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Silvicultural treatments for converting loblolly pine to longleaf pine dominance: effects on ground layer and midstorey vegetation

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Keywords
Ecological restoration; Fertilization; Functional group; Herbicide; Midstorey stem density

Abbreviations
H = chemical control of woody vegetation
H+F = chemical control plus fertilization
NT = untreated.

Nomenclature
Weakley (2010)

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Abstract

Questions: How do management practices used to enhance longleaf pine (*Pinus palustris*) seedling survival and growth under a loblolly pine (*Pinus taeda*) canopy alter the structure of midstorey and ground layer vegetation? Do management treatments achieve general restoration targets for longleaf pine ecosystem structure?

Location: Marine Corps Base Camp Lejeune, NC, USA within the Middle Atlantic Coastal Plain Ecoregion.

Methods: Four levels of timber harvest were applied to loblolly pine stands: Control (uncut, basal area ~16.2 $m^2 \cdot ha^{-1}$), MedBA (residual basal area ~9.0 $m^2 \cdot ha^{-1}$), LowBA (residual basal area ~6.4 $m^2 \cdot ha^{-1}$) and Clearcut (residual basal area of 0 $m^2 \cdot ha^{-1}$). Within each canopy treatment, we applied three cultural treatments selected to facilitate longleaf pine seedling success: NT (untreated), H (chemical control of woody vegetation) and H + F (chemical control plus fertilization). Vegetation responses, including the abundance (cover) of ground layer vegetation and midstorey stem densities, were reported for three growing seasons (2008–2010) following canopy removal.

Results: The ground layer was dominated by woody vegetation, and total vegetation cover generally increased with increasing canopy removal. Canopy treatment effects varied through time. Clearcut plots had higher total herbaceous and graminoid cover than MedBA and Control plots in 2008, while woody cover was significantly lower on Control plots than on LowBA and Clearcut plots in 2009. Clearcut plots had higher densities of loblolly pines than Control plots in 2009 and 2010. The herbicide treatment reduced hardwood densities, but increased loblolly pine densities, especially in 2010.

Conclusions: Successful restoration prescriptions are often site-specific because of different land-use history, climate, site characteristics and starting conditions. To achieve the restoration objective of creating an open midstorey with an herbaceous-dominated ground layer when converting loblolly pine stands to longleaf pine dominance on relatively productive sites with abundant hardwoods and aggressive loblolly pine natural regeneration, canopy retention can slow the rate of development of loblolly pine regeneration and herbicides reduce hardwood stem densities. Frequent, repeated burning would likely be required to further reduce woody vegetation and increase the relative abundance of herbaceous vegetation.

Introduction

In the southeastern United States, longleaf pine (*Pinus palustris*) ecosystem restoration is a common objective for many forest landowners. Logging, land-use changes and fire exclusion and suppression reduced the extent of historically dominant longleaf pine ecosystems to approximately 2.2% (or 1 million ha) of the acreage prior to

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European settlement (Wahlenburg 1946; Frost 1993, 2006; Oswalt et al. 2012). Many upland sites suitable for longleaf pine were reforested with faster-growing species, such as loblolly pine (*Pinus taeda*), which coincided with anthropogenic disruption of frequent fire regimes common to southern pine forests (Frost 2006). Consequently, the stand structure of the resulting second-growth loblolly pine forests commonly included a dense canopy of loblolly pine, a well-developed shrub/midstorey layer and sparse herbaceous ground layer vegetation (Hedman et al. 2000). In contrast, the structure of longleaf pine forests is generally characterized as a variable canopy dominated by longleaf pine, an open midstorey layer and a grass-dominated, species-rich herbaceous ground layer (Walker 1993; Landers et al. 1995; Peet 2006).

Restoration targets for longleaf pine ecosystems commonly include certain compositional and structural attributes (e.g. establishing longleaf pine trees, reducing midstorey abundance, increasing the abundance and diversity of herbaceous vegetation), as well as re-establishing frequent fire as a disturbance process (Walker & Silletti 2006; Martin & Kirkman 2009). Objectives for structural restoration in the longleaf pine ecosystem are rarely specified, as they are variable in time and space. Consequently, early restoration efforts were mostly directed toward establishing longleaf pine as a future canopy species by afforestation on non-forested sites or conversion on sites occupied by other forest types. Conventional regeneration methods involving clear-cutting, site preparations and planting have generally been effective for the establishment of longleaf pine (Boyer 1988; Brockway et al. 2006; Knapp et al. 2006). However, the effects of practices intended to maximize the desired response of one restoration objective (e.g. longleaf pine seedling establishment) must also be evaluated for impacts on other restoration objectives (e.g. vegetation response or ability to manage with fire). Treatments designed to improve conditions for planted longleaf pine seedlings, such as site preparation or release, may simultaneously favour objectives related to ground layer vegetation (e.g. Freeman & Jose 2009) or, conversely, may result in undesirable responses.

