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Effects of overstory retention, herbicides, and fertilization on sub-canopy vegetation structure and functional group composition in loblolly pine forests restored to longleaf pine

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ABSTRACT

The desirable structure of longleaf pine forests, which generally includes a relatively open canopy of pines, very few woody stems in the mid-story, and a well-developed, herbaceous ground layer, provides critical habitat for flora and fauna and contributes to ecosystem function. Current efforts to restore longleaf pine to upland sites dominated by second-growth loblolly pine require information about how restoration treatments affect sub-canopy vegetation. We established a field experiment at Fort Benning in Georgia and Alabama, USA to determine the effects of four levels of approximately uniform canopy density (Control [$\sim$16 m^2/ha basal area], MedBA [$\sim$9 m^2/ha basal area], LowBA [$\sim$5 m^2/ha basal area], and Clearcut [0 m^2/ha basal area]) and three cultural treatments (NT [untreated], H [chemical control of woody and herbaceous vegetation] and H + F [chemical control plus fertilization]) on vegetation structure and functional group composition for three growing seasons following canopy removal. In general, cover (a measure of abundance) of ground layer vegetation increased with the amount of canopy removal. The ground layer was dominated by herbaceous vegetation in each year. Canopy trees generally suppressed the cover of graminoids in the first two years after treatment but only the Control plots had lower graminoid cover than Clearcut plots after the third growing season. Forb cover was significantly lower on Control plots than on Clearcut plots after only the first growing season, and woody stems/shrubs had lower cover on Control plots than on LowBA or Clearcut plots in each year. Vegetation cover increased following the first year after canopy removal, and the relative dominance of functional groups did not change through time. Canopy retention limited the development of mid-story woody stems, with the greatest stem densities in the Clearcut plots. The herbicide treatment (on both H and H + F) significantly reduced woody stem density in the mid-story in 2009, but the effect was no longer significant in 2010. Traditional methods for converting stands of other pine species to longleaf pine commonly include clearcutting followed by planting, but our results suggest that clearcutting may release woody vegetation to increase mid-story stem densities and will reduce the amount of pine needles in the fuel bed. Retaining low to moderate levels of canopy density (5–9 m^2/ha basal area) in loblolly pine stands may provide an effective balance for reaching multiple restoration objectives that include maintaining desirable vegetation structure and creating fuel conditions for a frequent fire regime.

1. Introduction

In the southeastern United States, the historical conversion of upland sites from longleaf pine (*Pinus palustris* Mill.) to loblolly pine (*Pinus taeda* L.) has been largely associated with land-use history (e.g., timber clearing, agriculture) and forest management decisions (e.g., use of plantation systems, fire exclusion) (Frost, 1993; Van Lear et al., 2005). Following widespread logging of historically dominant longleaf pine forests in the 1800s and early

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1900s, many upland sites were reforested with faster-growing species or allowed to follow natural succession processes, largely in the absence of fire (Frost, 2006; Schultz, 1999). Consequently, loblolly pine is currently found on many upland sites that are well-suited for longleaf pine. The differences between the two forest types are not limited to canopy composition. The stand structure of second-growth loblolly pine forests is often quite different from that of fire-maintained longleaf pine forests. For example, Hedman et al. (2000) reported that second-growth loblolly pine forests had lower ground layer herbaceous cover and higher mid-story stem densities than longleaf pine forests and largely associated such differences with land-use history and fire management. Currently, restoration of longleaf pine forests and woodlands is a widely shared goal among public and private landowners in the southeastern United States.

While many different restoration objectives could be identified, ranging from the presence of selected species or groups of species to recreating the historic disturbance regime, measures of characteristic stand structure are arguably among the most useful. The stand structure of longleaf pine forests with high conservation value is generally characterized by an open canopy that is dominated by longleaf pine, little to no mid-story, and a ground layer that is dominated by herbaceous vegetation (e.g., Gilliam et al., 2006; Peet, 2006). The ground layer typically includes large bunchgrasses that create a matrix of overlapping plant tissue and form an often continuous layer of well-aerated fuels. When combined with needlefall from canopy pines, this fuel layer burns readily as low-intensity surface fires (e.g., Clewell, 1989; Noss, 1989; O'Brien et al., 2008). Frequent surface fires reduce encroachment from hardwood species and maintain the dominance of herbaceous species (Brockway and Lewis, 1997; Glitzenstein et al., 1995). The importance of ground layer vegetation (particularly large bunchgrasses) as a fuel source, coupled with the need for burning to perpetuate the desired structure, represents a positive feedback cycle that becomes difficult to re-establish once disrupted (Martin and Kirkman, 2009). Thus, restoring the desired structure is necessary for restoring ecological dynamics.

Further, where restoring wildlife habitat or conditions suitable for characteristic plant species is an explicit objective, restoring structure is critical. For example, the gopher tortoise (*Gopherus polyphemus*) and many other reptile specialists in longleaf pine habitats require open stands for foraging herbaceous ground layer plants (Guyer and Bailey, 1993). Perhaps the most well-known faunal species associated with the longleaf pine ecosystem is the red-cockaded woodpecker (*Picoides borealis*), which uses live longleaf pine trees for nesting cavities and prefers open stands for foraging (U.S. Fish and Wildlife Service, 2003). Recent reports suggest that RCWs living in habitats dominated by herbaceous plants have higher reproductive potential than those in habitats dominated by shrubs (James et al., 1997), in part due to the diverse arthropod community supported by herbaceous ground layers plants (Folkerts et al., 1993; Hanula and Engstrom, 2000).

The management and land-use histories that contributed to the conversion of upland sites from longleaf pine to loblolly pine also altered the sub-canopy vegetation. For example, many such sites have experienced a recent history of fire exclusion that has resulted in the establishment and growth of hardwood species in the sub-canopy layers. As hardwoods gain dominance, herbaceous species such as grasses and forbs become less abundant due to competition for resources and the development of hardwood litter on the forest floor (Harrington and Edwards, 1999; Hiers et al., 2007). Such changes in the vegetation composition and structure lead to changes in the characteristics of the fuels in the forest, with shifts from the well-aerated, continuous fine fuels of the herbaceous layer to a less pyrogenic and patchier hardwood litter (Mitchell et al., 2009; Williamson and Black, 1981). Consequently, the ability to manage with frequent surface fires becomes more difficult, and the hardwood mid-story continues to develop (Mitchell et al., 2006).

Several studies have been designed to determine methods for restoring the desired vegetation structure and associated fuel matrix to longleaf pine sites. Herbicides that target woody vegetation can be used to eliminate woody competitors and increase dominance of herbaceous species in the ground layer (Brockway et al., 1998; Freeman and Jose, 2009; Jose et al., 2010). Other studies have used mechanical treatments, or mechanical treatments combined with herbicides, to control woody species for the restoration of desirable longleaf pine vegetation (Harrington and Edwards, 1999; Martin and Kirkman, 2009; Outcalt and Brockway, 2010; Provencher et al., 2001a). To sustain the longleaf pine ecosystem over the long-term, frequent prescribed fire must be incorporated into management, and prescribed burning is an important tool for restoring the vegetation structure of the longleaf pine ecosystem (Freeman and Jose, 2009; Outcalt and Brockway, 2010; Provencher et al., 2001a). Burning alone, over long timeframes, has been shown to reduce woody vegetation and increase the abundance of herbaceous vegetation (Brockway and Lewis, 1997; Haywood et al., 2001; Waldrop et al., 1992), and results from recent research suggest that fire alone may be effective at restoring vegetation composition in longleaf pine forests (Kirkman et al., 2013). However, responses of the vegetation community following restoration treatments are likely to vary in magnitude or effect according to local site factors or the initial condition of the vegetation community. Few studies have incorporated variability among sites into the evaluation of such treatments (see Gliztenstein et al., 2003; Haywood, 2005), but previous studies have demonstrated the importance of site characteristics, such as soil texture or moisture, in affecting the productivity or composition of vegetation in longleaf pine forests (Gilliam et al., 1993; Kirkman et al., 2001, 2004; Mitchell et al., 1999). As a result, more information is required to understand the effects of state variables on the responses of the vegetation community to restoration treatments.

