Effects of reproduction methods and overstory species composition on understory light availability in longleaf pine–slash pine ecosystems

Ajay Sharma a,⁎, Shibu Jose b,1, Kimberly K. Bohn c,2, Michael G. Andreu d,3

a School of Forest Resources and Conservation, University of Florida, 369, Newins-Ziegler Hall, P.O. Box 110410, Gainesville, FL 32611, USA
b The Center for Agroforestry, University of Missouri, 203 Anheuser Busch Natural Resources Bldg., Columbia, MO 65211, USA
c University of Florida, West Florida Research and Education Center, 5988 Hwy 90, Bldg. 4900 Milton, FL 32583, USA
d School of Forest Resources and Conservation, University of Florida, 351, Newins-Ziegler Hall, P.O. Box 110410, Gainesville, FL 32611, USA

A R T I C L E   I N F O

Article history:
Received 1 March 2012
Received in revised form 14 July 2012
Accepted 16 July 2012

Keywords:
Uneven-aged silviculture
LAI
Digital Hemispherical Photography
Group selection
Single tree selection

A B S T R A C T

The restoration of longleaf pine (Pinus palustris Mill.) ecosystem types ranging from xeric uplands to hydric flatwoods is the goal of significant management efforts in the southeastern United States. Overstory species composition across ecosystem types varies from pure longleaf to mixed species stands, with slash pine (Pinus elliottii Engelm.) becoming more predominant on hydric soils, though species rich understories are prevalent throughout the landscape. Understory light regime has been determined to be one of many important environmental factors affecting regeneration and understory diversity; however it is not clear how different management regimes across ecosystem types affect light levels during restoration of degraded sites. In this study, we used Digital Hemispherical Photography (DHP) at multiple sites in north-west and north-central Florida to examine understory light availability in longleaf/slash pine forests treated with shelterwood and uneven-aged systems relative to uncut control plots. Basal area in these stands ranged from approximately 5.0 m² ha⁻¹ to 40 m² ha⁻¹ and species composition ranged from pure longleaf pine to pure slash pine. As expected, these management systems led to significant decreases in leaf area index (LAI), cover fraction, direct fraction of Absorbed Photosynthetically Active Radiation (fAPAR) and diffuse fAPAR, and increase in visible sky. These changes indicated increased light availability in shelterwood and uneven-aged stands compared to uncut control stands. Mean LAI ranged between 1.7 and 1.8 for control plots and from 0.3 to 0.9 for the various management systems. Shelterwood systems generally had the highest amount of understory light availability, while the greatest variability was observed in the group selection system. The overstory species composition also affected understory light availability. For a given basal area, longleaf pine showed greater understory light availability than slash pine. Light availability in mixed species stands differed significantly from pure longleaf pine stands only when the proportion of slash pine basal area was 70% or higher. Our observations suggest advantages of group selection management over the other management systems when understory restoration is a primary objective, but long-term monitoring of the understory will be needed for confirmation.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Restoration and management of longleaf pine (Pinus palustris Mill.) ecosystems of the southeastern United States is currently of high ecological and economic concern (Alavalapati et al., 2002; Brockway et al., 2005b; Jose et al., 2006; Kirkman et al., 2007). Longleaf pine ecosystem types range from xeric uplands to hydric flatwoods, and vary in overstory composition from pure longleaf to mixed-species stands. In fact, in hydric flatwoods slash pine (Pinus elliottii Engelm.) may comprise a significant component of the overstory. However, all of these ecosystems are characterized by some of the highest species-richness among ecosystems of North America, mainly attributable to an understory wherein over 40 species per square meter have been reported (Peet and Allard, 1983). These ecosystems once occupied an estimated 37 million hectare (ha) in the southeastern United States, with 23 million of pure longleaf pine and 14 million ha of mixed pine species, but have been reduced to a fraction of their original extent mainly due to conversion to commercial pine plantations or through degradation as a result of fire-exclusion (Frost, 1993, 2006; Landers et al., 1995). Thus, currently, these ecosystems have been designated as critically threatened (Means and Grow, 1985; Noss,
Successful restoration and management of these diverse ecosystems, however, is dependent upon an understanding of the biophysical processes that affect species performance. The opening of the canopy following cutting treatments generally leads to an increase in the availability of light (Palik et al., 1997; McGuire et al., 2001; Gagnon et al., 2003), soil moisture (Brockway and Outcalt, 1998), and nitrogen (Palik et al., 1997). Cutting method and intensity also influences the amount and spatial distribution of fuels within the stand (Brockway and Outcalt, 1998; Brockway et al., 2006; Mitchell et al., 2009), which is important in these fire-driven ecosystems because of the effect on fire dynamics and subsequent reductions in competing vegetation. All these environmental factors and their interactions may affect the survival and growth of longleaf pine regeneration and the maintenance of understory species richness.

While soil moisture may be critical to longleaf pine regeneration in xeric sandhills sites (Brockway and Outcalt, 1998), light is certainly an important factor in mesic sites with richer soils where soil moisture and nutrient availability are not limiting factors (Palik et al., 1997; McGuire et al., 2001; Gagnon et al., 2003). In general, light and its distribution across a stand have been determined to be a good indicator of regeneration, growth, and maintenance of understory species richness in these ecosystems (Palik et al., 1997, 2003; McGuire et al., 2001; Gagnon et al., 2003, 2004). Light is one of the primary factors that limit growth of longleaf pine seedlings both in artificial (Gagnon et al., 2003) as well as naturally created gaps (Gagnon et al., 2004). Greater understory light has also been associated with a greater abundance of understory vegetation, particularly herbaceous plants (Wolters et al., 1973, 1981; Platt et al., 2006), and increased growth in basal area and crown width in longleaf pine (Harrington and Edwards, 1999; Harrington, 2006). However, diversity in growing conditions may be needed to maintain the broad range of species in the understory in these ecosystems (Harrington, 2006).

