

## Chapter IV

### The Effect of Spatially Variable Overstory on the Understory Light Environment of an Open-Canopied Forest

## **ABSTRACT**

The variable retention harvest system has been proposed as a silvicultural technique to manage the longleaf pine (*Pinus palustris* Mill.) ecosystem. With this technique, residual basal area can be spatially distributed in different patterns that cause various understory light environments. The spatial distribution of the forest canopy structure can greatly influence the total understory light availability as well as its spatial distribution. In this study, the relationship between spatial structure of a longleaf pine canopy and spatial distribution of light were investigated by using three replicates of one uncut treatment and three harvest treatments: single tree, small gap (0.1 ha), and large gap (0.2 ha). Each harvest retained similar residual basal area but with different spatial patterns of the residuals, ranging from uniformly dispersed (single tree) to different degrees of aggregation (small and large gap). Within each treatment, hemispherical photographs were taken at 75 stations to estimate light availability with gap light index. For each treatment, the average stand level light availability, distribution of light availability, and spatial distribution of light availability were determined. Average stand level light availability increased by 20% by aggregating residual trees. In addition, the range and distribution of light availability differed between the harvest treatments. The variation of light availability increased as canopy gaps became larger and greater portions of the variation was explained by the spatial pattern of the canopy structure. Spatial autocorrelation range was twice as large in the small gap harvest than the other harvest treatments. It is suggested that seedling growth response to these differences in spatial patterns of light may differ between the different harvests.

## INTRODUCTION

The use of variable retention harvest systems has been promoted as a silvicultural technique to maintain and aid in rapid restoration of abiotic factors associated with structurally complex forests (Kohn and Franklin 1997). This technique allows a forest manager to decide the type and density of structures to retain, as well as the spatial pattern in which to arrange the retention. Currently, most longleaf pine forests are managed with even-aged management (Boyer and White 1989); however, the canopy structure of natural longleaf pine (*Pinus palustris* Mill.) forests is more like a mosaic of multi-aged patches of longleaf pine trees (Schwartz 1907). The use of a variable retention harvest system might be an appropriate technique to mimic the canopy structure of natural longleaf pine forest. However, the use of this technique in this system may have negative effects on the survival and growth of regeneration due to resource (light, moisture, and nutrients) competition from the residual overstory. In addition, it is unknown how the spatial arrangement of the residual trees (dispersed vs aggregated) will affect resource availability for the regeneration layer.

Studies have shown that overstory longleaf pines influence the growth of seedlings through competition for light and nitrogen (Palik et al 1997, McGuire 1999). The mechanism controlling seedling development can be explained by examining the competitive effects-response paradigm (Goldberg and Landa 1991). The competitive effect of the overstory on light availability was shown as an upward curvilinear relationship between increasing gap light index (a measure of light availability) and decreasing overstory basal area (Palik et al 1997). The seedling response to light availability was also curvilinear with increased seedling growth as light availability increased (Palik et al 1997). At gap light index values >70% seedling growth increased linearly (Palik et al 1997, McGuire 1999). Palik et al (1997) suggested stand-wide growth of regeneration could be maximized by manipulating the spatial arrangement of residual overstory toward a more aggregated distribution thus increasing the proportion of the area in a stand that has light availability >70%.

The spatial distribution of forest canopy structure can greatly influence total understory light availability as well as its spatial distribution (Horn 1971, Baldocchi and Collineau 1994, Brown and Parker 1994, Nicotra et al 1999). The recognition of the scale of spatial dependence of light availability is an important factor to consider when developing spatially explicit models that predict forest dynamics. This recognition allows the investigator to sample at the appropriate scale for independent data points. The ability to predict spatial variation in understory light environment under a wide range of partial-cutting systems is critical to our ability to predict forest dynamics following harvests in longleaf pine forests, however, this has not been addressed for longleaf pine ecosystems. Studies in other systems suggest that spatial distribution of light may have great importance for community-level processes (Clark et al 1996, Nicotra et al 1999, Denslow and Guzman 2000). Thus, learning more about the interaction of the understory environment with overstory canopy in terms of competition, canopy structure, and light will increase the ability to successfully manage this and other forests (Van Pelt and Franklin 1999).

The purpose of this study was to determine what effect different arrangements of residual overstory had on the average, frequency distribution, variation, and spatial pattern of the understory light environment. This was investigated by using three replicates of one uncut treatment and three harvest treatments: single-tree, small gap (0.1 ha), and large gap (0.2 ha). Each harvest retained similar residual basal area but with different spatial patterns of the residuals, ranging from uniformly dispersed (single tree) to different degrees of aggregation (small and large gap). We hypothesized that light availability and variation at the stand level would increase as residual basal became more aggregated due to the greater percentage of open areas. In addition, we expected the range of light availability would follow the same trend (*ie.* as residuals in the stands become more aggregated there will be a wider range of light availability and a shift in the distribution toward higher light levels due to larger openings in the canopy). We expected the more aggregated stands to have a ‘coarse-grained’ patch structure of light availability due to the lower probability of overstory interception of light. In addition, dispersed

residual basal area will have a ‘fine-grained’ patch structure of light availability due to more interception of light by the overstory.