A recently developed restoration model for converting slash pine (*Pinus elliottii*) plantations to longleaf pine suggests that retaining canopy pines during longleaf pine seedling establishment can maintain continuity of ecosystem processes during restoration (Kirkman et al. 2007). The fuel inputs provided by needle-fall from the existing canopy pines are important for introducing or maintaining frequent fire regimes in longleaf, slash and loblolly pine forests (Kirkman et al. 2007; Mitchell et al. 2009; Knapp et al. 2011). Several studies have shown that longleaf pine seedlings are capable of establishing beneath canopies of longleaf pine (Palik et al. 1997; Pecot et al. 2007), slash pine (Kirkman et al. 2007) and loblolly pine (Hu et al. 2012a; Knapp et al. 2013), although seedling growth is reduced by the retention of canopy trees. However, the regeneration and development of undesirable tree species in the midstorey may also be slowed by canopy retention (Kirkman et al. 2007; Jack et al. 2010; Knapp et al. 2014). A recent study at Fort Benning in Georgia and Alabama found that retaining low to moderate levels of canopy density may provide an effective balance for maintaining desirable vegetation structure and creating fuel conditions for a frequent fire regime during conversion of loblolly pine stands to longleaf pine dominance (Knapp et al. 2014).

The outcomes of restoration treatments are likely to vary in magnitude or effect according to local site factors or the initial condition of the vegetation community (Brudvig & Damschen 2011). Previous studies within longleaf pine forests have demonstrated the importance of site characteristics, such as soil texture or moisture, in affecting productivity or composition of vegetation (Gilliam et al. 1993; Mitchell et al. 1999; Kirkman et al. 2001, 2004). Regional variation associated with soils, climate and historic biogeography may signal regional variation in responses to management. Restoration studies, particularly those using partial retention approaches in the longleaf pine ecosystem, have been conducted in very few locations in the southeastern US (e.g. Palik et al. 1997; Pecot et al. 2007), with none in the Atlantic Coastal Plain Ecoregion. Progress toward a general restoration model will require a comprehensive understanding of system responses across the range of starting conditions, both natural and anthropogenic, at broad (e.g. ecoregional) as well as local spatial scales.

To fill a gap in our understanding of regional variation in responses to restoration management protocols, we established this field experiment in the Middle Atlantic Coastal Plain near the northern range of the longleaf pine ecosystem. We investigated management to gradually convert loblolly pine forest to longleaf pine dominance using partial canopy retention. Treatments designed to facilitate longleaf pine seedling establishment were evaluated for their effects on underplanted longleaf pine seedlings (Hu et al. 2012a,b), fuels and fire behaviour (Knapp et al. 2011) and, in this study, the structure and composition (by selected plant groups) of ground layer and midstorey vegetation. The specific objectives of this paper are to report how four canopy and three cultural treatments affect: (1) ground layer vegetation cover of selected functional groups; and (2) the density of three midstorey woody stem groups in loblolly pine stands on moderately well- to well-drained sites at Camp Lejeune, NC.

Methods

Study area

This study was conducted at the United States Marine Corps Base Camp Lejeune (Camp Lejeune) in Onslow County, NC (~34.68° N, 77.33° W). The study area is located within the Atlantic Coastal Flatlands Section of the Outer Coastal Plains Mixed Forest Province (Bailey 1995) and falls within the White Oak watershed in Onslow County, as defined by the North Carolina Department of Water Quality (USMBC Camp Lejeune 2006). The climate is classified as warm humid temperate with hot, humid summers and mild winters. Mean annual temperature is 16 °C, and annual precipitation averages 1420 mm and is evenly distributed throughout the year with a slight increase from Jun to Sept (National Climatic Data Center, Asheville, NC, US). The study sites are on moderately well- to well-drained soils with low to moderate water-holding capacity and low nutrient-holding capacity (Barnhill 1992). Texture and nutrient content of soils in each block are described in Appendix S1.

Based on Camp Lejeune's Integrated Natural Resource Management Plan (INRMP) and communications with local forest managers, the study locations were selected on sites that were historically longleaf pine communities but are currently occupied by other species, such as loblolly pine. We selected seven mature loblolly pine stands as replication blocks. Four blocks (Blocks 1–4) were located in loblolly pine plantations that were established in 1971, with mean DBH ranging from 26.4 to 33.9 cm. The remaining blocks (Blocks 5–7) were located in loblolly pine stands that were established around 1945, with mean DBH ranging from 38.7 to 44.3 cm. None of the blocks had been managed with frequent fire in the past few decades. Prior to treatment application, midstories were dominated by sweetgum (*Liquidambar styraciflua*), ranging from 4900 stems·ha^{-1} in Block 2 to 14 300 stems·ha^{-1} in Block 7. The cover of ground layer vegetation prior to study establishment (in 2006) was dominated by woody vegetation (Appendix S2; USMCB Camp Lejeune 2006).

Experimental design

The study used a randomized complete block, split-plot design, with the location of individual loblolly pine stands used as the blocking factor. Each block consisted of four whole plot treatments that included different levels of timber harvest in which residual canopy trees were distributed approximately uniformly within each whole plot: Control (uncut, mean basal area of 16.2 m^2·ha^{-1}), MedBA (harvest to a residual basal area of 9.0 m^2·ha^{-1}), LowBA (harvest to a residual basal area of 6.4 m^2·ha^{-1}) and Clearcut (complete canopy removal). Whole plots were 100 × 100 m (1 ha) with the exception of Clearcut plots, which were 141 × 141 m (2 ha) to create clearcut conditions in the plot centre. Small trees were marked for removal in the timber harvest, thus favouring the retention of large, vigorous trees. Harvesting was completed in all blocks between Feb and May 2007. We measured residual basal area following harvest and found that the LowBA and MedBA treatments in two blocks (Blocks 3 and 4) were similar, so both were considered to be the same canopy treatment (LowBA). In addition, we abandoned one canopy treatment plot (LowBA in Block 4) in 2010 due to conflicts with military training. As a result, we used data from seven blocks and 27 canopy treatment plots for analyses in this study.