Various silvicultural management systems, including uneven-aged reproduction methods such as single-tree or group selection methods, as well as traditional even- or two-aged shelterwood methods, are being proposed as appropriate techniques to restore and sustainably manage these ecosystems for the provision of multiple benefits including timber production and biodiversity because they are suggested to mimic natural disturbance regimes that historically maintained these ecosystems (Masters et al., 2003; Brockway et al., 2005a,b; Van Lear et al., 2005; Jose et al., 2006). However, these proposed management systems vary in the amount and distribution of residual basal area across a stand (Smith et al., 1997), which leads to varying levels of horizontal as well as vertical heterogeneity in the distribution of canopy gaps. This results in alteration of light availability not only at the stand but also at the tree level (Beaudet and Messier, 2002; Davi et al., 2008). Understanding these changes in light regimes created by different management systems is critical for guiding appropriate management actions.

Use of light transmittance, typically measured by leaf area index (LAI), has recently gained popularity as a management tool to predict regeneration and tree growth following silvicultural activities (Jiëffers et al., 1999; Hale, 2003; Yirdaw and Luukkanen, 2004; Jelaska et al., 2006; O’Hara et al., 2007). However, most studies to date have examined light availability as a function of thinning in even-aged stands. In most cases, effects of thinning on light regime were studied by simply observing relationships between transmittance and overstory basal area for both conifer and broadleaf forests (Kuusipalo, 1985; Cutini, 1996; Mitchell and Popovich, 1997; Hale, 2003; Davi et al., 2008) and occasionally as a function of both stand density and basal area (Hale et al., 2009). More sophisticated, spatially explicit models to predict canopy transmittance and understory light have also been developed for some conifer species, such as MAESTRO for Sitka spruce (Wang and Jarvis, 1990) and tRAYci for Douglas fir (Brunner, 1998). Still, the effect of thinning in even-aged stands may not be the same as using uneven-aged methods that can alter both the horizontal and vertical distribution of the canopy and residual basal area. Overstory–understory interactions may also operate differently in these stands (Oliver and Larson, 1996). The use of only basal area as a management recommendation ignores the spatial distribution of trees and gaps, and age- or size-related variations and thus may be unsuitable for estimating light regimes in stands managed under two-aged or uneven-aged systems.

Light regimes have been studied in longleaf pine ecosystems, but have sometimes given conflicting results possibly as a result of using different sampling techniques or due to differences in site conditions. Brockway and Outcalt (1998) reported that light availability in a naturally regenerated uneven-aged longleaf pine forest in sandhills sites was uniformly distributed across the forest floor of entire canopy gaps because the light could reach the understory through numerous “interstitial spaces” in the open canopy stands. However, other studies carried out in mature second growth longleaf pine stands on more productive sites have found significantly higher light availability in the gap centers than at the gap edges as a result of tree removal (Palik et al., 1997, 2003; McGuire et al., 2001; Battaglia et al., 2002, 2003). The most comprehensive study among these was conducted by Battaglia et al. (2002, 2003) who estimated light availability in longleaf pine stands treated to three different retention harvest treatments (single-tree, small-group, and large-group selection) and found that spatial structure of the longleaf pine stand strongly regulated understory light and its distribution across the stand. In that study, treatments differed in spatial distribution of residual trees but not residual basal area (11.9–12.3 m² ha⁻¹) and the large-group selection cut led to the highest light availability. Since proposed management systems for longleaf pine encompass a broader range of residual basal areas from as low as 5 m² ha⁻¹ (for shelterwood systems) to approximately 13 m² ha⁻¹ (for selection systems) at the stand level (Franklin, 1997; Brockway et al., 2005a, 2006; Johnson and Gjerstad, 2006), there is still a gap in knowledge regarding the entire range of proposed management systems and canopy biophysical variables such as LAI and canopy cover fraction related to light regimes in forest stands. Additionally, restoration of plantations to natural longleaf pine ecosystems often results in different mixes of species composition during the transition phase. Longleaf pine ecosystems also often occur naturally as mixed stands with slash pine in its distribution range (Peet and Allard, 1993). Because canopy transmittance may vary among species (Canham et al., 1994; Yirdaw and Luukkanen, 2004), light availability in mixed stands could be different from pure stands for a given basal area. Kirkman et al. (2007) reported that the canopy transmittance characteristics are significantly different in longleaf pine and slash pine stands. Thus, the understanding of understory light availability in longleaf pine ecosystems as influenced by basal area, spatial distribution of trees, and overstory composition is required to fine-tune silvicultural recommendations so that favorable light conditions could be created in the stands.

The first objective of this study was to quantify the effects of silvicultural systems on understory light regimes in longleaf pine ecosystems. We characterized light regimes in longleaf pine stands managed under single-tree selection, group selection, and shelterwood systems, along with an uncut control. The second objective of the study was to evaluate whether light regimes in these ecosystems were affected by overstory species composition (proportional stocking of longleaf pine and slash pine). The study was carried out in a variety of stand conditions in north-west and north-central
Florida, and employed high resolution Digital Hemispherical Photography (DHP) for greater accuracy (Frazer et al., 2001).

