EARLY IMPACTS OF MIDSTORY HARDWOODS AND OVERSTORY DENSITY ON LONGLEAF PINE SEEDLING ESTABLISHMENT ON XERIC SITES

Jacob Henry, John L. Willis, David K. Schnake, Scott D. Roberts, Heather D. Alexander, and Heidi Renninger

Abstract—Competition has long been considered a constraint on longleaf pine (*Pinus palustris* Mill.) regeneration. However, observational evidence suggests that neighboring vegetation may facilitate longleaf pine seedlings on xeric sites. To explore this notion, we established a manipulative experiment across a gradient of overstory basal area (9 to 25 m^2/ha) with or without a hardwood midstory in the North Carolina Sandhills. After 2 years, seedling survival averaged 80 percent, differed significantly among overstory density groupings (p = 0.0006), and was lowest (73 percent) under high overstory density (greater than 18 m^2/ha). Seedling survival also varied significantly among midstory treatments (p = 0.0261), with the highest survival occurring beneath an intact midstory (84 percent). Seedling biomass averaged 10.5 g, varied significantly among overstory groupings (p = 0.0007), and was greatest (10.9 g) under low overstory density (less than 12 m^2/ha). The presence of a hardwood midstory did not significantly impact seedling growth.

INTRODUCTION

Decades of silvicultural research have highlighted competition as a contributing factor to longleaf pine (*Pinus palustris* Mill.) regeneration failures. Multiple studies have demonstrated that grass stage longleaf pine seedlings compete poorly for resources with established mature trees, midstory hardwoods, and herbaceous vegetation (Brockway and others 1998, McGuire and others 2001, Pecot and others 2007). Consequently, natural regeneration prescriptions for longleaf pine typically involve reducing overstory density through harvesting and applying low-intensity prescribed fire or herbicides to control understory competition prior to seed fall (Kush and others 2004, Menges and Gordon 2010). Collectively, these treatments are thought to provide longleaf pine with the optimal high resource environment needed to expedite development out of the grass stage.

In some situations, however, longleaf pine regeneration must be accomplished within the structure of additional natural resource objectives, thus preventing the use of established silvicultural techniques. For example, managing mature longleaf pine stands for red-cockaded woodpecker (*Picoides borealis* Viellot) (RCW) habitat has become a common natural resource objective (Walters 1991). RCW is an endangered bird found in the longleaf pine ecosystem that prefers large diameter trees for cavities (Rudolph and Conner 1991) and extensive longleaf forests for foraging (Henry 1989). When managing for RCW, overstory trees are maintained at a target density of 12 to 18 m^2/ha to provide sufficient cavity trees and the open canopy that is preferred by RCW (U.S. Fish and Wildlife Service 2003). This target density is, however, a potential impediment to longleaf pine seedling development (Croker and Boyer 1975).

Following the traditional model of longleaf regeneration also may not be appropriate for all sites. Many of the studies documenting the effects of intense understory competition on longleaf pine seedlings have been conducted on mesic sites, where resource competition is magnified. In contrast, on more xeric sites, seedling persistence under stressful growing conditions may be more important than resource competition. Moreover, on xeric sites, neighboring vegetation may facilitate longleaf pine seedling development by providing partial shade (Allen 1954) or redistributing water in the upper soil profile (Espeleta and Donovan 2002). Evidence of facilitative effects of competing vegetation on longleaf pine seedlings on xeric sites has been accumulating

Author information: Jacob Henry, Graduate Student, Department of Forestry, Mississippi State University, Mississippi State, MS 39762; John L. Willis, Research Scientist, U.S. Department of Agriculture, Forest Service, Southern Research Station, Auburn, AL 36849; David K. Schnake, Forest Research Operations Manager, Research Stations Division, North Carolina Department of Agriculture and Consumer Services, Raleigh, NC; Scott D. Roberts, Emeritus Professor, Department of Forestry, Mississippi State University, MS 39762; Heather D. Alexander, Associate Professor, Department of Forestry, Mississippi State University, MS 39762; and Heidi Renninger, Assistant Professor, Department of Forestry, Mississippi State University, MS 39762.

