Abstract—Management of longleaf pine woodlands and savannas in areas that have multiple objectives including conservation of biodiversity is increasingly common on public and private lands, and various silvicultural approaches have been proposed to meet the diverse objectives. While considerable work has investigated how alternative silvicultural systems influence longleaf pine regeneration patterns, few studies document how competing understory hardwoods respond to the proposed silvicultural alternatives. We examined pine regeneration and understory hardwood response as part of a larger study in a mature longleaf pine forest with replicated blocks randomly assigned one of four silvicultural treatments: control (no cutting), single-tree selection, small-group selection, and large-group selection. Following harvest, understory woody (non-pine) plants increased their growth more than 3-fold due to decreased competition with the pine overstory in the gap-based approaches. This resulted in increased hardwood litter in the gaps, which subsequently resulted in fire feedbacks that increased the potential for perpetuating hardwood domination of gaps intended for pine regeneration.

INTRODUCTION

Fire has molded forests for millennia (Bird and Cali 1998), influencing the manner in which they are structured and regulating their functions. The impact that fire has on ecosystems is perhaps nowhere more evident than in the longleaf pine (Pinus palustris Mill.) woodlands and associated communities in Coastal Plain landscapes of the Southeastern United States. Historically, longleaf pine dominated areas of the Coastal Plain, unbroken in its range except for moist, bottomland sites (Wahlenburg 1946). Schwarz (1907) described longleaf pine forests as having an open, park-like appearance with a monotypic pine overstory and a grass-dominated herbaceous understory. The forest was all-aged, with even-aged cohorts regenerating in small patches formed in the largest gaps. This forest structure is found in today’s landscape only in the presence of frequent fire.

The species distribution, abundance, and stature of hardwoods (Quercus and associated species) reflect interactions between site resources and historical disturbance in longleaf pine forests. The Southeastern Coastal Plain has been described as Southern Mixed Hardwood forests (Kuchler 1964), oak-hickory association (Oosting 1956), and beech-magnolia forests (Delcourt and Delcourt 1987, Pessin 1933). All these classifications represent the potential community outcome if fire is suppressed for sufficient periods of time. However, even with frequent fire many longleaf pine forests are really mixed pine-hardwood forests (see Jacqmain and others 1999), with hardwoods at best relegated to small sprouts as advance regeneration on many sandhills and intermediate sites (flat hardwoods at best relegated to small sprouts as advance regeneration on many sandhills and intermediate sites (flat-canopy longleaf pine forests have sufficient light for vigorous hardwood development, where light rarely falls below 30 percent of full sunlight and many sites experience > 50 percent full sunlight (Battaglia and others 2002, 2003; McGuire and others 2001; Palik and Pederson 1996). However, the degree that competition, especially below ground, from adult pines regulates oak development has been little studied.

Gap-based approaches to management of longleaf pine forests have been suggested as a way to mimic natural disturbance patterns, allowing for regeneration to develop and for the use of frequent fire (Boyer and Peterson 1983). Recommended gap sizes in these approaches are based upon the idea that longleaf pine is an intolerant species (Boyer 1990) and can only be regenerated in large openings (Brockway and Outcalt 1998). However, fire behavior in created gaps may be altered by a lack of needles and greater hardwood litter, initiating feedbacks that discourage fire and increase the dominance and growth of fire-sensitive species (Williams and Black 1981).

To better understand how silvicultural alternatives influence pine seedlings and oaks in the understory, we harvested a second-growth longleaf pine woodland using single-tree selection and two group selection approaches (Battaglia and others 2002, 2003; Jones and others 2003; Palik and others 2003; Pecot and others 2006). The objective of this work, which was part of a larger study, was to investigate the manner in which longleaf pine interacts with hardwood sprouts and longleaf pine seedlings across ranges of pine stocking and gap sizes.

METHODS

Study Site

The research was conducted at the Joseph W. Jones Ecological Research Center in southwest Georgia on the Coastal Plain region of the Southeastern United States. The climate is subtropical with mean daily temperature ranging from 11 °C to 27 °C. Annual precipitation averages 132 cm/year, evenly distributed throughout the year. Soils of the study site are of the Orangeburg series, a fine-loamy, siliceous, thermic typic Paleudult. The site is dominated in the overstory by 70-
90-year-old second-growth longleaf pine and in the under-
story by a species-rich groundcover, including wiregrass
(Aristida stricta Michx.) (Kirkman and others 2001).