2. Material and methods

2.1. Study sites

The study was carried out at the Blackwater River State Forest (BRSF), Goethe State Forest (GSF), and Tate’s Hell State Forest (THSF) in Florida, USA (Fig. 1). Blackwater River State Forest (30.94N, 86.81W) is a well-drained middle coastal plain upland site covering about 848.1 km² in the western Florida panhandle. It has an elevation of approximately 60 m above mean sea level (amsl) with a nearly level to gently inclined topography (0–5%). Soils are deep well-drained and sandy, low in organic matter and nutrients and low to moderate in water-holding capacity. Site index for longleaf pine was estimated to be 25 m at 50 years (Brockway, personal communication). The study site was occupied by second growth longleaf pine forest that naturally regenerated following clearcutting of the original forest during 1920s and was subjected to improvement cuts in 1981 and 1991 prior to installation of the study treatments as well as some salvage harvesting in 2005 following hurricane Ivan. The overstory was dominated by longleaf pine with lesser components of slash pine and sporadic hardwoods (primarily oaks (Quercus spp.)). Tree seedlings common in the understory were mostly oaks and longleaf pine. Understory vegetation consisted of a variety of shrubs, primarily dangleberry (Gaylussacia frondosa), blueberries (Vaccinium spp.), blackberries (Rubus spp.), wax myrtle (Myrica cerifera), and gallberry (Ilex glabra). The herbaceous layer was well-developed and consisted of a variety of forbs, such as silverthread goldenaster (Pityopsis graminifolia), morning glory (Ipomoea spp.), noseburn (Tragia urens), and St. John’s wort (Hypericum spp.) and grasses, such as wiregrass (Aristida beyrichiana), broomsedge bluestem (Andropogon virginicus), and witchgrass (Dichanthelium spp.). The site had been managed under prescribed burning since 1970. The prescribed fire regime had been winter-season burning on a 2–3 year cycle since 1970, and was changed to late summer burning in 1995 and finally to spring burning in 2003 (Brockway and Outcalt, 2010; Brockway, personal communication).

Goethe State Forest (29.19N, 82.57W) covers about 217 km² of poorly-drained lower coastal plain flatwood site in north-central Florida. The stands used in the study had an elevation of approximately 15 m amsl with nearly level (0–2%) topography. The soils belong to Smyrna soil series, which are deep and characterized by poor drainage, low organic matter and nutrients and low water-holding capacity. Site index of these areas ranged from 21 to 25 m at 50 years for longleaf pine. On stands clearcut in the late 19th and early 20th century, sporadic planting was done during the period of 1940–1980 with subsequent thinnings between 1997 and 2004. The overstory was dominated by longleaf pine with some slash pine and sporadic hardwoods (mostly oaks). Tree seedlings were infrequent in the understory and included mostly longleaf pine, water oak (Quercus nigra) and sweetgum (Liquidambar styraciflua). Shrubs, primarily saw-palmetto (Serenoa repens) and gallberry, dominated the understory vegetation, and the herbaceous layer consisted of some grasses, mainly wiregrass, witchgrass, broomsedge bluestem, nodding fescue (Festuca obtusa) and panic grass (Panicum spp.). Forbs were infrequently present. The prescribed fire regime is currently winter-season burning on a 3 year cycle (Brockway and Outcalt, 2010; Brockway, personal communication). The site experienced an aggressive lightning-initiated fire in April–June 2011 which burned nearly 2000 ha of forest area, affecting some of the study plots and severely burning one of the control plots.

Tate’s Hell State Forest (29.83N, 84.79W) consists of about 820 km² of poorly-drained lowland hydric flatwood site between the Apalachicola and Ochlockonee rivers in panhandle Florida. It has elevation ranging from 0 to 10 m amsl with nearly level topography. Four poorly drained hydric soil types account for the...
majority of the soils, namely, (a) Scratch–Rutlege, (b) Plummer–Surrency–Pelham, (c) Meadowbrook–Tooles–Harbeson, and (d) Pamlico–Pickney–Maurepas (Gilpin and Vowell, 2006). The site was once a swampy mosaic of wetlands and pine flatwoods communities, but large-scale silvicultural operations and hydrological manipulations during 1960s through 1980s converted extensive areas to slash pine plantation using intensive mechanical site preparation, bedding and planting at high densities. Current restoration efforts include thinning planted pines and shrubs and conducting prescribed burns to restore and maintain a fire frequency of every 1–4 years since 1994. The study stands consisted of pure slash pine plantations subject to prescribed burns 1–3 times in the past 10 years. The understory mainly consisted of titi (Cliftonia monophylla), swamp titi (Cyrilla racemiflora), gallberry, and fetterbush (Lyonia lucida), saw-palmetto, blueberries, dangleberry, and St. John’s wort. The herbaceous layer was poorly developed in denser stands and well developed in open stands and consisted mainly of bracken fern (Pteridium aquilinum), flatsedges (Cyperus spp.), wiregrass, bluestem grass (Andropogon spp.), and yellow-eyed grass (Xyris spp.).

2.2. Stand characteristics and treatments

To examine the effect of management system on light availability, we utilized the long-term experimental treatments established by Brockway and Outcalt (2010) at Blackwater River and Goethe State Forests. Single tree selection (STS), group selection (GS), and shelterwood (SW) cutting treatments were each replicated on three 9-ha treatment plots with basal area ranging from 10.3 to 12.9, 9.1 to 12.6, and 4.2 to 7.4 m² ha⁻¹ respectively across the study sites (Table 1). Goethe State Forest had an additional three replications of shelterwood treatments compared to Blackwater, which were intended to further evaluate traditional shelterwood methods with a ‘shelterwood with reserves’ (or irregular shelterwood) treatment. Because the final removal cut within the traditional shelterwood treatment had not taken place when our measurements were taken, we considered these treatments equivalent and grouped the treatment plots in our analyses (Table 2). Longleaf pine represented 30–100% of the overstory in different stands with mostly slash pine and hardwood trees as the remainder.