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(Hiers and others 2014, Loudermilk and others 2016, Wahlenberg 1946), potentially bringing into the question our understanding of stand dynamics on xeric sites. However, little information exists detailing whether understory facilitation interacts with overstory density, or the processes through which longleaf pine seedlings are being facilitated.

To explore these questions, we established a stand-level manipulative experiment examining the growth and survival of planted seedlings across a gradient of overstory density in both the presence and absence of midstory hardwoods on a xeric site in the Sandhills Ecoregion. Specifically, we were interested in how the survival and growth of longleaf pine seedlings respond to (1) overstory density, (2) the presence of midstory hardwoods, and (3) the interaction of overstory density and midstory hardwoods. Clarifying the contributions of overstory density and midstory hardwoods to longleaf pine seedling performance will refine our understanding of competitive interactions on xeric sites and provide land managers with information to help improve regeneration prescriptions.

MATERIALS AND METHODS

Site Description

Our experiment was conducted in the Sandhills Ecoregion of North Carolina (35º 03' 34.6932" N, 79º 22' 22.0872" W) on the McCain Tract, managed by the Research Stations Division of the North Carolina Department of Agriculture and Consumer Services. Average monthly temperatures in Raeford, NC, (1981 to 2010) ranged from highs of 11.1 ºC (January) to 32.1 ºC (July) to lows of -1.7 ºC (January) to 20.6 ºC (July) (Arguez and others 2010). Average monthly rainfall (1981 to 2010) ranged from 77 mm (November) to 138 mm (July) (Arguez and others 2010), with an average annual total precipitation of 1182 mm. All experimental plots were established within mature longleaf pine stands growing on the Candor soil series (USDA NRCS 2019). The relevant characteristics of this series are that it has rapid permeability with no flooding frequency and is sandy throughout the entire soil profile while somewhat clayey and loamy at the deepest soil horizons (1.5 to 2.0 m). Longleaf pine was the dominant overstory species at the site, with basal areas ranging from 2 to 41 m^2/ha. The midstory (6,228 stems/ha) was dominated by turkey oak (*Quercus laevis* Walter; 82.3 percent) with admixtures of blackgum (*Nysssa sylvatica* Marsh; 9.1 percent) and sassafras (*Sassafras albidum* (Nutt.) Nees; 6.6 percent). Across the site, hardwood heights ranged from 0.1 m to 6.7 m, with an average height of 1.2 m. The herbaceous layer was dominated by wiregrass (*Aristida stricta* Michx.). The site was primarily managed to maintain RCW habitat with a secondary objective being longleaf pine regeneration. To accomplish both objectives, the stand was treated with a dormant season (December to February), low-intensity prescribed fire on a 3-year return interval.

Experimental Design

The experiment was established as a randomized complete block design. In February 2016, 15 experimental blocks (0.10 ha) were established across a gradient of longleaf pine overstory density (2 to 41 m^2/ha). Nine plots (0.002 ha) were nested within each block. Overstory basal area was determined at the plot level with a 10-basal area factor prism, and plots were then placed into one of three groups of overstory density based on RCW management guidelines (Costa 1992): less than 12 m^2/ha (low), 12 to 18 m^2/ha (prime), and greater than 18 m^2/ha (high). Each plot was planted with 16 containerized, 1-year-old longleaf pine seedlings spaced approximately 1 m apart. Midstory hardwoods were controlled by treating prior to planting (R0), treating after 1 year (R1), or left untreated (UN) for the entirety of the experiment (2 years, 2016 and 2017). Plot treatments consisted of cut stump treatment of midstory hardwoods following mechanical removal with brush saws in one-third of the plots with Brushtox Brush Killer herbicide (61.6 percent Triclopyr, Ragan and Massey, Inc., Gig Harbor, WA) mixed with methylated seed oil in a ratio of one part oil to nine parts herbicide each year in May with the goal of eliminating the hardwood midstory. For any hardwood sprouts that survived the cut stump treatment, the foliage was sprayed with the same herbicide the following summer. Plots with lowest oak densities were selected as (R0) in order to ensure adequate and less variable midstory hardwood stocking in the remaining plots. All other treatments were randomly assigned to remaining plots. To eliminate potential edge effects, each plot was separated by at least one buffer plot that received the same treatment as its nearest planted plot.

