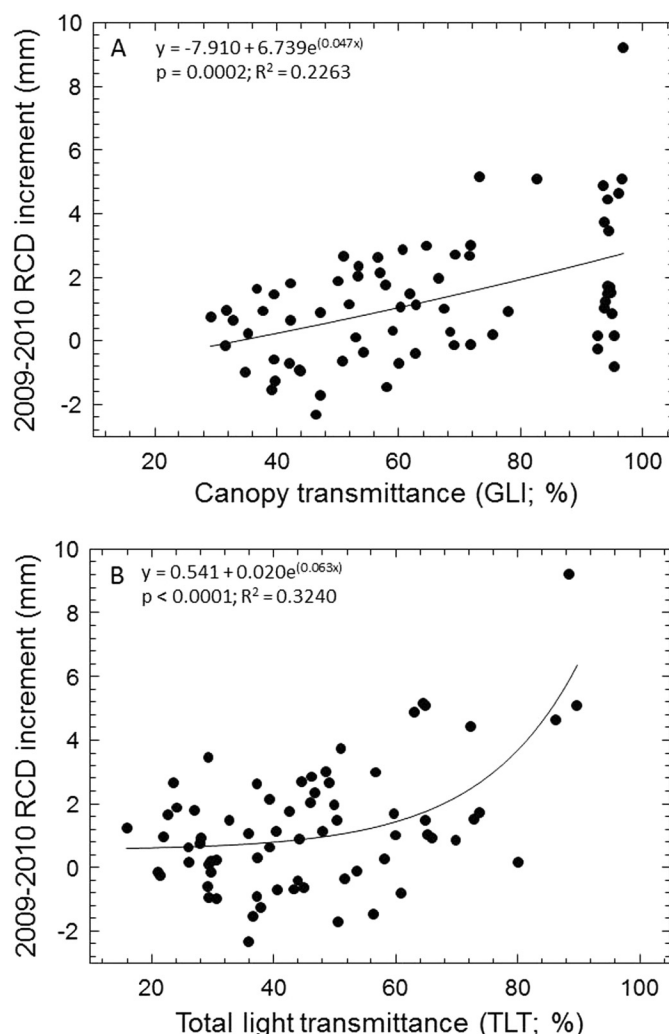
similar to those in second-growth longleaf pine stands. Previously, a negative, exponential relationship between overstory basal area and light availability (measured as GLI; $R^2 = 0.71$) was reported in longleaf pine forests, with a range from around 30% light availability at a basal area of 25 m²·ha⁻¹ to around 80% light availability at basal area <5 m²·ha⁻¹ (Palik et al. 1997). Similar relationships were also reported between canopy transmittance and OAI in longleaf pine forests (Battaglia et al. 2003; Pecot et al. 2007). Comparing the relationships between overstory basal area and GLI previously reported in loblolly pine stands (Hu et al. 2012a) with our results (Fig. 2) indicates that the overstory density of loblolly pine forests affects canopy light transmittance in similar ways in two ecologically distinct regions in the southeastern United States.

Reducing the density of canopy trees not only increases light availability for planted longleaf pine seedlings, but also increases resource availability for other subcanopy vegetation, often resulting in greater abundance of subcanopy vegetation following canopy removal (Grelen and Enghardt 1973). The interactions of canopy and subcanopy vegetation abundance regulate the net availability of resources for understory plants. Our results indicate that the greater abundance of understory vegetation on Clearcut plots may intercept nearly 40% of the available sunlight before it reaches the forest floor, and a previous study demonstrated that competition for light following canopy removal could

limit longleaf pine seedling growth (Knapp et al. 2008). However, effects of subcanopy vegetation on the availability of light at the forest floor are dependent on the type of vegetation present and are temporally dynamic. Woody vegetation that puts on secondary growth and increases in stature each year has the potential to reduce light levels through time. As a result, the presence of woody subcanopy species can shade out low growing species that require high light levels (Brockway and Lewis 1997; Harrington and Edwards 1999). In contrast, herbaceous vegetation generally follows annual cycles of growth and dieback, with less potential for the interception of light to increase through time. Thus, the role of canopy trees in controlling light levels at the forest floor could be modified by the type and abundance of vegetation in the subcanopy strata.