Despite an understanding of the importance of ground layer vegetation in this ecosystem, longleaf pine restoration efforts on sites that have been converted to other canopy species often initially focus on the establishment of longleaf pine seedlings. Traditionally, artificial regeneration of longleaf pine has been accomplished following clearcutting of the existing canopy and the use of release treatments (e.g., Freeman and Jose, 2009; Johnson and Gjerstad, 2006; Knapp et al., 2006). Although this approach is expected to maximize longleaf pine seedling growth, complete canopy removal may also release sub-canopy hardwoods and make fire management more difficult by changing the fuels. Therefore, retaining canopy trees during the conversion of other pine forests to longleaf pine may provide additional benefits for meeting restoration objectives (Kirkman et al., 2007). Recent studies suggest that retaining low to moderate levels of canopy basal area may be a viable practice during the establishment of longleaf pine seedlings in loblolly pine stands (Hu et al., 2012; Knapp et al., 2011, 2013).

To make informed restoration decisions, land managers require information on how alternative silvicultural treatments affect vegetation structure during longleaf pine restoration. This study was designed to determine the effects of various levels of canopy retention and cultural treatments used during longleaf pine restoration on the structure and functional group composition of the sub-canopy vegetation in loblolly pine stands. Moreover, we established our study on two broad categories of soil texture, and we used this opportunity to determine the effects of soil texture on certain vegetation responses. Our specific objectives are to determine: (1) how canopy density and cultural treatments affect ground layer vegetation total cover and the cover of selected functional groups;

(2) how ground layer vegetation cover changes through time in response to canopy density manipulation; (3) how canopy density and cultural treatments affect the abundance of mid-story woody vegetation; (4) how soil texture affects the abundance and response of sub-canopy vegetation to study treatments; and (5) how restoration treatments affect fine fuels (bunchgrasses and pine needles) that are important to fire management. Although our results have implications for fire management due to the fuel complexes created by the vegetation, a complete analysis of the effects of our study treatments on fire management is outside the scope of this study.

2. Materials and methods

2.1. Study site

This study was conducted at Fort Benning Military Installation (~32.38°N, 84.88°W) in Muscogee and Chattahoochee Counties, GA and Russell County, AL. Prior to establishment as a U.S. military installation in 1918, much of the land was used for cotton production and then reforested with loblolly pine following the abandonment of agriculture (Fort Benning, 2001). Currently, Fort Benning occupies 74,000 ha, of which approximately one-third (22,500 ha) is dominated by loblolly pine and approximately 15,000 ha support pure or mixed longleaf pine stands (Fort Benning, 2001). Fort Benning falls within two ecoregions, with the northeastern two-thirds in the Sand Hills Subsection of the Lower Coastal Plains and Flatwoods Section and the southwestern one-third of the installation within the Upper Loam Hills Subsection of the Middle Coastal Plain Section (Bailey, 1995). Soils are generally low in organic matter and nutrient holding capacity, although those of the Upper Loam Hills have higher silt and clay 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 terrain of Fort Benning is predominately rolling, and elevation is highest in the Sand Hills of the northeast (225 m above sea level) and lowest near the Chattahoochee River in the southwest (58 m above sea level). The 50-year mean annual precipitation at Fort Benning (through 2011) was 1225 mm, with a 50-year mean temperature of 18.4 °C.

For this study, we selected six upland sites (study blocks) dominated by second-growth loblolly pine and targeted for longleaf pine restoration by land managers at Fort Benning. Many such sites have been managed to improve RCW habitat over the past few decades, and recent management activities have included frequent prescribed burning (Table 1). Three of the study blocks were in the Sand Hills Subsection and the other three study blocks were in the Upper Loam Hills Subsection. Prior to the installation of the study, we conducted block-level surveys of overstory basal area with variable-radius prism plots and established six random transects throughout each stand to coarsely quantify the densities of mid-story stems and cover of ground layer vegetation prior to treatment (Table 1). Common ground layer species include bunchgrasses (e.g., *Andropogon* spp., *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum* spp.) and herbaceous species such as legumes (e.g., *Desmodium* spp., *Lespedeza* spp.) and composites (e.g., *Eupatorium* spp., *Solidago* spp.). Woody species, including sweetgum (*Liquidambar styraciflua* L.), persimmon (*Diospyros virginiana* L.), oaks (*Quercus* spp.), and hickories (*Carya* spp.), were common in the understory and mid-story.

2.2. Experimental design and treatments

The experiment used a randomized, complete block, split-plot design, with the location of individual loblolly pine stands as the blocking factor ($n = 6$). Each block was divided into four main treatment plots and each main-plot received an overstory treatment. Main-plots were 100 × 100 m (1 ha), with the exception of the Clearcut plots, which were 141 × 141 m (2 ha) to create clearcut conditions in the plot center. The main-plot treatments included four treatments that resulted in the uniform distribution of canopy pines: Control (uncut; residual basal area ~16 m^2/ha); MedBA (canopy tree removal with the target basal area of 9 m^2/ha); LowBA (canopy tree removal with the target basal area of 5 m^2/ha); and Clearcut (all trees removed to basal area of 0 m^2/ha).

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 removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid) mixed with 2.24 kg/ha 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 × 3.7 m spacing, for a total of 1495 seedlings per hectare. Planting began in mid-November 2007 and was completed by January 2008. All study areas were burned with dormant season prescribed fire, applied between the second and third growing seasons (January–April 2010). This burn was applied to meet the management objective of maintaining or introducing frequent fire on these sites and was not applied as a study treatment.

Split-plot treatments included additional cultural practices designed to enhance ecosystem restoration, through either improvement of the growing conditions for planted longleaf pine seedlings or changes to ground layer vegetation. The split-plot treatments included an untreated control (NT), competition control with herbicides (H), and competition control with herbicides combined with fertilizer (H + F). Main-plot treatments were each divided into four equal sections for cultural treatment application. Split-plot treatments were randomly assigned to three of the sections, and split-plot treatments were applied to a 30 × 30 m area centered on a 20 × 20 m measurement plot. The herbicide treatment included an application of 1% imazapyr plus 0.25% non-ionic surfactant applied directly to the foliage of woody vegetation in October 2008. Because herbaceous vegetation was abundant on these sites, we applied an additional mix of 63.2% hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] and 11.8% sulfometuron methyl {Methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl]benzoate} at a rate of 0.84 kg/ha, sprayed in approximately 1 m wide bands over the top of longleaf pine seedlings in March 2009. The H + F treatment included the herbicide treatments described above as well as an application of 280 kg/ha 10-10-10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009, with care taken to evenly distribute the fertilizer throughout each treatment area.