Sampling Design

Seedling survival and growth were measured in October 2017 at the end of the second growing season. Seedling survival was recorded for every seedling and averaged at the plot level. Growth was assessed through aboveground dry biomass (g) obtained from a random subsample of four seedlings per plot. Seedlings sampled for biomass were cut at the ground-line, stored in sealed plastic bags in a cooler with ice packs, transported to Mississippi State University, dried in an oven for 48 hours at 70 ºC, and subsequently weighed.

Statistical Analysis

Linear mixed models were utilized to explore the impacts of overstory basal area, midstory hardwood presence, the interaction between overstory density and midstory hardwoods, and block on longleaf seedling growth and survival. Overstory basal area and midstory treatments were considered fixed effects, while block was considered a random effect. The response variables of longleaf pine seedling survival and growth were averaged at the plot level (n = 135). Mixed model selection was accomplished through backwards selection, where all effects were placed in the model, and subsequently removed when results of Type 3 tests were nonsignificant. Significant fixed effects were then further explored with Tukey-Kramer multiple comparison tests, to identify significant differences between midstory treatments or overstory groupings. Use of the variance components covariance structure was required for model convergence. All tests were evaluated at α = 0.05 level. Residuals were evaluated for all models to ensure assumptions of normality, equal variance, and independence were not violated. All analyses were performed in SAS 9.4 (SAS Institute Inc., Cary, NC).

RESULTS

Seedling Survival

Seedling survival was best explained by a model containing the fixed effects of midstory treatment and overstory groupings, and the random effect of block. Seedling survival differed significantly among overstory groupings (p = 0.0006), with seedlings growing beneath a low density overstory (86 ± 11 (SE) percent) having greater survival than those growing beneath high overstory density (73 ± 16 percent) (p = 0.0001) (fig. 1). Seedling survival in midstory treatments differed significantly (p = 0.0261), with seedlings growing beneath an intact midstory (UN) (84 ± 13 percent) having greater survival than seedlings whose hardwood midstory was removed after 1 year (R1) (76 ± 17 percent) (p = 0.0280) (fig. 2). The interaction of midstory hardwoods and overstory groupings did not significantly impact seedling survival.

Seedling Growth

Seedling biomass was best explained by a model containing the fixed effect of overstory groupings, and the random effect of block. Seedling biomass in overstory groupings differed significantly (p = 0.0007), with seedlings being significantly larger in the low-density grouping (10.9 ± 1.2 g) compared to both prime density (10.3 ± 1.0 g) and high density (10.0 ± 0.7 g) (fig. 3). Seedling biomass did not vary among midstory treatments (fig. 4). Midstory treatments and their interaction with overstory groupings did not significantly impact seedling biomass, and were therefore not included in the model.

DISCUSSION

Tree regeneration on xeric sites is a long-term process. Thus, the results of our 2-year study should be viewed only as a preliminary indicator of longleaf pine seedling performance under a variety of competitive positions. Future analyses featuring longer term data and more

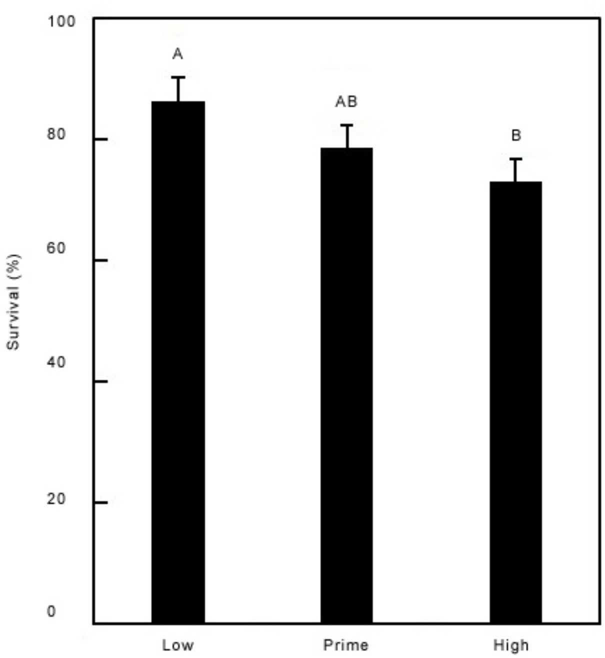

Figure 1—Average 2-year survival (percent) of planted longleaf pine seedlings among overstory groupings (less than 12 m^2/ha (low), 12 to 18 m^2/ha (prime), greater than 18 m^2/ha (high)). Error bars represent one standard error. Bars with differing letters denote a significant difference at the 0.05 level from Tukey-Kramer multiple comparison tests.