At Blackwater River and Goethe State Forests, tree marking for selection systems was based on the Proportional B method (Brockway and Outcalt, 2010; Brockway et al., 2011) where the proportion of residual basal area among three diameter classes (<15 cm, 15–30 cm, and >30 cm) is retained in the ratio of 1:2:3. In all of the cutting treatments, slash pine was selectively marked and harvested in the stands to increase the proportion of longleaf pine in the stands. The single-tree selection cuttings removed individual trees to create openings for regeneration with gap sizes less than 0.1 ha. The group selection cuttings created gaps in the stands ranging from 0.1 to 0.8 ha in size and of variable shape. Shelterwood treatments were applied using a seed cut that reduced the basal area uniformly across the stand. No cutting treatments were done in the experimental control.

To evaluate the effect of species composition at various levels of residual basal area, we sampled five stands at Tate’s Hell State Forest in addition to those stands described above. Stands here were established in the 1970s and consisted of mature pure slash pine plantations which were either uniformly thinned to varying levels of residual basal area or were unthinned. Basal area ranged from 5.5 to 40 m² ha⁻¹. Tree marking in thinned plots followed the principles of low thinning (Smith et al., 1997).

2.3. Data collection

Digital Hemispherical Photography (DHP), recognized as one of the most accurate and robust techniques for studying canopy transmittance and understory light availability (Battaglia et al., 2003; Valladares and Guzmán, 2006; Garrigues et al., 2008; Khabba et al., 2009), was employed to quantify understory light availability. We used a Nikon 5000 camera equipped with a Nikon

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Reproduction cutting method/management system</th>
</tr>
</thead>
<tbody>
<tr>
<td>Origin (year)</td>
<td>1920, 1935–48</td>
</tr>
<tr>
<td>Time of reproduction cuttings</td>
<td>November–December 2006</td>
</tr>
<tr>
<td>Approximate slope (%)</td>
<td>0–2, 0–5</td>
</tr>
<tr>
<td>Mean BA prior to cut (m² ha⁻¹)</td>
<td>11.0, 15.6</td>
</tr>
<tr>
<td>Mean BA in 2009 3 years after cut (m² ha⁻¹)</td>
<td>10.3–13.3, 16.0–18.3</td>
</tr>
<tr>
<td>Approximate species composition (% basal area constituted) by LLP⁶</td>
<td>85–95, 30–70</td>
</tr>
<tr>
<td>Site index (m) at 50 years</td>
<td>24.4, 21.3–24.0</td>
</tr>
</tbody>
</table>

⁶ The values represent the approximate percent basal area constituted by longleaf pine (LLP) at stand level. The remaining basal area was mostly constituted by hardwoods and some slash pine at Blackwater River State Forest, and slash pine at Goethe State Forest. The measurement plots had variable composition ranging from 25% to 100% longleaf pine by basal area.

Table 2

<table>
<thead>
<tr>
<th>Reproduction cutting method/management system</th>
<th>Number of measurement plots/treatment</th>
<th>Date of acquisition of DHPs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>26</td>
<td>BRSF</td>
</tr>
<tr>
<td>STS</td>
<td>9</td>
<td>24</td>
</tr>
<tr>
<td>GS</td>
<td>8</td>
<td>33</td>
</tr>
<tr>
<td>SW</td>
<td>10</td>
<td>48</td>
</tr>
</tbody>
</table>

The values represent the approximate percent basal area constituted by longleaf pine (LLP) at stand level. The remaining basal area was mostly constituted by hardwoods and some slash pine at Blackwater River State Forest, and slash pine at Goethe State Forest. The measurement plots had variable composition ranging from 25% to 100% longleaf pine by basal area.
fish eye FC-E8 0.21X lens and calibrated it to compute the optical center of the camera-fish eye lens system (Baret, 2004). The camera had an adaptable rotating LCD panel which was pulled out from the camera body, swung out horizontally 180°, and rotated up and over so that it faced the same direction as the lens towards the canopy. Orienting the camera-lens assembly magnetic north, we placed a two way spirit level over the LCD panel to take perfectly horizontal photographs (see Supplemental material A). This method eliminated the need of using a tripod to level the camera, which can be cumbersome in forest with dense understory. The photographs were taken with F1 setting of the camera at the widest zoom setting (Nikon User Manual). All the photographs were acquired by a single person, ensuring that all photographs were acquired at a single height of 1.6 m from forest floor. The pictures were recorded and saved in TIF format at the highest possible resolution (2560 x 1920 pixels, 14.1 megabytes). The DHPs were acquired in December 2009, June 2010, and later in October 2011 (Table 2), nearly 3–5 years after the last reproduction cuttings.

To collect light data as related to management systems, we utilized only the experimental treatment plots at the Blackwater River State Forest and Goethe State Forest as described in Section 2.2. For each management system or uncut control, we randomly assigned 25 m x 25 m measurement plots across any of the treatment plot replications. Each measurement plot was inventoried for its composition and basal area, and a DHP was acquired at the center. The number of measurement plots varied by cutting treatments and site, and ranged from 8 to 26 per treatment at Blackwater River and 9 to 48 at Goethe State Forests (Table 2).