2.3. Data collection

In each split-plot, we randomly located the starting points of two 20 m transects that ran parallel to one split-plot boundary (Fig. 1). We then randomly selected ten numbers between 2 and 17 to serve as starting distances (m) for sampling quadrats along each transect. We did not sample along the edges of each transect to avoid the potential disturbance to the vegetation caused by transect establishment and plot layout. At each sampling location, we established a 1 × 1 m sampling quadrat and recorded ocular estimates of percent cover of all vegetation <1 m tall that overlapped the area within the quadrat. We estimated cover as the

Table 1
Description of characteristics (stand structure, soil texture, and site history) in 2006, prior to treatment application, for the six study blocks at Fort Benning.

Type	Variable	Block					
		1	2	3	4	5	6[a]
Stand structure	BA (m^2/ha)	11.9	13.4	17.7	14.9	14.7	–
	DBH (cm)	38.0	29.2	25.7	33.9	41.5	–
	Mid-story density (stems/m^2)	0.0	1.0	0.2	0.5	1.2	–
	Total ground-layer vegetation cover (%)	52.4	71.7	55.7	50.2	57.5	–
Soil texture	Sand content (%)	66.7	75.9	87.2	88.7	76.1	86.9
	Silt content (%)	17.2	14.0	5.3	5.5	14.0	6.3
	Clay content (%)	16.1	10.1	7.5	5.8	9.9	6.8
	Texture class	Sandy loam	Sandy loam	Loamy sand	Sand	Sandy loam	Loamy sand
Site history	Age	40	47	47	53	45	48
	Land use in 1944[b]	Agriculture	Forested	Forested	Mixture	Agriculture	Agriculture
	Total burns since 1981	10	7	15	9	9	8

[a] Stand structural data were not recorded prior to treatment in Block 6 due to access issues.
[b] Land use in 1944 was determined from aerial photographs from 1944.

percentage of the plot that would be covered by vegetation when viewed from directly overhead. Cover was recorded using the following 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 quadrat could sum to over 100% if vegetation overlapped. We estimated cover by functional group (bunchgrasses, other graminoids, ferns, forbs, woody stems, and woody vines) and by common species for woody vegetation (i.e., *P. taeda*, *L. styraciflua*, *Rubus* spp., other). These woody species were selected because they were common but also because they either posed a threat to restoration objectives due to their potential to establish and dominate the regeneration layer (e.g., *P. taeda* and *L. styraciflua*) or because their growth form does not develop into the mid-story (e.g., *Rubus* spp.). We also recorded the cover of pine needles and the amount of mineral soil exposed in each quadrat. Ground cover data were recorded in October 2008, 2009, and 2010. To determine the density of mid-story, woody stems (>1 m tall but <4 cm in diameter at breast height (DBH)), we used each transect as the center of a 2-m wide sampling belt (1 m on each side of the transect). Within each belt transect, we tallied all woody stems by species in October 2008, 2009, and 2010.

2.4. Data analysis

Cover data were converted to the mid-point of each class, and we calculated mean values at the split-plot level for analyses. We used split-plot Analysis of Variance (ANOVA) with a random block effect to test for main-plot effects, split-plot effects, and main * split-plot interaction effects on total vegetation cover, herbaceous vegetation cover, woody vegetation cover, and vegetation cover by functional group. Analyses were conducted for each year separately because the split-plot treatment application occurred between the first and second growing seasons. In 2008, no split-plot treatments had been applied, and we tested for only main-plot effects. To determine the change in vegetation cover over time, we conducted a repeated measures ANOVA to test for year effects and year * main-plot treatment effects. For the repeated measures test, we used data from only NT split-plots because the split-plot treatments were applied after the first growing season. We determined the average number of woody stems per hectare at the split-plot level by species, and we used split-plot ANOVA with a random block effect to test for main-plot effects, split-plot effects, and main * split-plot interaction effects on woody stem density in each year.

We tested for effects of soil texture on the cover of herbaceous vegetation in the ground layer, the cover of woody vegetation in the ground layer, and the density of mid-story stems in response to the study treatments by including soil texture in a separate ANOVA model with the 2009 data. Our study was not explicitly designed to test the effects of soil texture on vegetation response, but the distribution of study blocks at Fort Benning provided the opportunity to conduct such a test. The 2009 data were selected because they provided a split-plot analysis, represent main-plot effects after two years of recovery following harvest, and had not yet been burned post-treatment. Blocks 1, 2, and 5 were grouped together as 'loamy soils' and Blocks 3, 4, and 6 were grouped together as 'sandy soils'. The block effect was nested within the soil type for the analyses. For each ANOVA test described above, we used transformations as necessary to satisfy assumptions of constant variance and normality. Treatment differences were determined using Tukey's HSD test, and degrees of freedom were calculated using the Satterthwaite approximation. Treatment effects were determined to be significant when $p < 0.05$.

3. Results

3.1. Treatment effects on ground layer vegetation cover

There was no interaction between main-plot and split-plot effects on total vegetation cover in 2009 or 2010 ($p \geq 0.2734$), but total vegetation cover was significantly affected by the main-plot treatments in each year (Fig. 2A, C, and E). Generally, total vegetation cover increased with decreasing overstory density, although total vegetation cover was not significantly different between Clearcut and LowBA plots or between LowBA and MedBA plots in any year. The uncut Control plots had the least amount of vegetation cover in each year. The split-plot treatments had a significant effect on total vegetation cover in 2009, when the H + F plots had higher total cover than the H plots (Fig. 2D). The split-plot effect was no longer significant in 2010 (Fig. 2F).

Regardless of the treatment applied, herbaceous vegetation dominated the ground layer, with more than twice as much cover as woody vegetation in all years (Fig. 2). In 2008, the canopy treatment effect was significant for cover of herbaceous and woody vegetation, with the pattern in vegetation response similar to that for total cover. The greatest cover of herbaceous and woody vegetation was on Clearcut plots, and the least cover was on Control plots. In 2009, there was a significant interaction between the main-plot and split-plot effects ($F_{6,40} = 2.39$; $p = 0.0459$) for herbaceous cover. The split-plot treatment effect was only significant on MedBA main-plots, and the canopy treatment effect was significant on NT and H split-plots but not on H + F split-plots. Within the main-plot treatments, herbaceous cover in MedBA main-plots was significantly lower in H than in H + F split-plots; within the