Canopy tree removal affects soil moisture through two primary processes: (i) reducing soil moisture through drying of the soil following increased exposure to solar radiation (Londo et al. 1999; Moroni et al. 2007; Redding et al. 2003), and (ii) increasing soil moisture in the absence of uptake and transpiration by canopy trees (Aussenac and Granier 1988; Bréda et al. 1995; Elliott et al. 1998). Understory plants quickly fill root gaps created by canopy tree removal (Jones et al. 2003) and provide an additional source of uptake of soil moisture. The distribution of root systems of understory plants within the soil profile varies by functional group; root systems of herbaceous plants are commonly concentrated at the soil surface, but woody plants are able to develop root systems deeper in the soil profile (Walter 1971). Consequently, the dynamics of overstory–understory interactions with soil moisture vary according to vegetation type and location within the soil profile (Pecot et al. 2007). Similar to the results from loblolly pine stands in North Carolina (Hu et al. 2012a), we found no effect of canopy density on soil moisture at a depth of 6 cm, where competition with herbaceous vegetation is expected to be high. However, we observed a slight, nonsignificant pattern of greater soil moisture at greater canopy densities in both years. This pattern was coincident with lower soil temperatures in plots with greater canopy densities, suggesting that the shade of canopy pines may slightly moderate soil heating and alter evaporative drying of the soil surface. We also found no effect of herbicide release on soil moisture, suggesting that competition from subcanopy vegetation did not strongly affect soil moisture on these sites.

Our results demonstrate that competition with canopy trees can result in reduced concentrations of foliar N, P, and K of longleaf pine seedlings. It is likely that competition from subcanopy vegetation also reduced foliar concentrations of N, because the herbicide release treatment had greater foliar N than the NT treatment in 2009. Previous studies have shown that overstory density is negatively related to the availability of N in the soil in the absence of understory vegetation in longleaf pine forests (Palik et al. 1997; Pecot et al. 2007) and that the presence of understory vegetation reduces N availability regardless of overstory density (Pecot et al. 2007). In contrast to our study, Haywood (2007) found that releasing longleaf pine seedlings from competing vegetation did not significantly increase foliar N concentrations after six growing seasons in Louisiana. In addition, it was reported that loblolly pine canopy density had no effect on foliar concentrations of N or K in planted longleaf pine seedlings (Hu et al. 2012a), suggesting that site-specific factors also contribute to the availability and utilization of soil resources.

Critical thresholds, or sufficiency levels, are often used with foliar nutrient analyses as a means to assess the nutritional status of trees (Blevins et al. 1996). For longleaf pine, foliar sufficiency levels for N, P, and K have been reported to be 0.95%, 0.08%, and 0.30%, respectively (Blevins et al. 1996). According to these standards, retaining high levels of overstory density in loblolly pine stands will likely result in nutrient deficiencies of N and P for planted longleaf pine seedlings on sites similar to those used in this study. However, our results suggest that fertilization, at the

rate used in this this study, does not improve the nutritional status of longleaf pine seedlings planted on sites similar to those used in this study.

Longleaf pine seedling response to resource availability and growing conditions

In longleaf pine forests, the relationship between seedling size and canopy density has been described by a negative, exponential function in which seedling size is strongly reduced by canopy densities greater than 6 m²·ha⁻¹ (Palik et al. 1997). Furthermore, the temporal patterns of longleaf pine regeneration in second-growth longleaf pine stands fit into a three-stage model of canopy density thresholds (Kirkman and Mitchell 2006; Mitchell et al. 2006). At high canopy densities (basal area ~17 m²·ha⁻¹) seedling establishment may occur, but survival through 5 years is not expected and regeneration is inhibited. Seedling are able to persist with moderate growth beneath stands with basal areas between 8 and 17 m²·ha⁻¹; however, grass stage emergence and subsequent height growth accelerates when basal area is less than ~8 m²·ha⁻¹ (Mitchell et al. 2006). Our results generally support this model for longleaf pine seedling establishment in loblolly pine stands. Although we found that survival through three growing seasons remained relatively high for seedlings beneath comparatively dense canopies (Knapp et al. 2013), it is not clear how long seedlings will persist with limited growth. Similar to the results from longleaf pine forests, we observed moderate increases in seedling growth between loblolly pine canopy basal areas of around 7 to 14 m²·ha⁻¹, with accelerated seedling growth with less than 7 m²·ha⁻¹ basal area.