We established substantially higher numbers of measurement plots on some treatments than others, particularly in shelterwood treatments plots at Goethe State Forest because they provided opportunities for data collection on light regimes in various proportions of mixed slash pine-longleaf pine to be used for the second part of our study. Similarly, control plots at Blackwater River Forest and single tree selection at Goethe State Forests were largely of pure longleaf pine. Group selection plots at Goethe State Forest also had a relatively greater number of measurement plots to account for the heterogeneous spatial distribution of residual trees in these treatments. For additional analysis to evaluate light availability with regard to different locations in the group selection plots at Goethe State Forest, we classified these measurement plots into three classes, namely, (1) gap, (2) matrix, and (3) new regeneration cohort. We defined matrix as the portion of group selection stands at least 10 m from a gap edge. This led to allocation of 8 gap plots on some treatments than others, particularly in shelterwood treatments, also called black sky JAPAR and white sky JAPAR respectively (Weiss et al., 2004). The ratio of these components may influence the ratio of red and far red radiation (Pecot et al., 2005). LAI is defined as one half the total leaf area per unit ground surface area (see Jonckheere et al., 2004). LAI is related to Photosynthetically Active Radiation (PAR) (400–700 nm) transmission as given by the Beer–Lambert law (Vose et al., 1995). Cover fraction, on the other hand, is the fraction of sky covered by vegetation viewed in the nadir direction integrated over a range of zenith angles (0–10°). Over all, greater sky implies greater light availability at the forest floor while greater LAI, JAPAR, and cover fraction generally mean lesser canopy transmittance to the forest floor.

Among the various measures of LAI computed by CAN_EYE, we chose true LAI to present in our results because it takes into account the clumping index of the overstory species. Also, it may be pointed out that the term LAI has been used as proxy for PAI (Plant Area Index) because all parts of the trees including stems, leaves and branches are accounted for by CAN_EYE in the analysis (Weiss and Baret, 2010).

2.4.1. Effect of management systems on light availability
Mean and coefficient of variation for each of the five response variables (sky, cover fraction, LAI, direct JAPAR, diffuse JAPAR) were calculated for each of the management systems and control plots at Blackwater River and Goethe State Forests, and analysis of variance (ANOVA) was carried out to evaluate the effect of management on each response variable for each site separately, with each measurement plot forming one replication of the treatment. The number of replications varied among the treatments (Table 2). Tukey’s HSD (Honesty Significant Difference) test was performed at α = 0.05 to test for significant differences.

Similarly, ANOVA were carried out to evaluate the effect of position (gap, matrix, and regeneration cohort) within group selection plots, and the effect of wildfire on each of the response variables at Goethe State Forest. Again, Tukey’s HSD (Honesty Significant Difference) test was performed at α = 0.05 to test for significant differences.

2.4.2. Effect of overstory species composition on light availability
For this portion of the analysis, we utilized the measurement plots across each of the three study sites, which differed in proportional overstory species composition as well as basal area. Regardless of site or cutting treatment, we selected and classified the measurement plots into the following five categories based on proportional overstory species composition: (1) pure longleaf pine (>90% basal area constituted by longleaf pine), (2) 70% longleaf pine (65–75% basal area constituted by longleaf pine), (3) 50% longleaf pine (45–55% basal area constituted by longleaf pine), (4) 30%
longleaf pine (25–35% basal area constituted by longleaf pine), and (5) pure slash pine (>90% basal area constituted by slash pine). A total of 164 measurements consisting of 94 for pure longleaf pine, 22 for 70% longleaf pine, 14 for 50% longleaf pine, 11 for 30% longleaf pine, and 23 for pure slash pine were considered. We then used analysis of covariance (ANCOVA) with the five proportional species compositions as a categorical variable, each of the response variables as a dependent variable, and basal area as the covariate (Crawley, 2005). All the data were analyzed using the statistical program R 2.14.0 and XLstat 2012 (http://www.xlstat.com, Addinsoft).

3. Results

3.1. Effect of management systems

As would be expected, the cuttings associated with the management systems at both Blackwater River State Forest and Goethe State Forest led to significant decreases in LAI, direct fAPAR and indirect fAPAR, and increase in sky compared to the uncut control plots (p < 0.001). At Blackwater River State Forest, cover fraction was lower in only group selection as compared to the uncut control (Table 3). Although the mean values of some of the response variables differed between the two sites, overall trends between the management systems and patterns of the coefficient of variation were largely consistent between the two sites. LAI at both sites averaged 1.7–1.8 for the control plots and ranged from 0.3 to 0.9 for the various management systems.

At Blackwater River State Forest, the group selection and shelterwood treatment resulted in significantly higher values of sky than single-tree selection and control, and correspondingly lower values for LAI, and direct as well as diffuse fAPAR (Table 3). The group selection showed the highest variability (coefficient of variation) in the values of cover fraction, LAI, direct and diffuse fAPAR, while sky was more variable in single-tree selection. Though the ratio of direct: diffuse fAPAR was not significantly different among the various management systems, the greatest variability was again observed in group selection system at this site.
### Table 3