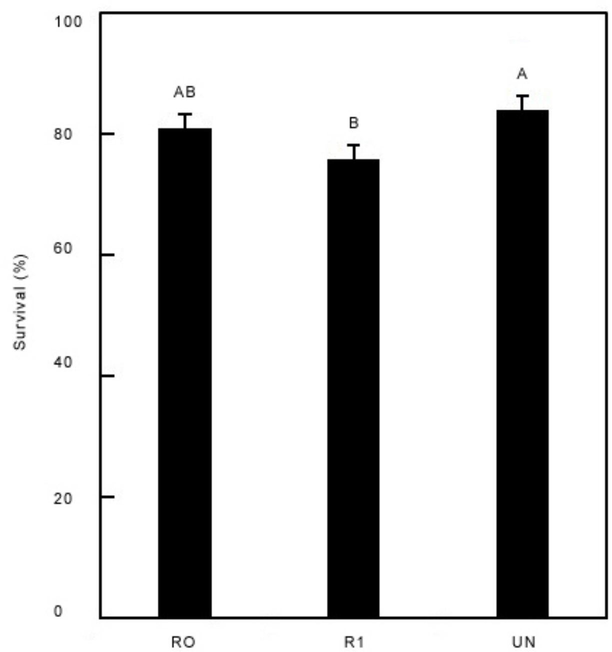

Figure 2—Average 2-year survival (%) of planted longleaf pine seedlings among midstory treatments (treatment prior to planting (R0), treatment after 1 year (R1), or left untreated (UN)). Error bars represent one standard error. Bars with differing letters denote a significant difference at the 0.05 level from Tukey-Kramer multiple comparison tests.

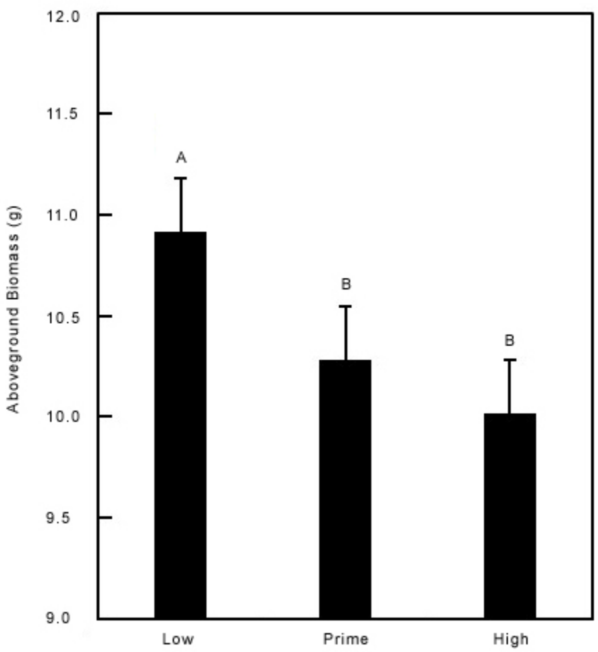

Figure 3—Average 2-year aboveground biomass (g) of longleaf pine seedlings among overstory groupings (less than 12 m^2/ha (low), 12 to 18 m^2/ha (prime), greater than 18 m^2/ha (high)). Error bars represent one standard error. Bars with differing letters denote a significant difference at the 0.05 level from Tukey-Kramer multiple comparison tests.