Following timber harvest, all study sites were mechanically prepared by mulching all standing midstorey vegetation with a Fecon Bull Hog® rotary mulcher in the summer of 2007 and by prescribed burning in autumn 2007. One-year-old container-grown longleaf pine seedlings were planted by hand in Dec 2007 at a spacing of 1.8 × 3.0 m (approximate 1800 seedlings·ha^{-1}). Because re-introducing frequent fire into these stands was considered a critical part of restoration, all study areas were burned with dormant season prescribed fire between the second and third growing seasons (Jan to Mar 2010). Thus, the 2007 site preparation mulching/prescribed burning and the 2010 dormant season prescribed burns were applied as operational treatments and were not included as study treatments.

The split-plot treatments, hereafter referred to as cultural treatments, included additional practices designed to maximize longleaf pine seedling establishment and early growth by increasing resources directly (fertilization) or indirectly (competition control). The cultural treatments included an untreated control (NT), woody competition control with herbicides (H) and competition control with herbicides plus fertilization (H + F). Each whole plot was divided into four equal sections and three of the sections were randomly selected for cultural treatment application. Within each section, cultural treatments were applied to a 30 × 30 m area centered on a 20 × 20 m measurement area. The herbicide treatment included 4.8 g acid equivalent·l^{-1} of imazapyr applied in a 1% solution with 1/4% non-ionic surfactant applied as a direct foliar application to target woody vegetation in Oct 2008. The H + F treatment included the herbicide treatment described above as well as an application of 10-10-10 NPK granular fertilizer evenly broadcast at a rate of 280 kg·ha^{-1} in early May 2009. A detailed timeline of all treatments applied during the study period is shown in Fig. 1.

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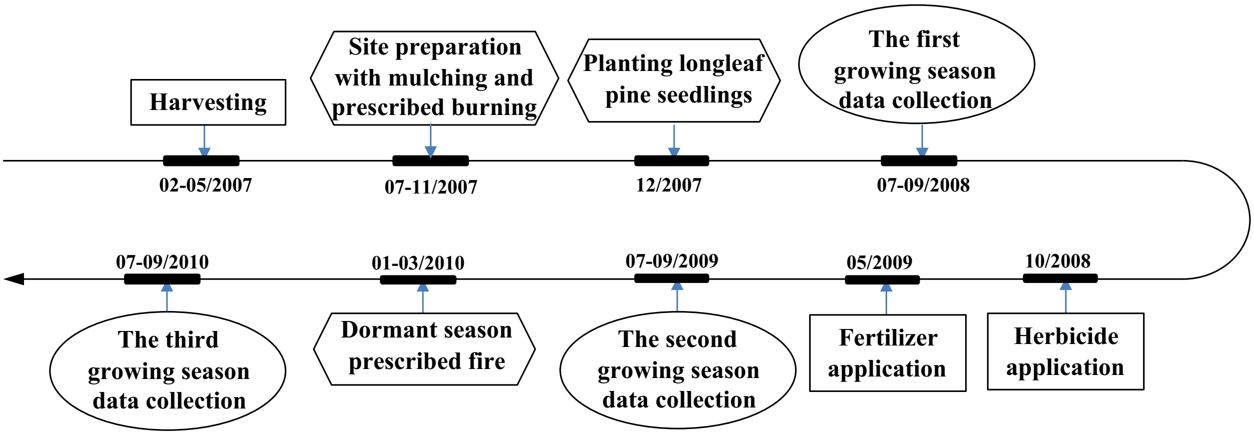

Fig. 1. Timeline of treatment application and data collection during the study period. The shapes in the diagram indicate the type of treatment: rectangles indicate study treatments, hexagons indicate management practices used on all study areas, and ellipses indicate data collection periods.