<table>
<thead>
<tr>
<th>Site</th>
<th>Management system</th>
<th>Sky Cover fraction</th>
<th>LAI</th>
<th>Direct fAPAR</th>
<th>Diffuse fAPAR</th>
<th>Direct fAPAR: Diffuse fAPAR</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SE (CV%)</td>
<td>Mean ± SE (CV%)</td>
<td>Mean ± SE (CV%)</td>
<td>Mean ± SE (CV%)</td>
<td>Mean ± SE (CV%)</td>
<td>Mean ± SE (CV%)</td>
</tr>
<tr>
<td><strong>Basal area (m² ha⁻¹)</strong></td>
<td>Control</td>
<td>17.66 ± 1.17 (33.65)</td>
<td>0.47 ± 0.01 a (9.20)</td>
<td>0.30 ± 0.03 b (44.69)</td>
<td>1.81 ± 0.06 c (17.10)</td>
<td>0.79 ± 0.01 c (5.97)</td>
</tr>
<tr>
<td></td>
<td>STS</td>
<td>11.22 ± 0.46 (12.29)</td>
<td>0.68 ± 0.02 b (10.91)</td>
<td>0.19 ± 0.04 a,b (67.64)</td>
<td>0.92 ± 0.11 b (36.85)</td>
<td>0.55 ± 0.04 b (19.73)</td>
</tr>
<tr>
<td></td>
<td>GS</td>
<td>9.82 ± 3.38 (68.74)</td>
<td>0.76 ± 0.02 c (9.22)</td>
<td>0.05 ± 0.04 a (222.53)</td>
<td>0.35 ± 0.13 a (104.30)</td>
<td>0.30 ± 0.10 a (89.31)</td>
</tr>
<tr>
<td></td>
<td>SW</td>
<td>7.58 ± 0.91 (37.93)</td>
<td>0.76 ± 0.01 c (3.14)</td>
<td>0.20 ± 0.07 a,b (104.14)</td>
<td>0.50 ± 0.06 a (39.14)</td>
<td>0.39 ± 0.02 a (13.91)</td>
</tr>
<tr>
<td><strong>Basal area (m² ha⁻¹)</strong></td>
<td>Control</td>
<td>22.07 ± 2.61 (35.55)</td>
<td>0.49 ± 0.01 a (6.24)</td>
<td>0.19 ± 0.04 b (57.41)</td>
<td>1.73 ± 0.12 c (20.09)</td>
<td>0.46 ± 0.02 d (10.48)</td>
</tr>
<tr>
<td></td>
<td>SW</td>
<td>4.42 ± 0.46 (52.16)</td>
<td>0.84 ± 0.00 d (3.26)</td>
<td>0.05 ± 0.01 a (149.68)</td>
<td>0.28 ± 0.02 a (52.99)</td>
<td>0.17 ± 0.01 a (26.69)</td>
</tr>
</tbody>
</table>

**Note:**
- BRSF = basal reproduction system
- GSF = group selection system
- STS = single tree selection system
- SW = shelterwood system

At the Goethe State Forest, shelterwood treatment had significantly higher value of sky and lower value of direct fAPAR than both of the other treatments and the control. As at Blackwater, LAI and diffuse fAPAR were similar in shelterwood and group selection but were significantly lower than single tree selection and control. Cover fraction did not differ significantly among the treatments, but was lower than the control. The coefficient of variation was highest in group selection only for LAI, direct fAPAR and diffuse fAPAR. At this site, shelterwood treatment had the highest coefficient of variation in cover fraction and ratio between direct to diffuse fAPAR, while single tree selection observed highest coefficient of variation for sky.

Within the group selection plots at Goethe State Forest, the position with regard to gap, matrix, and regeneration cohort significantly altered light conditions ($p < 0.001$). The new cohorts of regeneration in gap openings, after nearly 5 years since the last reproduction cuttings, led to a significant decrease in sky and increase in cover fraction, direct fAPAR, and diffuse fAPAR, within the regeneration clusters compared to open gap area and matrix portion in the group selection plots. LAI in regeneration clusters was similar to the matrix portion but, as expected, higher than at gap portion. Sky and cover fraction in regeneration clusters were also significantly higher than in the uncut controls whereas LAI and diffuse fAPAR were significantly lower. Although, direct fAPAR was similar in regeneration clusters and uncut control, the ratio between direct fAPAR and diffuse fAPAR was significantly higher in regeneration clusters than in control (Figs. 3 and 4).

The incident of wildfire in the control plot of Goethe in 2011 significantly increased understory light availability ($p < 0.001$) by reducing basal area to approximately 2.7 m² ha⁻¹. This resulted in significant changes in all of the response variables (values of LAI = 0.16; cover fraction = 0.02; direct fAPAR = 0.10; diffuse fAPAR = 0.10) as compared to the unburned control. The mean and variability of light conditions created by the wildfire were closest to the shelterwood systems in Goethe State Forest.

#### 3.2. Effect of overstory species composition

Overstory species composition and basal area had a significant effect on understory light availability ($p < 0.001$) (Table 4). For a given basal area, pure longleaf pine stands had the highest amount of light availability while pure slash pine stands had the least understory light availability. Sky, LAI, and diffuse fAPAR differed significantly in pure longleaf pine stands and pure slash pine stands, while cover fraction was similar among different composition categories. Direct fAPAR showed inconsistent patterns possibly due to difference in dates of DHP acquisition. However, total fAPAR (obtained by summing direct fAPAR and diffuse fAPAR for each observation) was also found to differ significantly between pure slash pine and pure longleaf pine. Stands containing longleaf pine and slash pine in varying proportions of basal area generally resulted in significant reductions in light availability relative to pure longleaf pine only when the proportion of slash pine in the overstory was 70% or higher.

### 4. Discussion

#### 4.1. Comparison of management systems on light transmittance

Understory light availability in forest ecosystems can be critical for successful tree regeneration and growth as well as maintenance of understory species richness and abundance (Canham and Marks, 1985; Parrotta, 1995; Yirdaw and Luukkanen, 2004; Platt et al., 2006). This is of particular concern in ecosystems with high biodiversity and where the principal overstory species are...
light-demanding, such as are slash and longleaf pine (Wahlenberg, 1946; McGuire et al., 2001; Platt et al., 2006). The management challenges in longleaf pine ecosystems are to regulate the canopy structure and light transmittance in a manner that will create favorable light conditions for successful regeneration and maintenance of understory biodiversity while also retaining sufficient overstory stocking to provide fine fuels to maintain periodic fires or to provide some acceptable level of timber production where desired. Historically, longleaf pine has been managed as even-aged stands and natural regeneration has been obtained by the well-researched and very successful shelterwood system. More recently, however, there has been significant interest in using other regeneration systems that mimic smaller scale natural disturbance in longleaf pine (Brockway et al., 2005b).