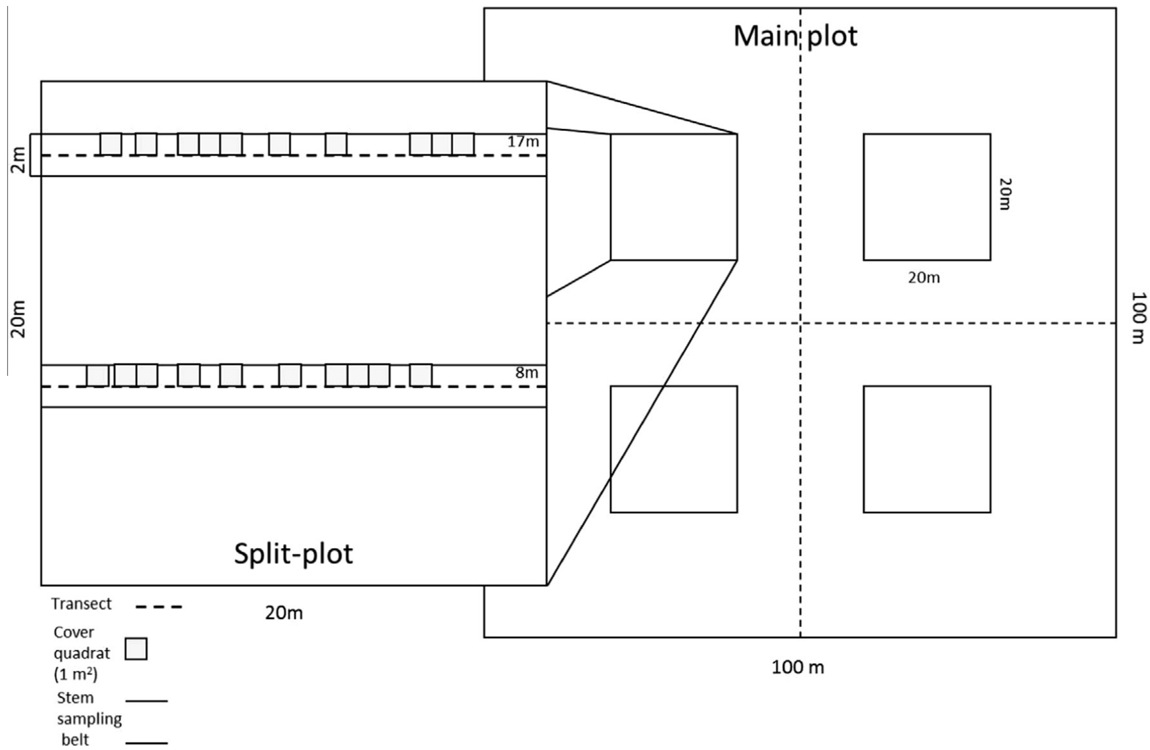

Fig. 1. Illustration of the main-plot and split-plot layout and the sampling design used to quantify cover of the ground layer vegetation (<1 m tall) and mid-story stems (>1 m tall but <4 cm diameter at breast height).

split-plot treatments, the Clearcuts plots had greater vegetation cover than the Control plots on NT and H split-plots (Table 2). There was no interaction effect on woody vegetation in 2009 ($F_{6,30}$ = 0.47; p = 0.8241), and the Clearcut and LowBA plots had significantly greater woody vegetation cover than the Control plots (Fig. 2C). Split-plot treatments did not significantly affect woody vegetation cover in 2009. In 2010, there was no significant interaction effect for herbaceous ($F_{6,40}$ = 1.57; p = 0.1825) or woody ($F_{6,40}$ = 0.55; p = 0.7670) vegetation. There was no longer a significant main-plot treatment effect on herbaceous vegetation, but woody cover was significantly greater on Clearcut and LowBA plots than on Control plots (Fig. 2E). We found no significant effect of the split-plot treatments on herbaceous or woody vegetation in 2010.

In 2010, *Rubus* spp. made up more than half of the total woody cover in all main-plot treatments. Loblolly pine and sweetgum made only minor contributions (<2% cover) to the woody species cover for any main-plot treatment. Other common species that contributed to the woody vegetation in the ground layer included blueberries (*Vaccinium* spp.), oaks and hickories. Despite the significant main-plot effects on total woody vegetation cover in 2010 (Fig. 2), there was no significant main-plot effect on the cover of *Rubus* spp. ($F_{3,15}$ = 2.62; p = 0.0887) or loblolly pine ($F_{3,15}$ = 0.34; p = 0.7980). The main-plot treatments significantly affected the cover of sweetgum in the ground layer ($F_{3,15}$ = 3.32; p = 0.0485), with greater cover on the LowBA plots (1.8%) than on the Control plots (0.1%). Split-plot treatments did not significantly affect the cover of *Rubus* spp. ($F_{2,40}$ = 0.94; p = 0.3989) or loblolly pine ($F_{2,40}$ = 1.72; p = 0.1918) by the end of the third growing season, but sweetgum ($F_{2,40}$ = 4.71; p = 0.0145) had significantly greater cover on NT plots (2.1%) than on H + F plots (0.2%).

There were no interactions between main-plot and split-plot treatment effects for any functional group in any year. In 2008, the main-plot treatments significantly affected the cover of graminoids, forbs, and woody stems. For each functional group, the greatest amount of cover was on the Clearcut plots and the least amount of cover was on the Control plots (Table 3). For forbs and woody stems, the intermediate density treatments (MedBA and LowBA) resulted in intermediate vegetation cover. For graminoids, cover was similar among all treatments that retained canopy trees but greater on the Clearcut plots. In 2009 and 2010, the patterns of vegetation response were similar to those in 2008, but only the graminoid and woody stem groups were significantly affected by the canopy density treatments. In both years, the Clearcut plots had greater cover of graminoids and woody stems than the Control plots. There were no split-plot treatment effects on any functional group in either 2009 or 2010 (Table 3).

3.2. Changes in vegetation cover over time

Results from the repeated measures analyses show that total vegetation cover increased over time ($F_{2,38.5}$ = 12.18; p < 0.0001), with no interaction between year and treatment effects ($F_{6,38.3}$ = 2.13; p = 0.0719). Total cover was significantly higher in 2010 and in 2009 than in 2008, but total cover in 2009 was not significantly different from that in 2010 (Fig. 3). Graminoids, ferns, woody stems, and woody vines followed similar patterns as that of total vegetation cover over time, but there was an interaction between treatment and year effects for forbs ($F_{6,37}$ = 4.18; p = 0.0026). Forb cover did not change over time on MedBA and LowBA plots, but forb cover increased over time on Control plots and decreased over time on Clearcut plots (Fig. 4).

3.3. Treatment effects on mid-story vegetation

The number of woody stems in the mid-story layer was significantly affected by canopy density in 2008, with greater stem density on the Clearcut and LowBA plots than on the Control and MedBA plots (Fig. 5A). There were no interactions between main-plot and split-plot effects in 2009 or 2010 ($p \geq 0.1560$). Stem density was higher on Clearcut plots than on Control plots in 2009 and

2010, and by the end of the 2010 growing season the Clearcut plots averaged 1222 woody stems per hectare and the Control plots averaged 42 woody stems per hectare in the mid-story. The split-plot treatment effect was significant in 2009, with higher stem density on the NT plots than on H and H + F plots. In 2010, the split-plot treatment effect was not significant, despite a range of 1156 stems per hectare on the NT plots to 313 stems per hectare on the H + F plots. In each year, sweetgum was the most common species encountered in the mid-story layer, making up 72%, 65%, and 52% of the woody stems in the mid-story in 2008, 2009, and 2010, respectively. Other common species included oaks, loblolly pine, persimmon, hickories, winged sumac (*Rhus copallinum* L.) and wax myrtle (*Morella cerifera* (L.) Small).

3.4. Effects of soil texture on vegetation response

Soil texture had no effect on total cover of ground layer vegetation ($F_{1,4} = 5.12$; $p = 0.0865$) or on cover of woody vegetation in the