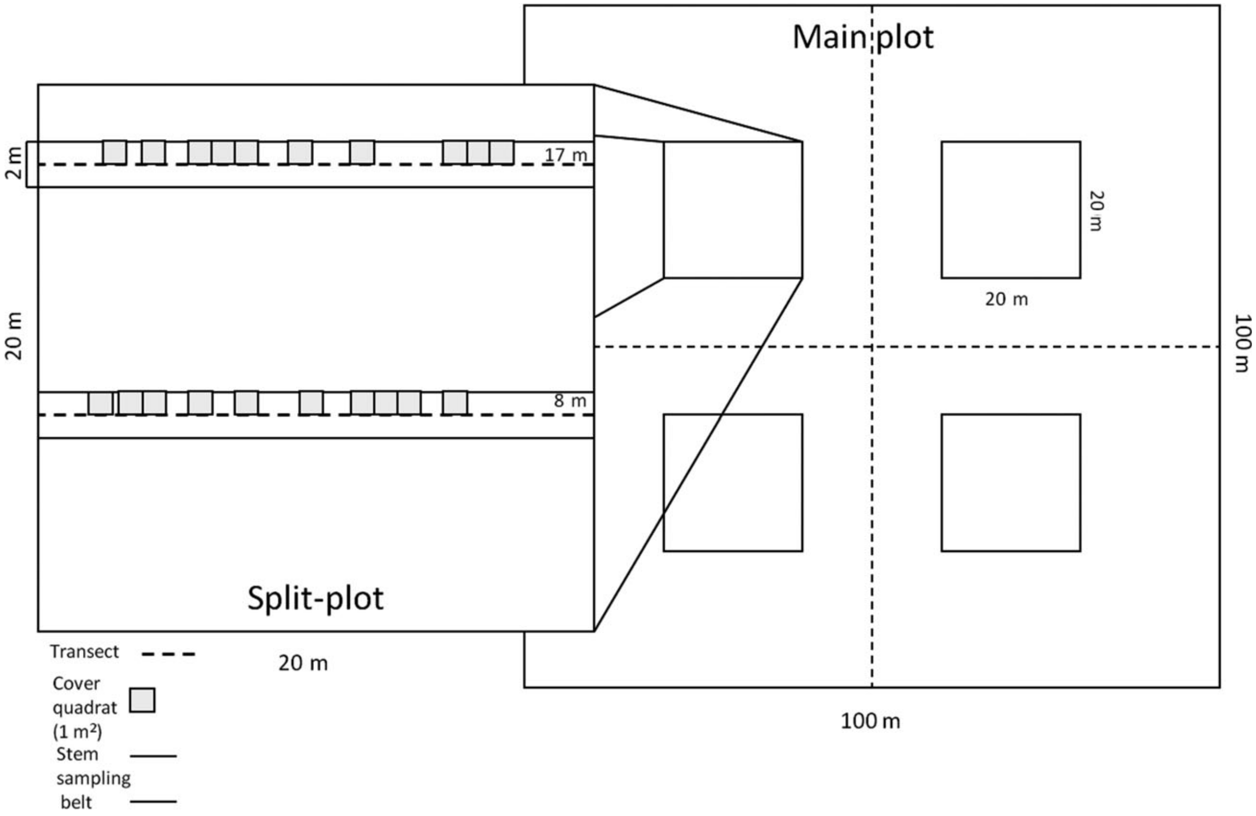

Fig. 2. Illustration of the whole plot and split-plot layout and the sampling design used to quantify cover of the ground layer vegetation (≤1-m tall) and midstorey stems (>1-m tall but <4 cm DBH).

Data collection

In each split-plot, we established two parallel, 20-m transects, with the starting location of each transect randomly located (Fig. 2). Along each transect, we then randomly located ten 1 × 1 m sampling quadrats. We did not sample near the ends 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 visual estimates of the percentage cover of all vegetation $\leq$1-m tall that overlapped the area within the quadrat. We estimated cover as the percentage of the plot that would be covered by vegetation when viewed from directly overhead. Cover was recorded using North Carolina Vegetation Survey cover classes (Peet et al. 1998): 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 more than 100% if vegetation overlapped. We estimated cover by functional group (graminoids including grasses, rushes, sedges; forbs; and woody species including shrubs, trees, woody vines). Cover of ground layer vegetation was recorded in Jul and/or Aug in each year after harvest (2008–2010).

To determine the density of midstorey woody stems (>1-m tall but <4 cm DBH), we used each transect as the centre 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.

Data analysis

Cover data were converted to the mid-point of each class for analyses. We also calculated the relative abundance of woody and herbaceous vegetation as follows:

Relative abundance of woody vegetation = (woody cover/total cover) ×100%;

Relative abundance of herbaceous vegetation = [(graminoid cover + forb cover)/total cover] × 100%.

Midstorey stem densities were compiled and analysed in three species groups: *Rubus* spp., loblolly pines and hardwood species [e.g. sweetgum, oaks (*Quercus* spp.), sweetleaf (*Symplocos tinctoria*)]. All variables were averaged at the split-plot level by year for statistical analyses.

An ANOVA (2008 data) and split-plot ANOVA (2009 and 2010 data) were used to determine the effects of canopy (whole plot) and cultural (split-plot) treatments on the cover of total vegetation, woody vegetation, herbaceous vegetation, graminoids and forbs, relative abundances of both woody and herbaceous vegetation and midstorey stem densities of *Rubus* spp., loblolly pines and hardwood species during each growing season. To determine the change in vegetation cover and midstorey stem density through time, we conducted a repeated measures ANOVA using only NT split-plot data because cultural treatments were not installed until 2009 (Fig. 1). The analyses used for each variable are specified in Appendix S3.

For each ANOVA test described above, we used transformations as necessary to satisfy assumptions of constant variance and normality (Krebs 1999). All analyses were performed using PROC MIXED in SAS9.1 (SAS Institute, Cary, NC, US) with mixed models and a random block effect. Tukey's honestly significant difference (HSD) test was used to determine differences in pair-wise comparisons among the canopy and cultural treatments for each variable. The level of statistical significance was set at $\alpha = 0.05$.

Results

Treatment effects on ground layer vegetation cover

There was no interaction between the canopy and cultural treatment effects on the cover of each functional group or the relative abundance of woody and herbaceous vegetation in either 2009 ($P \geq 0.087$) or 2010 ($P \geq 0.222$; Appendix S4). Canopy treatment effects were detected for total, herbaceous and graminoid cover in 2008, total and woody cover in 2009, and total cover in 2010 ($P \leq 0.029$; Table 1). In the 2008 growing season, both Clearcut and LowBA plots had higher total cover than Control plots

Table 1. Covers (%) of total vegetation, woody vegetation, herbaceous vegetation, graminoids, forbs and relative abundances (%) of woody and herbaceous vegetation by canopy treatment. Means are followed by SE in parenthesis. Means with the same letter within each year indicate no significant difference ($\alpha = 0.05$).