Our comparisons between management systems showed a predictable response in both the mean and variability of the light responses as can be attributed to the level of residual basal area and the distribution of residual trees across the stands for each cutting method applied. Not surprisingly, shelterwood systems resulted in the highest understory light availability and generally with the least amount of variability as these treatments had the lowest residual basal area and residual trees were purposefully left distributed evenly across the stands leading to homogenous canopy openings. Interestingly, the means of several light responses, e.g. fAPAR (direct and diffuse) or LAI, in the shelterwood system were not significantly different from those of group selection at Blackwater River State Forest or Goethe State Forest, where group selection treatments had greater stand basal area. That result likely occurred because the mean values for group selection included data from both open gaps as well as matrix forest such that the high light conditions from open gap conditions skewed the mean values downward and high variability made mean separation difficult. Differences in light availability between gap and matrix forest were quite large in some cases (Figs. 3 and 4) and thus led to the highest variability in light responses as a result of the aggregated distribution of trees following group selection cuts. Single tree selection, which maintained the same amount of residual basal area at the stand level as the group selection, in general had smaller variability in light measurements on par with shelterwood method as a result of the more even dispersal of residual trees.

Though the measures of light availability used in our study did not allow us a direct comparison to other studies (using different measures of light) in longleaf pine and other forest types, the overall patterns appear to be in alignment with these studies. For example, understory light availability was found to vary inversely with increasing overstory basal area in longleaf pine (Kirkman et al., 2007), and Sitka spruce and Scots pine (Hale et al., 2009). Also, for the same level of residual basal area, mean stand light availability (measured as gap light index) in longleaf pine increased significantly from 56% in the single tree cut to 63% in large group harvest (Battaglia et al., 2003; Palik et al., 2003). Similarly, in another study conducted in France on a variety of forest types, LAI decreased from 60% to 33% with a similar decrease in basal area, with higher LAI variability resulting from group and seed cuts than the uniform cuts (Davi et al., 2008).

While uniform higher light levels can have positive benefits for many species in longleaf ecosystems, heterogeneity of light across a stand has also been suggested to be more conducive to creating, improving, or maintaining understory species diversity, stand structural diversity, microenvironment and habitat (Holmes and Smith, 1977) by providing a greater number of ‘safe sites’ for regeneration to occur and greater resource availability at the stand level than other management systems (Palik et al., 2003). Spatial aggregation in group selection systems, which creates larger gaps, also exposes the stand to the maximum length of time over which understory and related fauna can respond to increased light

---

**Fig. 3.** Understory light conditions (sky, cover fraction, direct fraction of Absorbed Photosynthetically Active Radiation (fAPAR), and diffuse fAPAR) in various areas of the group selection system plots as compared to the uncut control plots approximately 5 years following reproduction cuttings at Goethe State Forest, FL, USA. The values with the same letter did not differ significantly.

**Fig. 4.** Understory light conditions (leaf area index (LAI), and ratio of direct fraction of Absorbed Photosynthetically Active Radiation (fAPAR) and diffuse fAPAR) in various areas of the group selection system plots as compared to the uncut control plots approximately 5 years following reproduction cuttings at Goethe State Forest, FL, USA. The values with the same letter did not differ significantly.
because larger openings are likely to fill in slower than the smaller openings created by other types of systems (Sprugel et al., 2009). After 5 years post-cutting in the group selection plots, dense clusters of new cohorts of longleaf pine regeneration originated in the centers of the gaps. While the large gaps were favorable for longleaf regeneration, the reduction in light availability we observed could, at least temporarily, have a negative effect on localized understory biodiversity enhancement and maintenance. However, this negative effect would be localized to the gap centers and might not have a large impact on biodiversity across the entire stand.

Our field observations and preliminary data 3 years following the reproduction cuttings suggest that group selection cuttings produce desirable conditions similar to those of the traditionally used shelterwood system by promoting longleaf pine regeneration and enhancing understory species richness (Brockway and Outcalt, 2010; Brockway, personal communication). On the other hand, long term management of longleaf pine following group selection may have more concerns than short term regeneration and understory dynamics. For example, as Mitchell et al. (2009) has noted, group selection might cause disruptions in fuel continuity and create hard edges which in turn might affect fire behavior leading to unpredictable consequences. Only long term studies will establish the suitability of group selection systems in managing longleaf pine ecosystems.

Management recommendations typically use stand level measures of stocking, such as basal area or more currently LAI as surrogates for regulating resource availability; however, variability in light conditions such as would be created by group selection may also have strong implications for understory dynamics. For example, regeneration and growth responses under a mature forest canopy are not linearly related to LAI and thus use of mean values may not be appropriate where variability of LAI across a stand is high (Davi et al., 2006). Also, the proportion of direct and indirect radiation can affect the ratio of red (660 nm) and far red (730 nm) light (R:FR) in the stand as diffuse radiation is low in far red light (Holmes and Smith, 1977; Pecot et al., 2005). This ratio has been reported to regulate important developmental processes including seed germination, specific leaf area, and stem elongation (Pecot et al., 2005). Although the reproduction cutting techniques did not differ significantly in mean ratio of direct to diffuse fAPAR in Blackwater River State Forest, the group selection cuttings did show the highest variability. The ratio has been reported to vary in longleaf pine ecosystems with respect to sky conditions, overstory stocking, and solar angles (Pecot et al., 2005). Though, our study did not examine these aspects, the inconsistency in the pattern of direct and diffuse fAPAR observed at the Goethe State Forest in contrast to Blackwater River State Forest was possibly because the data from the Goethe State Forest was collected in different months of year (June and October) when sun angles were different.