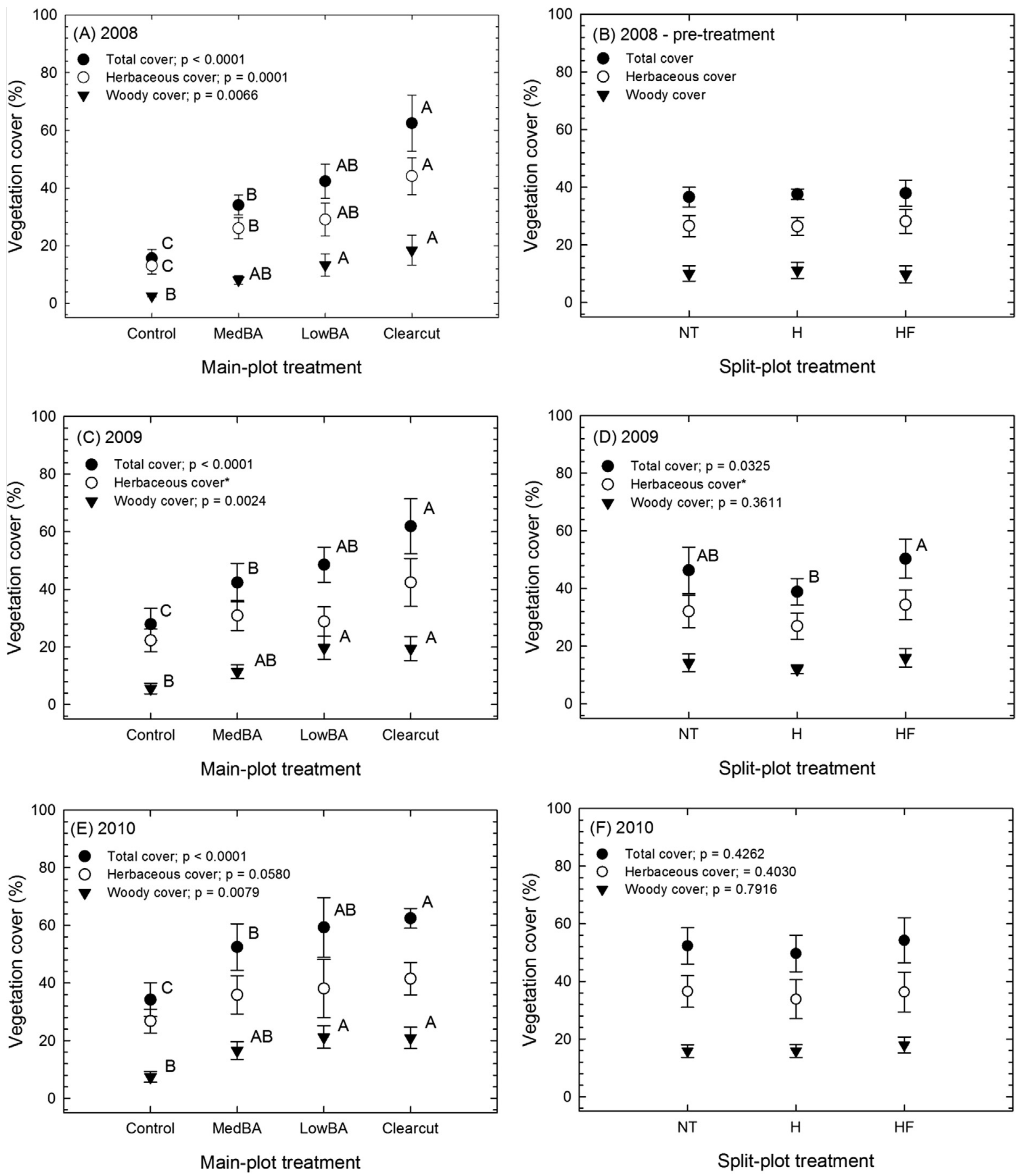

Fig. 2. Total, herbaceous, and woody vegetation cover (mean ± one standard error) by main-plot treatment (panels A, C, and E) and split-plot treatment (panels B, D, and F) in 2008, 2009, and 2010. The same letter within a vegetation type indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$. No analysis was performed on panel B because split-plot treatments had not been applied in 2008. [*]*p*-Values are not included for 2009 herbaceous cover because the main-plot $*$ split-plot interaction was significant.

ground layer in 2009 ($F_{1,4} = 1.10$; $p = 0.3527$). There were no interactions between soil texture and main-plot or split-plot effects for total cover or woody vegetation cover in the ground layer ($p \geq 0.3057$). We found a significant interaction between soil texture and main-plot treatment effects on herbaceous vegetation cover in the ground layer in 2009 ($F_{3,12} = 5.60$; $p = 0.0123$) (Fig. 6). On loamy soils, herbaceous vegetation was significantly higher on Clearcut plots than on any other treatment, but there was no effect of canopy density on vegetation cover on sandy soils. We found no effect of soil texture and no interactions between soil texture and main-plot treatments or between soil texture and split-plot treatments on mid-story stem densities in 2009 ($p \geq 0.1565$).

3.5. Treatment effects on fine fuel components

We found no interactions between main-plot and split-plot treatment effects on the cover of bunchgrasses or pinestraw in either 2009 or 2010 ($p \geq 0.1499$). The main-plot treatments significantly affected the cover of pinestraw in 2009 and 2010, with greater pinestraw associated with treatments that had higher canopy density (Fig. 7). Clearcut plots had almost no pinestraw ground cover, and Control plots had almost 50% cover of pinestraw in 2009. Although bunchgrasses appeared slightly more abundant on Clearcut plots in both years, there were no significant main-plot effects on bunchgrass cover in 2009 or 2010. The split-plot treatments did not significantly affect either bunchgrass or pinestraw cover in 2009 or 2010.

4. Discussion

Canopy removal can affect the residual plant community by altering both abiotic conditions and resource availability (e.g., Anderson et al., 1968; Roberts, 2004). Increased availability of plant resources (light, nutrients, and water) following canopy removal is generally associated with increases in the abundance of ground layer plants in a variety of ecosystems (e.g., Ares et al., 2010; Frederickson et al., 1999; Harrington and Edwards, 1999; Wilson et al., 2009; Zenner et al., 2006). In longleaf pine forests, Grelen and Enghardt (1973) reported an increase of herbaceous vegetation that was proportional to the intensity of canopy thinning. In 8- to 11-year old longleaf pine plantations at the Savannah River Site, GA, Harrington and Edwards (1999) found that forb, grass, vine, and shrub cover increased following experimental reductions of canopy density. Our results show a similar general increase in vegetation cover following canopy removal, although response patterns differed across functional groups and through time. In each year, both total vegetation cover and woody vegetation cover increased as canopy density decreased from uncut Control plots to Clearcut plots. In contrast, the response of herbaceous vegetation was not consistent through time. In the first year following treatment, herbaceous cover appeared strongly linked to canopy density, but by the third growing season there were no longer significant effects of canopy density. Moreover, the presence of canopy trees at any density (Control, MedBA, or LowBA) limited graminoid cover in 2008, but graminoid cover on Control plots was different only from Clearcut plots in 2010.

Table 2
Results of significant interaction between main-plot and split-plot effects for herbaceous vegetation cover (%) in 2009; the same upper-case letters indicate no significant differences within columns and the same lower-case letters indicate no significant differences within rows at $\alpha = 0.05$.

Main-plot	Split-plot						p-Value
	NT		H		H + F		
	Mean	SE	Mean	SE	Mean	SE	
Control	^{B}20.92	(4.50)	^{B}20.12	(5.19)	25.79	(4.13)	0.3614
MedBA	^{AB}34.44^{ab}	(7.18)	^{B}20.22^{b}	(2.61)	38.06^{a}	(7.44)	0.0003
LowBA	^{AB}27.05	(4.46)	^{AB}26.13	(5.23)	33.28	(6.38)	0.1991
Clearcut	^{A}45.85	(10.34)	^{A}41.12	(8.10)	40.2	(6.91)	0.3691
p-Value	0.0017		0.0040		0.1001		