Canopy treatment	Control	MedBA	LowBA	Clearcut
Cover				
Total				
2008	50.7 b (3.7)	62.9 ab (8.1)	70.7 a (5.1)	76.7 a (3.7)
2009	42.7 b (5.4)	54.4 ab (8.0)	69.5 a (6.2)	76.8 a (7.5)
2010	30.5 b (3.4)	38.4 b (5.3)	54.6 ab (5.4)	58.8 a (3.7)
Woody				
2008	31.3 a (1.4)	45.0 a (7.0)	44.1 a (4.4)	43.8 a (5.0)
2009	27.9 b (4.1)	42.1 ab (6.7)	48.0 a (5.2)	47.5 a (4.9)
2010	20.8 a (3.0)	27.2 a (5.5)	41.8 a (5.4)	40.2 a (4.0)
Herbaceous				
2008	19.4 b (2.5)	17.8 b (3.8)	26.6 ab (2.9)	32.9 a (4.8)
2009	14.8 a (2.6)	12.3 a (2.5)	21.5 a (2.7)	29.3 a (6.1)
2010	9.7 a (1.5)	11.2 a (2.0)	12.8 a (2.7)	18.6 a (3.2)
Graminoids				
2008	15.8 b (2.3)	16.2 b (3.7)	21.6 ab (2.5)	26.6 a (3.3)
2009	9.6 a (1.8)	7.7 a (2.1)	15.0 a (2.5)	23.3 a (5.1)
2010	7.5 a (1.4)	7.3 a (0.9)	9.3 a (2.0)	14.3 a (2.5)
Forbs				
2008	3.6 a (0.9)	1.6 a (0.4)	5.0 a (1.9)	6.3 a (1.9)
2009	5.2 a (1.7)	4.6 a (1.8)	6.5 a (1.6)	6.0 a (1.5)
2010	2.2 a (0.4)	3.9 a (1.7)	3.5 a (1.1)	4.3 a (1.0)
Relative abundance				
Woody				
2008	65.9 a (3.8)	71.3 a (6.2)	63.3 a (4.1)	57.8 a (5.6)
2009	62.0 a (5.4)	73.2 a (4.6)	68.8 a (3.4)	64.2 a (5.4)
2010	66.5 a (4.9)	62.0 a (7.0)	73.9 a (3.7)	67.1 a (6.0)
Herbaceous				
2008	34.1 a (3.8)	28.7 a (6.2)	36.7 a (4.1)	42.2 a (5.6)
2009	38.0 a (5.4)	26.8 a (4.6)	31.2 a (3.4)	35.8 a (5.4)
2010	33.5 a (4.9)	38.0 a (7.0)	26.1 a (3.7)	32.9 a (6.0)

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($P \leq 0.006$), and Clearcut plots had higher herbaceous cover and graminoid cover than Control and MedBA plots ($P \leq 0.040$). In the 2009 growing season, both Clearcut and LowBA plots had higher total cover and woody cover than Control plots ($P \leq 0.046$). In the 2010 growing season, Clearcut plots had higher total cover than Control and MedBA plots ($P \leq 0.032$). However, neither woody species relative abundance ($P \geq 0.154$) nor herbaceous relative abundance ($P \geq 0.112$) was affected by canopy treatment through the first three growing seasons (Appendix S5).

Cultural treatments significantly affected the cover of each functional group except herbaceous cover in 2009, and herbaceous, graminoid and forb cover in 2010 ($P \geq 0.120$; Table 2, Appendix S4). In 2009, the cover of total vegetation ($P < 0.001$), woody vegetation ($P < 0.001$), graminoids ($P \leq 0.002$) and the relative abundance of woody vegetation ($P \leq 0.002$) was higher in NT plots than in H and H + F plots. In contrast, forb cover ($P \leq 0.004$) and herbaceous relative abundance ($P \leq 0.009$) were lower in NT plots than in H and H + F plots. In 2010, NT plots had higher total cover ($P < 0.001$) and woody cover ($P < 0.001$) than H and H + F plots. All plots had higher relative abundance of woody cover than herbaceous cover, but the relative abundance of woody cover was significantly larger in NT plots than in H and H + F plots ($P \leq 0.002$; Appendix S5).

Table 2. Covers (%) of total vegetation, woody vegetation, herbaceous vegetation, graminoids, forbs and relative abundances (%) of woody and herbaceous vegetation by cultural treatment. Means are followed by SE in parenthesis. Means with the same letter within each year indicate no significant difference (α = 0.05).

Cultural treatment	NT	H	H + F
Cover			
Total			
2009	81.6 a (5.1)	52.0 b (5.4)	51.3 b (6.5)
2010	61.0 a (3.9)	39.0 b (4.0)	39.3 b (4.3)
Woody			
2009	60.7 a (3.4)	33.9 b (4.2)	30.0 b (4.1)
2010	48.6 a (3.6)	24.9 b (3.6)	26.3 b (4.0)
Herbaceous			
2009	20.8 a (3.2)	18.1 a (3.2)	21.3 a (4.2)
2010	12.5 a (2.0)	14.1 a (2.4)	13.0 a (2.4)
Graminoids			
2009	18.7 a (3.0)	11.2 b (2.5)	13.4 b (3.4)
2010	10.3 a (1.8)	9.9 a (1.6)	9.1 a (1.9)
Forbs			
2009	2.1 b (0.6)	7.0 a (1.7)	7.9 a (1.5)
2010	2.2 a (0.4)	4.2 a (1.1)	3.9 a (1.1)
Relative abundance			
Woody			
2009	77.1 a (2.6)	62.9 b (4.8)	59.9 b (4.0)
2010	80.1 a (2.6)	60.3 b (5.0)	63.6 b (4.8)
Herbaceous			
2009	22.9 b (2.6)	37.1 a (4.8)	40.1 a (4.0)
2010	19.9 b (2.6)	39.7 a (5.0)	36.4 a (4.8)