Treatment Design
The study design was described previously (Battaglia and
others 2002, 2003; Jones and others 2003; Palik and others
2003) and incorporates four overstory removal treatments
assigned randomly within three 2.5-ha blocks (3 replications).
The four treatments were (1) uncut control and basal area
reduction through (2) single-tree selection, (3) small-group
selection (approximately 0.10-ha circular gaps), and (4) large-
group selection (approximately 0.20-ha circular gaps). In
each cut treatment, residual overstory basal area was similar.
All trees > 10 cm d.b.h. were surveyed into Universal Trans-
verse Mercator (UTM) space. Next, we calculated an overstory
abundance index (OAI) for all locations on a 1 x 1 m grid. OAI
is a distance-weighted measurement of basal area within a
circumscribed area (Jones and others 2003, Palik and others
2003, Stoll and others 1994). We chose 15 m as the radius
for our circumscribed area (Jones and others 2003, Palik and
others 2003), since most overstory effects of longleaf pine on
plant responses are observed within that distance (Brockway
and Outcalt 1998, McGuire and others 2001). A total of 300
plots were established that spanned the range of OAI (data-
set A). Next, we established 60 additional plots to test the
influence of overstory effects on hardwood populations
(dataset B). In each large-group selection treatment area, we
established 10 plots (4m x 2m) in a randomly selected gap.
For each gap, four plots were established within the intact
(uncut) savanna matrix, four at the gap edge, and two in the
gap center. In each control treatment area, we also established
10 plots that had similar OAI values to those plots in the
large-group selection treatment areas. We randomly chose
half of the plots in each stand to receive a trenching treat-
ment which prevented overstory roots from regrowing into the plot
area over time (Pecot and others 2006). For datasets A and
B, we planted 10 1-year-old containerized longleaf pine seed-
lings, evenly distributed in the central portion of each subplot.
Finally, we examined the spatial response of hardwood bio-
mass in 2 randomly selected gaps in each of the small- and
large-group treatment areas (dataset C). We established plots
in 4 cardinal directions at 0, 1, 2, 4, 6, 8, 12, and 15 m from the
gap edge in the small gap with an additional location (25 m
down to gap edge) in each large gap, for a total of 816 plots.

Sampling
For dataset A, seedling survival was assessed monthly
throughout the duration of the study (February 1999 to
December 2001). In December, 2001, we measured total
(above- and below-ground) seedling biomass in 40 randomly
selected plots. For each seedling, we measured root-collar
diameter and height to the top of the bud to the nearest 0.1 mm.
We then carefully excavated and collected each root system.
Seedling components were dried at 70 °C to a constant mass
and weighed. In addition, we measured diameter at 1 cm
height and height to the top of the stem for all hardwoods in
a 0.75-m² circular area at each of these plots and used a
locally derived equation to predict biomass from d*h. For
dataset B, we measured diameter at 1 cm height and height
to the top of the stem for every hardwood stem in a 0.75-m²
circular ring randomly placed in each of the small and large
gaps and calculated biomass using the same equation as in
dataset A. For dataset C, we measured the aboveground
portion of all understory hardwoods 2 years after trenching
installation. These plants were clipped at ground level, dried
at 70 °C to a constant mass, and weighed. Mean plot
biomass (datasets A and B) and mean biomass of the four
cardinal directions at each gap location (dataset C) were
calculated.

Data Analysis
Prior to stand-level analyses, we weighted each plot measure-
ment to reflect the importance of that particular plot in the treatment area to improve the estimate of stand means. The
weights were the proportions of grid points falling in each ofive OAI classes, calculated separately for each treatment
area. Prior to all analyses, we determined if each variable met the assumption of a normally distributed variable and
transformed them as necessary. Statistical differences for all
tests were accepted as significant at α<0.05 (SAS for Windows
v. 9.1, SAS Institute, Inc., Cary, NC, USA). Regression anal-
ysis was used to test for effects of overstory abundance on
seedling and hardwood biomass (dataset A). We used a
randomized-block, mixed-models analysis of variance (Littell
and others 1996) to test for treatment effects (weighted to
stand level) on seedling biomass and survival and hardwood
biomass. For dataset B, we used nonlinear regression to
predict the relationship between seedling and hardwood
biomass. For dataset C, we tested for differences in under-
story hardwood biomass (expressed as percent of maximum
biomass observed across all savanna locations) with the
main effects of trenching and location. When interactions of
the main effects were present, a set of simple effects tests
were performed.