We observed different response patterns of herbaceous and woody vegetation, which may be related to several factors. First, the site preparation treatments used in this study, including broadcast application of non-selective herbicide, likely reduced the initial abundance of ground layer vegetation across treatments. Results from the repeated measures analyses showed that both herbaceous and woody vegetation increased through time. It is possible that the retention of canopy pines reduced the rate of recovery of the herbaceous community such that recovery on Clearcut plots occurred earlier than that on the MedBA or Control plots. Second, the morphology and life histories of herbaceous and woody vegetation may also contribute to differential responses. Pecot et al. (2007) suggested that below-ground competition with canopy trees limited the abundance of woody vegetation but competition for light more strongly controlled the abundance of herbaceous vegetation in longleaf pine forests. Given the relatively high light levels in pine forests, such a model could account for stronger control of canopy pine density on woody species than on herbaceous species. Finally, the prescribed fire that was applied to all study sites between the second and third growing seasons likely contributed to the response patterns in 2010. In longleaf pine ecosystems, repeated burning can reduce woody stems in the mid-story and increase the biomass of grasses and forbs (Brockway and Lewis, 1997; Gliztenstein et al., 2003; Haywood et al., 2001). We found that the cover of herbaceous vegetation was no longer significantly affected by canopy density in 2010, suggesting that the prescribed fire may have stimulated regrowth of herbaceous plants regardless of canopy density. However, the effects of a single fire on woody vegetation may be more variable than the effects of a single fire on herbaceous vegetation (Arthur et al., 1998). Our results showed that the prescribed fire did not reduce the cover of woody vegetation or the number of woody stems the year following burning. Although it is likely that the prescribed fire contributed to the vegetation abundance patterns observed in 2010, our study was not designed to test fire effects, and we cannot make conclusive interpretations about the role of fire on the observed vegetation response.

Objectives of longleaf pine ecosystem restoration commonly include reducing the abundance of woody vegetation in the ground layer and mid-story (Brockway et al., 2009; Mitchell et al., 2006; Provencher et al., 2001a), and we observed large differences in the abundance of woody vegetation among our study treatments. Previous reports have discussed concerns with gap-based longleaf pine management because canopy removal can result in the release and rapid growth of woody stems (Jack et al., 2006; Kirkman et al., 2007; Pecot et al., 2007). Our results support this finding and suggest that canopy retention can be used to limit the growth of hardwoods in the mid-story of loblolly pine stands. However, retaining canopy trees in loblolly pine stands can lead to additional challenges presented by natural loblolly pine regeneration (Knapp et al., 2011). In our study, loblolly pine regeneration was a relatively minor component of the ground layer and mid-story vegetation; in contrast, Hu (2011) found that loblolly pine dominated the mid-story of plots with heavy canopy reductions in a study with the same design as ours that was established at Camp Lejeune, NC. Thus, the control of loblolly pine regeneration must be an important consideration for managers restoring longleaf pine while retaining loblolly pine canopy trees (Knapp et al., 2011).

Given the challenges presented by hardwood encroachment during longleaf pine restoration, herbicides have been studied as

Table 3
Effects of main-plot and split-plot treatments on vegetation cover (%) by functional group in 2008, 2009, and 2010; the split-plot effect was not included in the 2008 analysis because treatments were not applied until 2009. The same superscript letter within an effect, functional group, and year indicates no significant differences at $\alpha = 0.05$.

Effect	Treatment	Graminoids		Forbs		Ferns		Woody stems		Woody vines	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
2008											
Main plot	Control	3.4^{b}	(0.7)	7.9^{b}	(2.4)	0.4	(0.2)	2.5^{b}	(0.4)	0.2	(0.1)
	MedBA	5.5^{b}	(0.9)	15.5^{ab}	(2.3)	1.6	(1.6)	6.2^{ab}	(1.2)	0.5	(0.1)
	LowBA	6.5^{b}	(1.1)	21.3^{ab}	(5.3)	2.0	(1.2)	13.8^{a}	(4.6)	0.6	(0.4)
	Clearcut	18.1^{a}	(4.7)	25.3^{a}	(5.0)	0.5	(0.3)	16.8^{a}	(5.8)	0.7	(0.4)
	p-Value	0.0006		0.0072		0.4723		0.0074		0.3334	
Split plot	NT	8.3	(1.4)	17.1	(3.0)	1.2	(0.7)	9.4	(2.8)	0.6	(0.4)
	H	7.3	(1.1)	17.6	(2.4)	1.5	(1.0)	10.5	(2.7)	0.6	(0.2)
	H + F	9.5	(1.1)	17.9	(3.6)	0.8	(0.4)	9.5	(2.9)	0.3	(0.1)
2009											
Main plot	Control	11.5^{b}	(3.0)	10.4	(2.1)	0.4	(0.2)	5.2^{b}	(1.9)	0.4	(0.2)
	MedBA	14.6^{ab}	(3.3)	15.9	(2.3)	0.5	(0.4)	10.4^{ab}	(2.0)	1.0	(0.6)
	LowBA	10.9^{b}	(1.6)	16.1	(3.7)	1.9	(1.5)	18.7^{a}	(4.4)	0.5	(0.2)
	Clearcut	23.6^{a}	(5.9)	18.1	(3.4)	0.7	(0.3)	18.4^{a}	(4.2)	1.1	(0.8)
	p-Value	0.0235		0.1240		0.5646		0.0056		0.4977	
Split plot	NT	15.9	(3.9)	15.0	(2.0)	1.1	(0.6)	13.2	(3.2)	0.7	(0.3)
	H	12.7	(3.2)	13.4	(1.6)	0.8	(0.4)	11.0	(1.7)	1.0	(0.4)
	H + F	16.9	(2.1)	16.9	(3.3)	0.6	(0.4)	15.3	(3.1)	0.6	(0.4)
	p-Value	0.1522		0.1668		0.5312		0.3048		0.3462	
2010											
Main plot	Control	13.2^{b}	(2.7)	12.6	(3.0)	1.5	(0.9)	6.3^{b}	(1.6)	0.7	(0.4)
	MedBA	18.5^{ab}	(3.9)	16.9	(3.2)	1.2	(0.9)	15.6^{ab}	(2.7)	2.2	(1.0)
	LowBA	16.7^{ab}	(3.8)	17.8	(5.3)	3.8	(2.7)	18.3^{a}	(4.0)	1.1	(0.7)
	Clearcut	23.6^{a}	(4.6)	16.7	(2.6)	1.3	(0.7)	22.3^{a}	(3.4)	1.1	(0.6)
	p-Value	0.0093		0.3829		0.5674		0.0020		0.1454	
Split plot	NT	18.4	(3.2)	16.0	(3.1)	2.1	(1.1)	14.9	(2.4)	1.0	(0.8)
	H	16.5	(3.7)	15.2	(2.9)	2.1	(1.0)	14.5	(2.4)	1.4	(0.6)
	H + F	18.3	(3.0)	16.8	(4.0)	1.2	(0.6)	17.0	(2.7)	0.9	(0.5)
	p-Value	0.5679		0.9346		0.7004		0.8286		0.0681	

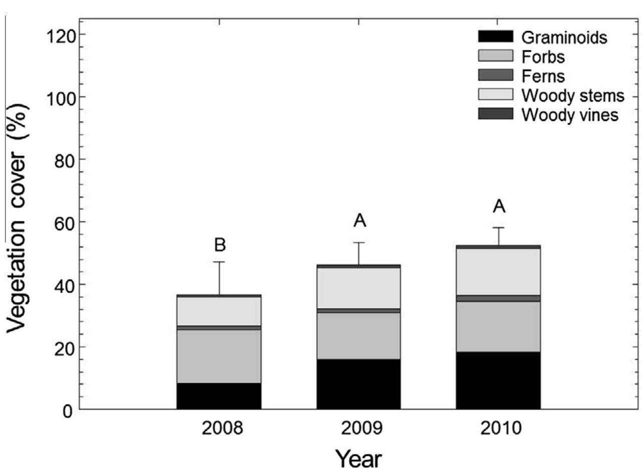

Fig. 3. Vegetation cover (%) by functional group in 2008, 2009, and 2010. Only NT split-plots were used for the analyses because split-plot treatments were applied in 2009. Error bars are one standard error of the mean total cover, and the same letter indicates pair-wise comparisons for total cover are not significantly different at $\alpha = 0.05$.