Previous studies have discussed the importance of belowground resources in regulating longleaf pine seedling establishment (e.g., Brockway and Outcalt 1998), and soil N has generally been found to be more closely related to longleaf pine seedling growth than soil moisture in field studies (McGuire et al. 2001; Palik et al. 1997). We found no evidence that soil water availability limited the growth of longleaf pine seedlings in our study; in fact, we observed a negative correlation between soil moisture and incremental seedling size that was significant in 2009. A study over the same time period in North Carolina reported negative, exponential relationships between soil moisture and seedling growth that explained 41% and 9% of the variation in longleaf pine incremental RCD in 2009 and 2010, respectively (Hu et al. 2012a). Similarly, longleaf pine seedling size was negatively related to soil moisture after two growing seasons on wet flatwoods sites in North Carolina, where volumetric soil moisture ranged from around 10% to 40% (Knapp et al. 2008). Our sites were considerably drier, ranging from 5% to 25% moisture by volume, suggesting that soil moisture is not the primary limitation to longleaf pine seedling growth across a range of site conditions.

In contrast to soil moisture, we found that foliar concentrations of N and K in 2009 were positively correlated to RCD increment, and each accounted for around 15% of the variability in growth during that year. Although fertilization had an apparent effect on foliar P concentration in 2009, the concentration of P was not significantly correlated with seedling growth in either year. Contrary to our results, foliar P was significantly related to incremental RCD of longleaf pine seedlings planted in loblolly pine stands in North Carolina (Hu et al. 2012a), suggesting that site-specific nutrient deficiencies may result in different patterns of seedling growth on different sites. However, relationships between foliar nutrient concentration and tree growth may be confounded by dilution effects associated with foliar biomass, such that foliar nutrient content may be more strongly related to growth than foliar nutrient concentrations (Barron-Gafford et al. 2003).

Conclusion

Recent studies on silvicultural techniques that include canopy retention during longleaf pine restoration suggest that group se-

lection or single-tree selection may be appropriate for seedling establishment in longleaf pine forests (McGuire et al. 2001; Mitchell et al. 2006; Palik et al. 2002; Pecot et al. 2007) and during conversion of stands dominated by other southern pines (Hu et al. 2012b; Kirkman et al. 2007). Developing silvicultural protocols for restoration in loblolly pine stands requires an understanding of how stand conditions and resource availability affect longleaf pine seedling response, and we found that relationships between seedling size and overstory density in loblolly pine forests were largely similar to those previously reported in longleaf pine forests. Successful longleaf pine seedling establishment is an important component of longleaf pine restoration, but maintaining a frequent prescribed burning program is critical to sustaining the ecosystem through time. Our study incorporated prescribed burning as a site preparation practice and after two growing seasons, as a standard management practice, across all treatments. Although we were unable to determine effects of prescribed burning on resource availability or seedling response from an experimental approach, it is important that silvicultural practices used for seedling establishment are compatible with prescribed burning (Kirkman et al. 2007; Knapp et al. 2011).

This study was designed to complement a similar experiment established in the Coastal Plain of North Carolina (Hu et al. 2012a, 2012b), and comparing results from these studies provides a unique opportunity to determine if responses may be generalized across sites. We found that the effects of canopy density on canopy light transmittance and soil moisture were similar, but our study reported effects of canopy density on longleaf pine seedling foliar N and K that were not previously detected (Hu et al. 2012a). Differences between these studies suggests the importance of considering site-specific factors but may also be related to differences in the "standard" management practices (e.g., site preparation and postplanting prescribed burning) between the studies. We acknowledge that the site preparation treatments used in our study (herbicide and fire), as well as the subsequent prescribed burn following two growing seasons, may have interacted with the study treatments to affect observed results. Additional research is warranted to determine how interactions between site quality and additional management practices may influence responses to canopy removal or herbicide release across sites throughout the longleaf pine range.

Given the interactions among vegetation structure, resource availability, and plant responses (e.g., Tilman 1985), it is often difficult to isolate the effects of specific resources on seedling growth or survival under field conditions. In a greenhouse experiment, interactions among resource limitations were found to affect longleaf pine seedling growth in dynamic ways; for example, increased light availability resulted in greater seedling growth only when soil moisture was not limiting (Jose et al. 2003). Despite the inherent challenges to determining the effects of specific resources on longleaf pine seedlings in the field, our results indicate that the availability of light most strongly limits longleaf pine seedling growth in loblolly pine stands. The N and P limitations affected seedling growth to a lesser degree, but we found no evidence that soil moisture limited seedling growth. Establishing longleaf pine seedlings in loblolly pine stands can be best accomplished by reducing canopy density to ≤7 m²·ha⁻¹, although complete canopy removal may require additional treatments to control rapid growth of subcanopy vegetation and allow for frequent fire management.

Acknowledgements

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