RESULTS AND DISCUSSION
As overstory abundance increased, the biomass of planted
pine seedlings declined (fig. 1a). The relationship is an expo-
entially decreasing form and the asymptote at an overstory
abundance correlating with approximately 60 percent canopy
closure. In contrast, above-ground biomass of hardwoods is
much more variable over the range of overstory abundance,
and no significant statistical relationship could be determined
(fig. 1b). Instead, the relationship appears to be more of an
upper boundary or threshold, where hardwood biomass
cannot be greater than the threshold at a particular overstory
abundance. This high degree of variability is likely due to the
wide range of starting conditions in gaps, including the initial
number of hardwood stems.

The relative location of pine seedlings or hardwood stems
within a gap also affected growth responses (fig. 2). The rela-
tionship is significant for pines and hardwoods, but the pine
response is less variable and does not separate by gap size
(fig. 2a). In contrast, the hardwood response was more vari-
able and differed with gap size (fig. 2b). There is a rapid
biomass response as distance from gap edge increases with
an asymptote reached at 15 and 10 m from gap edge for
seedlings and hardwoods, respectively.

The different harvest treatments resulted in similar growth
responses for the pine seedlings and hardwood stems (table
1). Compared to the seedling response, the response was
much stronger for the hardwood stems, with clear statistically
significant differences between the harvest treatments.
Figure 1—Total biomass (expressed as percent of maximum biomass observed in this study) of planted longleaf pine seedlings increased with decreasing longleaf pine overstory stocking (OAI) \(r^2=0.25, p<0.0001\) (A), but understory hardwoods were more variable and not related to OAI \(p>0.05\) (B). For clarity, figure 1a is presented using the log scale.

Figure 2—Biomass of planted longleaf pine seedlings increased with distance from gap edge \(r^2=0.61, p<0.0001\), but this response did not differ with gap size (A). Mean biomass of understory hardwoods increased with gap size, and in large gaps hardwood biomass increased to an asymptote at approximately 10 m from the gap edge \(r^2=0.62, p<0.0001\) (B).

Table 1—Total seedling biomass, understory hardwood biomass, and seedling survival from treatment plots on a 70- to 90-year-old longleaf pine forest, Baker County, GA. Letters following values indicate significant differences \(p < 0.001\) for each variable among overstory treatment levels.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Seedling biomass (g)</th>
<th>Understory hardwood biomass (g/m^2)</th>
<th>Seedling survival %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uncut control</td>
<td>6.61 ± 0.51 (a)</td>
<td>46.98 ± 6.45 (a)</td>
<td>80.15 ± 1.16 (a)</td>
</tr>
<tr>
<td>Single-tree</td>
<td>9.05 ± 1.25 (a)</td>
<td>68.17 ± 5.98 (ab)</td>
<td>76.82 ± 0.99 (ab)</td>
</tr>
<tr>
<td>Small groups</td>
<td>9.74 ± 0.55 (a)</td>
<td>96.72 ± 5.16 (bc)</td>
<td>72.77 ± 1.98 (b)</td>
</tr>
<tr>
<td>Large groups</td>
<td>21.38 ± 5.39 (b)</td>
<td>185.23 ± 29.17 (c)</td>
<td>75.07 ± 0.30 (c)</td>
</tr>
</tbody>
</table>
Furthermore, an interesting tradeoff between pine seedling growth and survival was apparent. In general, greater overstory canopy abundance led to higher survival for the pine seedlings (table 1). This response may be in part due to the long-term drought conditions during the study and a “nurse crop” effect from the overstory canopy. Still, in an operational sense, a balance between seedling growth and survival must be achieved to meet particular objectives. This balance must also take into account the retention of enough overstory to provide fuels to permit the use of prescribed fire.