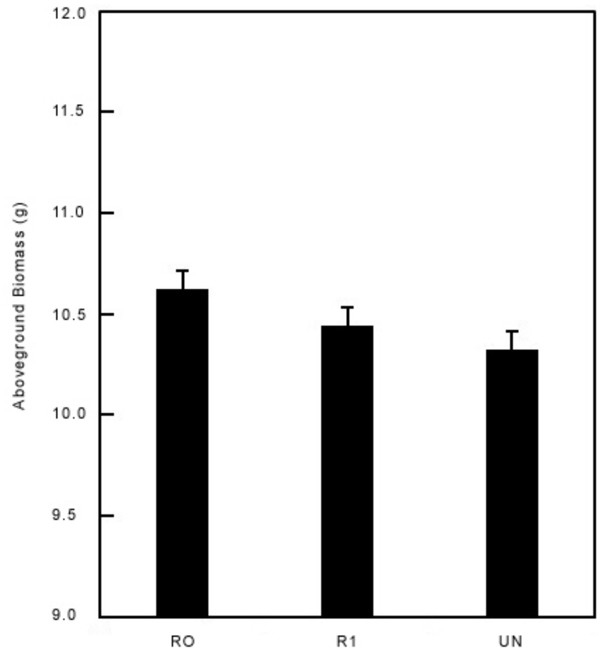

Figure 4—Average 2-year aboveground biomass (g) of longleaf pine seedlings among midstory treatments (treatment prior to planting (R0), treatment after 1 year (R1), or left untreated (UN)). Error bars represent one standard error. There were no significant differences among treatments at the 0.05 level from Tukey-Kramer multiple comparison tests.

detailed physiological evidence will provide better indicators of the complex relationships introduced here.

Overstory Density

Longleaf pine seedling survival exhibited an inverse relationship with overstory density, where survival decreased as overstory density increased. Interestingly, differences in survival were only detected between the low- and high-density groupings, indicating that managing overstory density within the prime RCW range did not have a strong negative influence on longleaf pine seedling survival after 2 years. This apparent competitive effect of high overstory density may have been caused by belowground competition (Brockway and others 1998), as even at the high overstory densities light availability averaged 1045 μmol/m^2/s, exceeding the favorable light threshold of 800-900 μmol/m^2/s (Jose and others 2003). Consistent with our findings, Grace and Platt (1995) demonstrated a similar negative relationship between overstory density and seedling survival. In contrast to our findings, a similar study conducted in southwestern Georgia, under xeric conditions, did not find a significant relationship between survival and overstory density after one growing season (Palik and others 1997). However, given the short measurement interval, it remains difficult to discern whether this finding reflected overstory facilitation or the short measurement duration.

Aboveground seedling biomass exhibited the same relationship as survival, where growth decreased as overstory density increased. These results support the findings of other studies (Grace and Platt 1995, Palik and others 1997, Pecot and others 2007) reporting a negative relationship between overstory density and longleaf pine seedling growth. However, in contrast to our findings on seedling survival, managing overstory density within the prime RCW range significantly reduced seedling growth. Assessing the effect of the overstory on growth is likely a more sensitive early indicator of overstory influence, as longleaf pine seedlings have been shown to persist in the grass stage in low-resource environments for up to 15 years (Boyer 1990).

Midstory Treatments

Understanding the role of midstory hardwoods on xeric sites is critical for future restoration efforts, as the current practice of burning or otherwise controlling hardwood midstory may be inadvertently contributing to longleaf regeneration failures. Our findings demonstrate that seedling survival was highest in the untreated plots. Moreover, seedling growth was not significantly impacted by the presence of a midstory. Collectively, these findings provide early evidence supporting the existence of midstory facilitation on xeric sites (Maestre and others 2009) and the findings of Wahlenberg (1946) and Loudermilk and others (2016). From a management perspective, this suggests prescribed burning to reduce competition on longleaf seedlings is not having the intended positive effect. It should also be noted that removing the midstory after one growing season did negatively impact longleaf pine seedling survival, which may have resulted in micro-environment change following midstory hardwood removal.

CONCLUSIONS

Plant competition has long been considered an influential factor influencing longleaf pine regeneration. Our preliminary findings suggest that maintaining overstory density within the prime RCW range is negatively influencing longleaf pine seedling growth, but not survival. In contrast, reducing midstory hardwood competition is benefiting neither seedling survival nor growth. After 2 years, we detected no interactions between overstory density and the presence of midstory hardwoods. Future analyses will provide further clarification on whether mature trees or the midstory are inhibiting or facilitating longleaf pine regeneration.

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