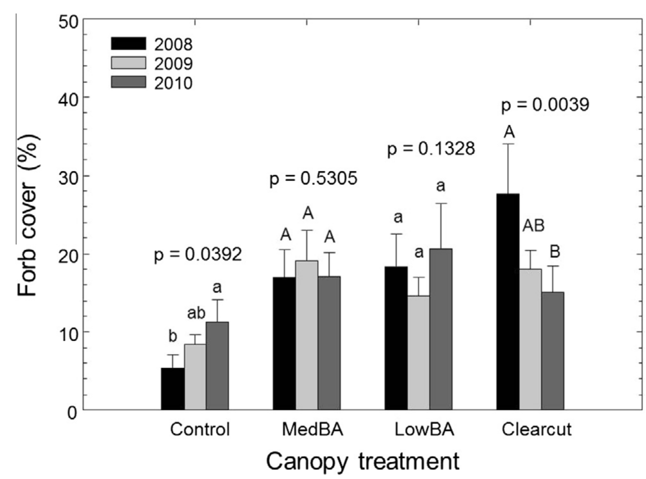

Fig. 4. Results of repeated measures ANOVA showing the significant year by treatment interaction for mean cover (+ one standard error) for forbs. *p*-Values relate to year effects within each treatment, and the same letter indicates pair-wise comparisons among years within each treatment are not significantly different at $\alpha = 0.05$.

a technique to rapidly change vegetation structure by reducing woody stem density and improving opportunities for fire management (e.g., Addington et al., 2012; Freeman and Jose, 2009; Haywood, 2009; Jose et al., 2010; Kush et al., 1999; Provencher et al., 2001b). The appropriate herbicide type is largely dependent on the initial vegetation density and composition, and previous studies have evaluated the effectiveness of different herbicide types, rates, and application methods for achieving restoration objectives (Litt et al., 2001). Herbicides that target woody vegetation, including imazapyr, hexazinone, and triclopyr, have been reported to increase longleaf pine seedling growth (Freeman and Jose, 2009; Jose et al., 2010; Knapp et al., 2006) or the cover of herbaceous vegetation (Brockway et al., 1998; Freeman and Jose, 2009). In our study, herbicides significantly reduced mid-story woody stem density in the first year following application, but high variability in stem densities resulted in no significant differences among split-plot treatments two years after treatment. The long-term effects of herbicides on stand structure are not well

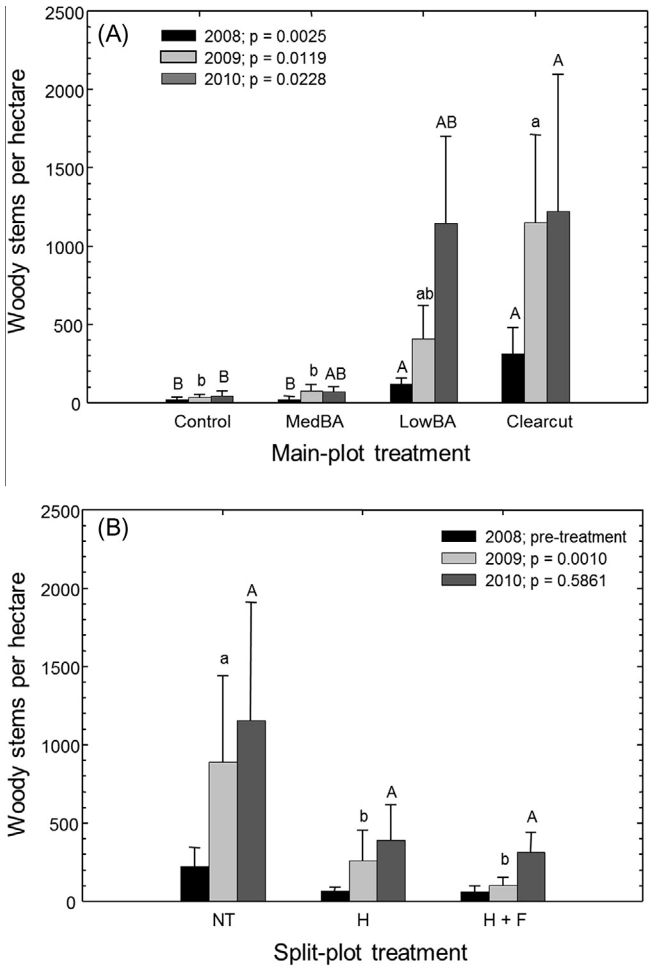

Fig. 5. Woody stem density in the midstory layer (mean + one standard error) in 2008, 2009, and 2010 by (A) main-plot treatment and (B) split-plot treatment. The same letter indicates pair-wise comparisons among treatments within each year are not significantly different at $\alpha = 0.05$.

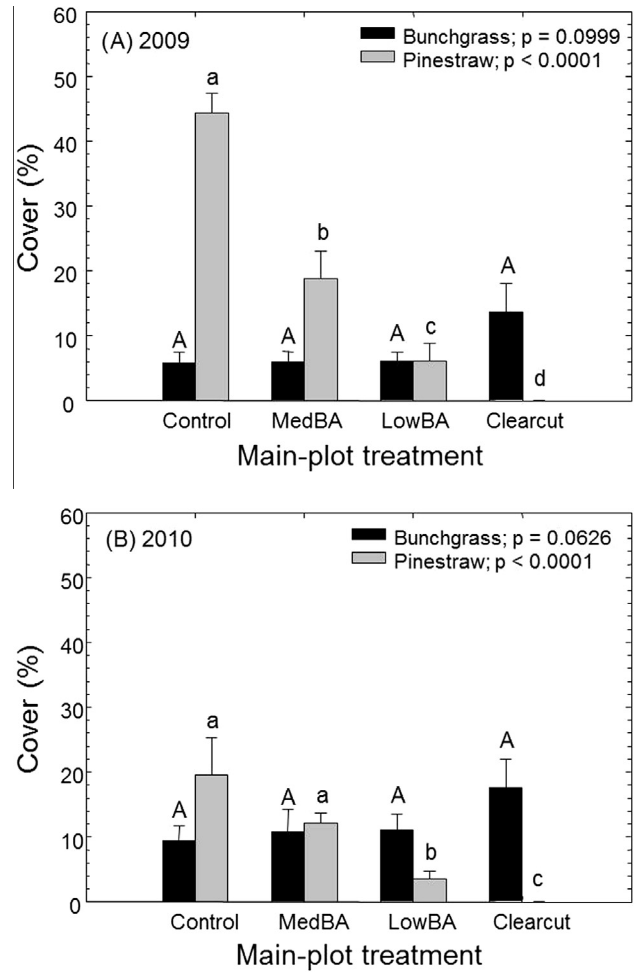

Fig. 7. Cover of important fine fuels (bunchgrasses and pine straw) by main-plot treatment in 2009 (panel A) and 2010 (panel B). The same letter within a response variable indicates pair-wise comparisons are not significantly different at $\alpha = 0.05$.