The shelterwood and uneven-aged management systems evaluated in our study were designed to mimic natural disturbances that have historically governed the dynamics of natural longleaf pine ecosystems. For example, the shelterwood method represents circumstances where a partial stand of longleaf pine is left following a catastrophic event such as wildfire or damage from tropical storms, while group selection and single tree selection represent smaller scale localized disturbances such as those resulting from insect and pathogen attacks or lightning strikes (Brockway and Outcalt, 2010; Brockway, personal communication). These disturbances create canopy gaps that allow higher resource availability at the forest floor resulting in longleaf pine regeneration (Platt et al., 1988). Although the change in resource availability as a result of disturbance will vary with its intensity and frequency, the incident of wildfire at Goethe State Forest led to increased availability of light, more than any of our treatments. The monitoring of understory succession and longleaf pine regeneration in the wildfire-affected stand at Goethe State Forest offers an opportunity for comparison with the treatments implemented at Goethe State Forest.

### 4.2. Effect of overstory species composition

The proportion of longleaf pine and slash pine in the overstory altered light conditions especially at higher proportions of slash pine. The capacity of a species to intercept light is affected by its crown structure including characteristics and spatial distribution of needles, shoots and branches (Stenberg et al., 1994). Clearly, crown morphology, needle length, and foliage clustering are quite distinct between the two species. While longleaf pine has a sparse porous crown consisting of long needles, slash pine has dense crown of shorter needles. In total, longleaf pine typically has less leaf area than slash pine for trees of the same sapwood area (Gonzalez-Benecke et al., 2011). These characteristics allow longleaf pine stands to transmit more light than those of slash pine. Light at a given point in a measurement plot (photopoint) was possibly affected by overstory composition outside the plot. Though we tried to control this effect by selecting measurement plots in more uniform stands, some variability in the observations is bound to occur. Although, significant changes in light availability were observed only at high proportion of slash pine in the overstory, more studies are required to tease out the specific differences in transmittance in these ecosystems.

Given that much of the area currently under slash pine plantations in the southeastern United States was formerly occupied by longleaf pine, restoration of these sites will involve a series of mixed stand stages of slash pine and longleaf pine in varying proportions during the process (Kirkman et al., 2007). Currently, the pure and mixed stands are managed under a basal area regulation approach without regard to overstory composition. As suggested in both our study and in Kirkman et al. (2007), the residual basal area required to maintain favorable understory light regimes in mixed stands will be different than in pure stands of longleaf pine or slash pine because of the difference in light transmittance of these species. Thus a basal area regulation approach must account for overstory composition to create desirable light regimes while restoring and managing these ecosystems. However, our results seem to suggest that appropriate recommendations based on species

### Table 4

<table>
<thead>
<tr>
<th>Proportional overstory composition</th>
<th>Sky</th>
<th>Cover fraction</th>
<th>LAI</th>
<th>Direct fAPAR</th>
<th>Diffuse fAPAR</th>
<th>Total fAPAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pure LLP</td>
<td>0.68a</td>
<td>0.16a</td>
<td>0.92a</td>
<td>0.43a</td>
<td>0.23a</td>
<td>0.66a</td>
</tr>
<tr>
<td>70% LLP</td>
<td>0.71b</td>
<td>0.10ab</td>
<td>0.84a</td>
<td>0.32a</td>
<td>0.29a</td>
<td>0.60a</td>
</tr>
<tr>
<td>50% LLP</td>
<td>0.69b</td>
<td>0.15b</td>
<td>0.77a</td>
<td>0.35b</td>
<td>0.28b</td>
<td>0.62a</td>
</tr>
<tr>
<td>30% LLP</td>
<td>0.59a</td>
<td>0.15b</td>
<td>1.26a</td>
<td>0.53a</td>
<td>0.29a</td>
<td>0.82a</td>
</tr>
<tr>
<td>Pure SLP</td>
<td>0.55a</td>
<td>0.16a</td>
<td>2.38b</td>
<td>0.40abc</td>
<td>0.40b</td>
<td>0.86b</td>
</tr>
</tbody>
</table>

* Total fAPAR was obtained by summing direct fAPAR and diffuse fAPAR for each observation.
proportions may only be critical during early restoration efforts when slash pine is the most dominant component of the overstory.

5. Conclusions

Our study examined the canopy structure and light transmittance 3–5 years following three different management systems. In general, management systems that create larger gaps in the canopy, i.e. group selection and shelterwood, result in greater amounts of light available to the understory. Differences in both the quantity and variability of understory light availability suggest that there may be trade-offs in determining which management systems may be most appropriate for meeting multiple objectives including tree regeneration and growth as well as understory diversity. For instance, shelterwood methods which led to high, uniform light levels may be conducive for promoting significant tree regeneration and establishment, while group selection system which created both overall greater amounts as well as variability in light conditions likely to result in a more heterogeneous and diverse understory species response. The group selection system also retains greater stocking than the shelterwood system. We suggest that understory and longleaf pine regeneration response should be monitored over a long period in these treatments to establish the suitability of group selection in managing longleaf pine ecosystems. Additionally, since the relative proportion of longleaf pine and slash pine affected the light conditions especially at higher proportions of slash pine, the residual basal area should be adjusted appropriately in mixed stands to create favorable light conditions.

Acknowledgements

The funding for this study was provided by Cooperative for Conserved Forest Ecosystems–Outreach and Research (CFEOR), and McIntire Stennis Funding. The authors would like to express their sincere gratitude to all the technicians, who helped in the field work: Justin McKeithen, Michael Morgan, Melissa Kreye and Jo-sincere gratitude to all the technicians, who helped in the field work: Justin McKeithen, Michael Morgan, Melissa Kreye and Jo-

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.07.023.

References