Treatment effects on midstorey stem density

Canopy treatments did not affect midstorey *Rubus* spp. density in any growing season ($P \geq 0.413$; Table 3, Appendix S6). The Clearcut treatment resulted in higher loblolly pine densities than the Control treatment during the 2009 ($P = 0.007$) and 2010 ($P = 0.004$) growing seasons. Hardwood stem density in LowBA plots was higher than in Control plots during the 2008 growing season ($P = 0.032$), an effect not observed in subsequent years. No interaction was detected between the canopy and cultural treatments for any species group in either 2009 ($P \geq 0.802$) or 2010 ($P \geq 0.517$). The responses of midstorey stem densities to cultural treatments varied by year (Table 4). In 2009, hardwood stem density was higher on NT plots than on H and H + F plots ($P < 0.001$), but cultural treatments had no effect on stem densities of *Rubus* spp. ($P = 0.576$) or loblolly pines ($P = 0.169$; Appendix S6). In 2010, *Rubus* spp. density was lower on NT plots than on H + F plots ($P = 0.017$); NT plots had higher hardwood stem density ($P \leq 0.020$) but lower loblolly pine density ($P < 0.001$) than H and H + F plots.

Changes in ground layer and midstorey vegetation through time

Results from the repeated measures analyses indicated that the cover of total vegetation, woody vegetation, herbaceous vegetation, graminoids and forbs, as well as the relative abundances of woody and herbaceous vegetation,

Table 3. Densities (stems·ha^{-1}) of midstorey *Rubus* spp., loblolly pines and hardwood species by canopy treatment. Means are followed by SE in parenthesis. Means with the same letter within each year indicate no significant difference (α = 0.05).

Canopy treatment	Control	MedBA	LowBA	Clearcut
Rubus spp.				
2008	42 a (18)	100 a (90)	203 a (106)	95 a (50)
2009	71 a (44)	0 a (0)	141 a (96)	30 a (21)
2010	280 a (140)	833 a (534)	745 a (246)	494 a (223)
Loblolly pines				
2008	12 a (12)	275 a (195)	193 a (146)	321 a (161)
2009	125 b (68)	1500 ab (622)	1385 ab (371)	2631 a (494)
2010	387 b (247)	1167 ab (570)	2729 ab (780)	5149 a (1266)
Hardwood species				
2008	1792 b (502)	2408 ab (841)	3646 a (732)	2393 ab (481)
2009	1065 a (403)	1492 a (608)	1974 a (600)	1768 a (632)
2010	673 a (216)	1242 a (505)	1880 a (613)	1268 a (405)

Table 4. Densities (stems·ha^{-1}) of midstorey *Rubus* spp., loblolly pines and hardwood species by cultural treatment. Means are followed by SE in parenthesis. Means with the same letter within each year indicate no significant difference (α = 0.05).

Cultural treatment	NT	H	H + F
Rubus spp.			
2009	79 a (41)	97 a (84)	28 a (17)
2010	144 b (70)	718 ab (255)	866 a (313)
Loblolly pines			
2009	1093 a (280)	1338 a (374)	1778 a (490)
2010	1097 b (371)	2870 a (927)	3412 a (919)
Hardwood species			
2009	4588 a (474)	125 b (45)	74 b (30)
2010	3463 a (484)	181 b (62)	227 b (104)

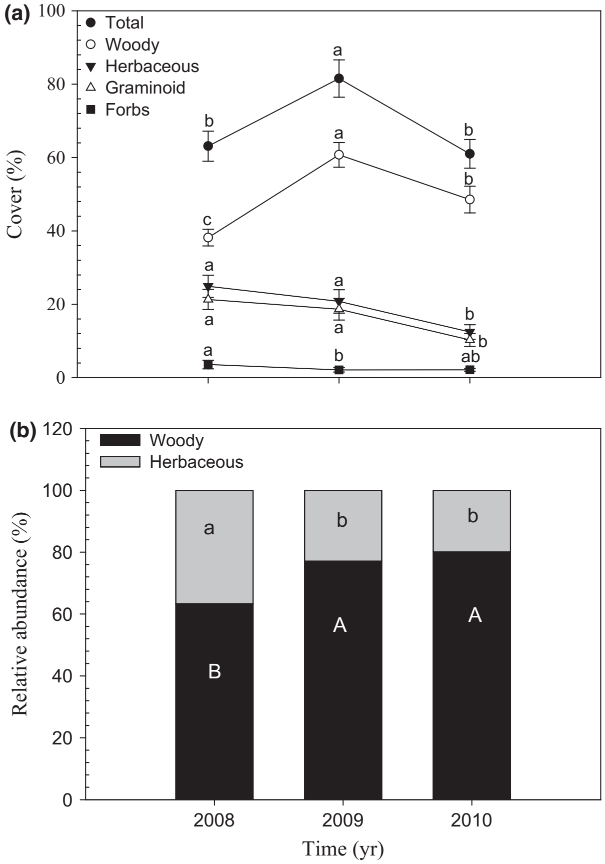

Fig. 3. (**a**) Covers (%; mean ± 1 SE) of total vegetation, woody vegetation, herbaceous vegetation, graminoids and forbs, and (**b**) relative abundances (%) of woody and herbaceous vegetation through time. The same letter in each functional group indicates no significant difference (α = 0.05) among years.