We were also interested in how changes in overstory abundance influence seedling and hardwood responses through altered resource availability. Table 2 shows that canopy manipulations greatly affected both above- and below-ground resource availability. When plots were trenched to remove below-ground competition, understory hardwood biomass increased significantly in the intact savanna and at the gap edge with trenching, but no trench effect was observed in the center of the gaps. Thus, an intact canopy retards hardwood stem growth by restricting the availability of both above- and below-ground resources, with below-ground competition perhaps exerting the strongest control.

Several factors likely affected seedling and hardwood responses observed in this study. Obviously, gap size and distance from the gap edge had an influence (fig. 2, table 1); however, it is important to note that the gap sizes in this study were smaller than are often prescribed in gap-based silvicultural approaches for longleaf pine. Because the seedling growth response levels off beyond 15 m from the gap edge, and the lack of overstory in the center of gaps results in a lower distribution of fine fuels to carry prescribed fire, it appears that smaller gap sizes can be recommended.

The harvest process itself has an effect on the structure of fine fuels in the forest. The heavy equipment and skidding of trees can severely disturb the groundcover and make burning more difficult. The presence of well-established hardwood stems decreases the ability to use fire following harvest, which can lead to shifts in mid- and overstory dominance. A related factor is historical fire management in harvested areas. If past fire management has allowed the development of a heavy under- or mid-story of hardwood stems (either through infrequent fire or poor burning conditions), it is more difficult to establish pine regeneration and to have fire alone adequately control the hardwood competition.

Table 2—Effects of removal of below ground competition through trenching location on understory hardwood biomass (g/m²) in a 70- to 90-year-old longleaf pine forest, on understory hardwood biomass (g/m²) Baker County, GA. Letters following values indicate significant differences (p < 0.0001) among trench treatments at each savanna

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Untrenched</th>
<th>Trenched</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intact savanna</td>
<td>20.38 ± 6.03 a</td>
<td>83.10 ± 18.45 b</td>
</tr>
<tr>
<td>Gap edge</td>
<td>8.09 ± 2.93 a</td>
<td>100.00 ± 21.13 b</td>
</tr>
<tr>
<td>Gap center</td>
<td>54.90 ± 19.76 a</td>
<td>51.89 ± 26.27 a</td>
</tr>
</tbody>
</table>

Characteristics of advance pine regeneration can also affect the relationships observed in this study. Well-established seedlings that can rapidly respond to increased resource availability following harvests are more likely to successfully capture the harvest-created gaps and compete well with hardwoods. It has been suggested that adequate advance regeneration is important to the success of gap-based silvicultural approaches (Farrar and Boyer 1991), and the results of this study further support this conclusion. Finally, the climatic conditions during the course of this study potentially affected the observed results. The harvest operations were conducted just prior to a multi-year, region-wide drought. These conditions likely increased the observed “nurse crop” effect of seedling survival and may have influenced hardwood growth in the understory (table 1).

CONCLUSIONS

The results of this study have some important implications for gap-based silvicultural approaches. First, the presence (or absence) of advance pine regeneration is an important consideration in choosing gaps to be created with harvests, as is the control of competing hardwoods in potential gaps. Second, gaps should be situated such that continuous fine fuels (especially pine needles) are available to carry prescribed fire. Once hardwoods are well-established in gaps, the burning conditions required to provide control are generally outside of the prescription parameters for the surrounding pine matrix. In cases where there are insufficient fuel sources, other operational treatments may be required to keep the hardwood competition under control.

The results of this study argue for the use of variable-sized openings based upon local (fine-scale) conditions rather than using a “cookie cutter” approach, where gap size and spatial distribution are fixed. Because of the threshold response of seedling growth in gaps, the response of hardwoods to overstory removal, and the need to maintain continuity of fuels, we recommend that gap size in general be smaller and dictated by the patterns of established seedlings that are to be released.

ACKNOWLEDGMENTS

This study was funded by the USDA NRI Ecosystems Grant program number 9700565 and the Robert W. Woodruff Foundation. We thank Preston Parker, Stacy (Hurst) Odom, Tom Hay, Mike Battaglia, Glen Stevens, and Dwan Williams for their hard work. Dr. Barry Moser provided thoughtful statistical advice.

LITERATURE CITED