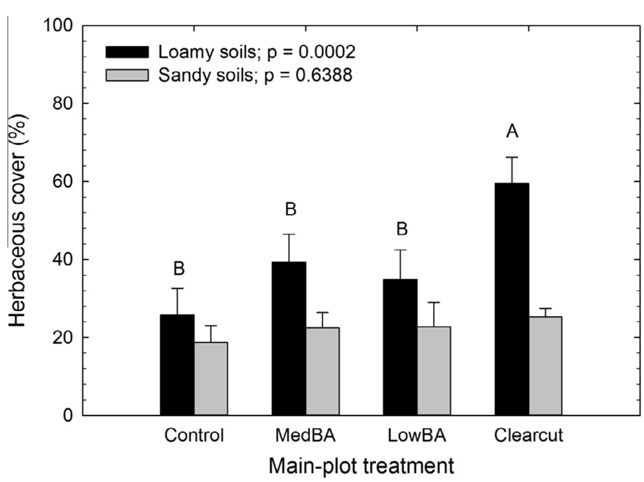

Fig. 6. Main-plot treatment effects on herbaceous vegetation cover in 2009 on loamy soils and sandy soils. The same letter indicates pair-wise comparisons among treatments within each soil type are not significantly different at $\alpha = 0.05$.

documented. However, Kush et al. (1999) reported that the understory biomass of woody vegetation was higher on plots treated with a single herbicide application than on untreated controls 23 years after treatment, suggesting that herbicide effects can be transient or may require multiple applications. Provencher et al. (2001a) found that prescribed fire was more effective for increasing herbaceous plant densities than herbicide control of woody vegetation, and it is not likely that short-term improvements in ground layer vegetation structure caused by herbicides can be maintained without frequent fire management (Brockway and Outcalt, 2000; Freeman and Jose, 2009). Thus, initial herbicide applications may be most useful for changing the vegetation structure to improve fire management. Once frequent prescribed fire can be applied, additional herbicide treatments may not be needed. It should also be noted that the site preparation used in this study was designed to control woody vegetation. As a result, the effects of the herbicide study treatment on woody vegetation represent control of vegetation not killed by, or established after, the site preparation treatment and are likely an underestimation of herbicide effects in the absence of site preparation.

The establishment success of artificially regenerated longleaf pine seedlings is often considered a priority during the conversion of other canopy species to longleaf pine. Consequently, additional cultural treatments, such as chemical weeding treatments or fertilization, may be used to improve seedlings establishment (Haywood, 2000, 2005; Ramsey et al., 2003). In our study, herbaceous vegetation control was applied in bands over the rows of longleaf pine seedlings, with the objective of localizing the herbicide effects around seedlings. As a result, approximately 30% of the study plots were treated with the herbaceous vegetation control treatment, and we found few effects of the herbicide treatment on herbaceous vegetation at the stand level. Targeted application of herbicides is often favored over broadcast application for restoration of sensitive plant communities and has been found to result in greater species richness and diversity than broadcast application in longleaf pine forests in Florida (Brockway and Outcalt, 2000). In contrast, the fertilization treatment used in this study was broadcast throughout the entire study plots. Despite having no effect on individual functional groups, the fertilizer resulted in a short-term increase in total vegetation cover when compared to the herbicide treatment but did not increase cover over that in the untreated plots, suggesting that fertilization has little effect on ground layer vegetation abundance.

5. Management implications

Converting existing loblolly pine stands to longleaf pine requires attention to the ground layer vegetation, a critical component that contributes to ecosystem function. The target stand conditions for longleaf pine restoration include a ground layer that is dominated by herbaceous species, with a minor component of hardwoods and few mid-story stems, and the desired herbaceous layer includes large bunchgrasses that serve as fine fuels for frequent surface fires and forbs that contribute to high levels of species richness. The structure and condition of ground layer vegetation at a given time are the reflection of land use history and management legacies, in addition to biotic and abiotic controls on plant establishment and persistence (Brudvig and Damschen, 2011). Consequently, the initial stand conditions will affect the response of the vegetation community to canopy removal. On our study sites, herbaceous plants dominated the ground layer vegetation, and both herbaceous and woody vegetation increased following canopy removal. However, we also found that soil texture affected the response of herbaceous vegetation cover to canopy density in 2009. Previous studies have identified soil texture and soil moisture to be important factors affecting productivity in longleaf pine forests (Mitchell et al., 1999; Kirkman et al., 2001). Although our study was not explicitly designed to determine the effects of soil texture on vegetation response, our results suggest that soil factors that affect productivity are likely to also affect the outcomes of restoration treatments.

Clearcutting is traditionally used for establishing longleaf pine seedlings on sites occupied by other pine species, and past studies have demonstrated rapid seedling growth in the absence of canopy trees (e.g., Freeman and Jose, 2009; Haywood, 2005; Hu et al., 2012; Knapp et al., 2006). Despite potential increases in seedling growth on Clearcut plots, the long-term effects of clearcutting on the vegetation structure may conflict with restoration objectives (Kirkman et al., 2007; Mitchell et al., 2006). For example, the characteristically high level of plant species richness in the longleaf pine ecosystem is largely found among the forb group in uplands sites. We found few effects of our treatments on forb cover throughout this study, except for a decrease in forb cover from 2008 to 2010 on the Clearcut plots. The reason for the decrease is not clear, but it is possible that an increase in woody vegetation and no change in graminoid cover resulted in increased competitive pressure for forbs. In addition, annual species associated with disturbance may have increased in Clearcut plots in 2008 and then decreased with time since the logging disturbance. Thus, the effect of silvicultural treatments on species composition is also an important consideration during restoration.

A frequent fire regime is critical to maintain the desired vegetation structure, and large bunchgrasses and pine needles from canopy trees are important fuels. Previous studies have demonstrated that prescribed fires burn hotter and more completely beneath canopy trees, where pine needle inputs increase fuel loads (Grace and Platt, 1995; O'Brien et al., 2008; Williamson and Black, 1981). We found that pine needle cover decreased with canopy removal, while bunchgrass cover was not significantly affected by canopy density. Previously, Knapp et al. (2011) found that the prescribed fires burned more completely on Control and MedBA plots than on the Clearcut plots. These results, along with the increased density of mid-story stems on Clearcut plots, suggest that clearcutting may have important, undesirable long-term effects on fire management in these stands (see Mitchell et al., 2006).

Our results indicate that low to moderate canopy removal can be used to maintain or encourage the early development of herbaceous vegetation while limiting the release of woody species into the mid-story during longleaf pine restoration. Previous work indicates that maintaining the basal area of canopy pines <9 m^2/ha can result in the establishment of underplanted longleaf pine in longleaf, slash, and loblolly pine forests (Hu et al., 2012; Kirkman et al., 2007; Knapp et al., 2013; Mitchell et al., 2006), suggesting that multiple restoration objectives could be reached simultaneously. The canopy structure created would be similar to that of an irregular shelterwood (Brockway et al., 2006), with the distinction that the desirable regeneration is the underplanted longleaf pine rather than natural regeneration in loblolly pine forests. If woody stems are abundant or if heavy canopy removal is used, herbicides that target hardwood vegetation are recommended to reduce the mid-story layer. Although the herbicides used in this study reduced woody stems in the mid-story, they had few effects on herbaceous cover in the ground layer. In situations in which herbaceous vegetation is dense enough to affect seedling performance, we recommend using band-spray herbicide application to reduce the stand-level effects on the herbaceous plant community. We found that fertilizer used in combination with herbicide increased the cover of ground layer vegetation compared to herbicide alone in the first year following application, but this effect was transient. The results presented here are relatively short-term, and it is not clear how our study treatments will affect stand development through time. However, continued management with frequent prescribed fire will be critical to improving and maintaining the desired vegetation structure and meeting longleaf pine restoration goals.

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