each changed through time ($P \leq 0.041$), with no interactions between year and treatment effects ($P \geq 0.130$; Appendices S4 and S5). However, the changes of these functional groups through three growing seasons differed (Fig. 3). For example, total cover significantly increased from 2008 to 2009 ($P < 0.001$), but total cover in 2010 was not significantly different from cover in 2008 ($P = 0.821$) due to a significant decrease from 2009 to 2010 ($P < 0.001$). Woody cover significantly increased from 2008 to 2009 ($P < 0.001$) and remained significantly different between 2008 and 2010 ($P < 0.001$), despite a significant decrease from 2009 to 2010 ($P < 0.001$). In contrast, the cover of herbaceous vegetation and the cover of graminoids did not significantly change from 2008 to 2009 ($P \geq 0.207$) but significantly decreased from 2009 to 2010 ($P \leq 0.003$), resulting in significant decrease from 2008 to 2010 ($P < 0.001$). Forb cover significantly decreased from 2008 to 2009 ($P = 0.033$), but forb cover in 2010 was not significantly different from cover in 2008 ($P = 0.486$) or 2009 ($P = 0.458$; Fig. 3a).

Regardless of the treatment applied, woody vegetation dominated the ground layer and contributed over 60% of the total cover through the first three growing seasons. Woody species relative abundance significantly increased from 2008 to 2009 ($P < 0.001$) and did not further change in 2010. Herbaceous relative abundance showed the inverse pattern, significantly decreasing from 2008 to 2009 ($P < 0.001$) and maintaining this decrease in 2010 ($P < 0.001$; Fig. 3b).

The midstorey *Rubus* spp. density did not change through three growing seasons ($P = 0.795$; Fig. 4a, Appendix S6). Hardwood stem density significantly increased from 2008 to 2009 ($P = 0.003$) but then decreased from 2009 to 2010 ($P = 0.007$; Fig. 4a). Loblolly pine density significantly changed through time, but there was an interaction between treatment and year effects ($P = 0.007$; Fig. 4b). Loblolly pine density did not change through time in MedBA and Control plots ($P \geq 0.146$). However, loblolly pine density significantly increased from 2008 to 2009 in LowBA and Clearcut plots ($P \leq 0.047$) and remained significantly different between 2008 and 2010 ($P \leq 0.036$).

Discussion

Effects of canopy treatments on sub-canopy vegetation

Previous studies from a variety of ecosystems have generally indicated that canopy removal results in short-term increases in the abundance of ground layer plants, largely due to increases in plant resource availability (e.g. Platt et al. 2006; Ares et al. 2009; Ruwanza et al. 2013). For example, in 28- to 31-yr-old longleaf pine plantations at the Savannah River Site of South Carolina, Harrington (2011) found that cover of herbaceous and woody plants both increased following experimental reductions of about half of the canopy density. Results from our study show a similar general increase in vegetation cover following

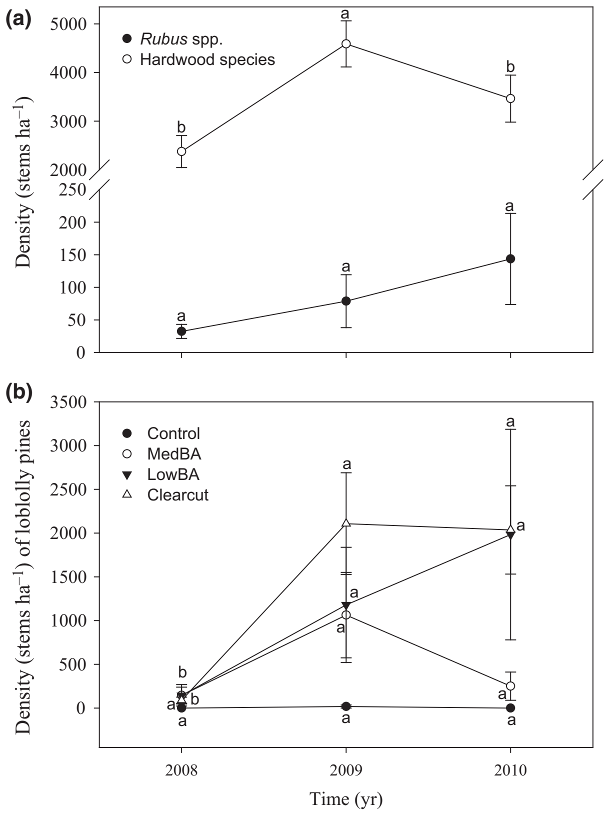

Fig. 4. Densities (stems·ha^{-1}; mean ± 1 SE) of midstorey (**a**) *Rubus* spp. and hardwood species, and (**b**) loblolly pines for each canopy treatment through time. The same lowercase letter in each group (**a**) or within each treatment (**b**) indicates no significant difference ($\alpha = 0.05$) among years.

canopy removal, although response patterns differed across functional groups and through time.

Longleaf pine restoration generally targets increased herbaceous vegetation in the ground layer, but previous studies on gap-based longleaf pine management showed that canopy removal also resulted in the release and rapid growth of woody plants (Jack et al. 2006; Kirkman et al. 2007; Pecot et al. 2007). Similar results were found in loblolly pine stands in Georgia and Alabama, where clearcut plots (1222 stems·ha^{-1}) had higher densities of woody stems than uncut plots (42 stems·ha^{-1}) in the midstorey after three growing seasons following harvest (Knapp et al. 2014). Our study resulted in higher densities of midstorey stems after three growing seasons, with nearly 6500 stems·ha^{-1} in Clearcut plots and over 1000 stem·ha^{-1} in uncut plots. The development of a dense midstorey layer following canopy removal threatens the objectives of an open stand structure during longleaf pine restoration, suggesting that additional treatments for woody vegetation control may be warranted in such cases.

Interestingly, we found that canopy treatment effects differed between naturally regenerated loblolly pines and hardwood species in our study, and it is likely that the mulching treatment used for site preparation affected the response patterns we observed. Mulching treatments are generally effective at initially reducing midstorey densities but have transient effects on hardwood species that resprout and grow quickly (Brockway et al. 2009; Outcalt & Brockway 2010). It is probable that rapid growth following resprouting allowed hardwood stems to reach the height threshold of >1 m for midstorey stems in our study, regardless of possible growth reductions due to canopy density levels. In contrast, loblolly pines in the midstorey originated from seed, and thus increased through time and demonstrated a pattern of higher abundance with lower canopy density.

Canopy removal increased the cover of herbaceous vegetation, predominantly in the graminoid group, in 2008. This transient response is likely attributed to the dominance of woody vegetation, which increased in relative abundance from 2008 to 2009. Development of woody vegetation in the midstorey through time can limit the abundance of herbaceous vegetation following canopy removal through competition for light and accumulation of a litter layer on the forest floor (Hiers et al. 2007; Pecot et al. 2007; Harrington 2011).

Effects of cultural treatments on sub-canopy vegetation

Herbicides have been reported to be an effective technique to rapidly change vegetation structure by reducing woody stem density and improving opportunities for fire management during longleaf pine restoration (e.g. Welch et al. 2004; Freeman & Jose 2009; Haywood 2009; Jose et al. 2010; Addington et al. 2012). Similar to previous studies, treatments that included herbicides in our study (H and H+F) significantly reduced the cover of woody plants in the ground layer without affecting the total cover of herbaceous plants, resulting in the observed increase in the relative abundance of herbaceous vegetation with herbicide use. Previous studies within longleaf pine forests reported that imazapyr has been used successfully to control hardwoods with beneficial (Welch et al. 2004; Freeman & Jose 2009) or neutral (Jose et al. 2010) effects on herbaceous species cover. On Tall Timbers Research Station in Florida, Welch et al. (2004) found significant increases in forb cover but no effect on graminoid cover 1 yr after applying imazapyr. Similarly, we detected a short-lived increase in forb cover in the first year after application, but we also observed a concurrent decrease in graminoid cover. These results suggest that the herbicide treatment might shift the composition of herbaceous vegetation toward forb species, but the effect we observed was transient.

Our results suggest that chemical control of hardwood stems may simply shift the composition of midstorey stems from hardwoods to naturally regenerated loblolly pines. Therefore, the benefits of herbicide application may be best realized if the treatment is combined with effective control of loblolly pine regeneration. Given the differences in vulnerability to mortality from fire between longleaf pine and loblolly pine, prescribed burning to control loblolly pine seedlings is critical on sites with abundant loblolly pine regeneration (Knapp et al. 2011).

In addition, our results indicate that fertilizing at the rate applied in this study has little effect on the structure and composition of sub-canopy vegetation.

Management implications

Across the southeastern US, land managers are targeting restoration objectives that include establishing a longleaf pine canopy and developing an herbaceous-dominated ground layer when converting existing loblolly pine to longleaf pine stands, particularly on sites with a history of fire exclusion that has resulted in a well-developed woody component (Brockway et al. 2005; Mitchell et al. 2006). However, successful restoration prescriptions are often site-specific because of different land-use history, climate, site characteristics and starting conditions. Considering our results in comparison to previous studies demonstrates several points:

1. Canopy removal generally increases the abundance of ground layer vegetation but can increase the dominance of woody vegetation in the ground layer.
2. The response of sub-canopy vegetation to restoration treatments may vary across productivity gradients. A recent study from Fort Benning in GA and AL showed that the abundance of woody vegetation in the understorey was negatively related to canopy density but only on soils of finer texture (sandy clay loams vs sandy loams and loamy sands; Addington et al. 2015).
3. Herbicides were effective at controlling the density of hardwood stems in the midstorey, but resulted in the release of naturally regenerated loblolly pines. Combined with suggestions from Knapp et al. (2011), both prescribed fire and herbicide application may be required to achieve structural restoration objectives in stands with abundant loblolly pine and hardwood regeneration.

Longleaf pine seedlings can be established with partial canopy retention (Kirkman et al. 2007; Hu et al. 2012a; Knapp et al. 2013). Combining the application of herbicides and prescribed fire with retaining moderate levels of canopy density (7–9 $m^2 \cdot ha^{-1}$) within loblolly pine stands may provide an effective balance for reaching restoration objectives that include establishing longleaf pine seedlings and reducing midstorey densities of regenerating loblolly pine. However, our treatments did not result in lasting increases in herbaceous vegetation, suggesting that additional treatments such as seeding native species may be necessary to improve the ground layer component of these sites. Given the short-term responses reported here, our recommendations should be regarded as tentative and most applicable to sites where woody species capable of prolific resprouting dominate the sub-canopy vegetation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Texture and nutrient content of soils for each block used in the study.

Appendix S2. Basic vegetation information before treatment applied for each block used in the study.

Appendix S3. Detailed description of data analyses used for each measured variable.

Appendix S4. Detailed statistical results for covers of ground layer vegetation.

Appendix S5. Detailed statistical results for relative abundances of ground layer vegetation.

Appendix S6. Detailed statistical results for densities of midstorey vegetation.

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