## **STUDY AREA**

The study was conducted at the Joseph W. Jones Ecological Research Center in southwestern Georgia, U.S.A (31°N, 84°W) from August 1998 to July 1999. It was part of a larger study investigating the role of overstory structure on regeneration processes in longleaf pine ecosystems. Measurements were taken in a 60-80 year old second-growth forest. The mean height of all trees > 4 cm dbh was  $20.87 \pm 5.77$  meters. Topography is gently sloped (1-5% slope) with some sinkholes present. The climate is humid subtropical (Christensen 1981) with an average annual precipitation of 131 cm which is evenly distributed throughout the year. Mean daily temperatures range between 21-34°C in summer and 5-17°C in winter. The soils are classified as excessively drained sites of the Orangeburg and Wagram series. The vegetation is maintained with prescribed fire with intervals ranging from 1 to 5 years, depending on moisture conditions and fuel accumulation. The understory is dominated by the perennial grass *Aristida stricta* Michx. with many other species of perennial grasses and forbs (Goebel et al. 1997).

## **METHODS**

### *Site selection*

As part of the larger study, three replicates of four overstory manipulation treatments were used to determine the effects of spatially variable overstory light competition on longleaf pine seedlings. The four treatments were randomly assigned to 12 plots grouped into 3 blocks and consisted of 1) uncut control, 2) basal area reduction through thinning of widely spaced individual trees, 3) basal area reduction through small gap harvesting (~0.10 hectare gap), and 4) basal area reduction through large gap harvesting (~0.20 hectare gap). For the three cut treatments, residual basal area was similar (10-15 m<sup>2</sup>/ha; Table 3.1 Chapter 3), but the residual overstory was spatially varied.

For each plot, a complete survey of tree height (m), dbh (cm), and GPS location was performed. The location of each individual tree was entered into a GIS database and maps were drawn for each plot. A 5 x 5 m grid was superimposed on the map to determine a competition index, overstory abundance index (OAI), for each grid point. OAI was calculated by summing the trees' basal areas within 5m (BA5), 10m (BA10), and 15m (BA15) from the point, dividing each value by the distance, and adding these three values together.

$$\text{OAI} = \text{sum} ((\text{BA5})/5) + \text{sum} ((\text{BA10})/10) + \text{sum} ((\text{BA15})/15) \quad (1)$$

This allowed a tree's size to be weighted by its distance from the point. A tree closer to the point is weighted more heavily than one 15 meters away. Once OAI was calculated for each gridpoint, a frequency distribution of OAI based on 20% intervals for each plot was calculated. Out of each interval class for each plot, five points were randomly selected to represent a measurement station. Thus, twenty-five stations were assigned to each plot for measurement.

### *Light measurements*

Hemispherical photographs were taken at all stations (n=300) during July and August 1998 on calm, cloudless mornings at sunrise and evenings prior to sunset. It was assumed that canopy openings in the coniferous forests do not change significantly throughout the year (Rich 1990). Photographs were taken on Kodak t-400 black and white film with a Nikon 35mm camera with an attached 180-degree equidistant fisheye lens (Sigma 8mm). The camera was oriented north for each photograph. Negatives were scanned into a computer and edited in Adobe PhotoShop (Adobe Inc, IL) to increase the contrast between the foliage and the visible sky. A threshold gray level was determined for each photograph to distinguish between the foliage and visible sky. In order to minimize observer error all photographs were taken, scanned, edited, and analyzed by the same person. Each photograph was analyzed using the image analysis program Hemiview v. 2.1 (Delta-T, UK). For each calculation, the hemisphere was divided into sectors with an azimuth and a zenith resolution of 20.

Hemiview was used to calculate the amount of light transmittance to the understory based on canopy openness by accounting for the location of canopy elements, the diurnal path of the sun, and seasonal changes in sun angle. Parameters used for the estimates of direct transmission factor ( $T_{\text{beam}}$ ) were transmissivity=0.65, beam fraction=0.5 and solar constant= $2510 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Diffuse transmission factor ( $T_{\text{diffuse}}$ ) was estimated using the Standard Overcast Sky (SOC) assumption (Anderson 1964) in which the brightness of a point in the sky at zenith angle is three times as bright as that near the horizon. With the estimates of direct and diffuse transmission factors, gap light indices (Canham 1988) were calculated. The gap light index (GLI) specifies the percentage of incident PAR transmitted through a gap to a point in the understory. GLI is calculated using the equation below (Canham 1988):

$$\text{GLI}=[(T_{\text{diffuse}} * P_{\text{diffuse}}) + (T_{\text{beam}} * P_{\text{beam}})]*100 \quad (2)$$

where  $P_{\text{diffuse}}$  and  $P_{\text{beam}}$  are the proportions of incident seasonal PAR received at the top of the canopy as either diffuse sky radiation or direct-beam radiation, respectively.  $T_{\text{diffuse}}$  and  $T_{\text{beam}}$  are the proportions of diffuse and direct-beam radiation that are transmitted through the canopy to the understory, respectively. A GLI of zero indicates that there is no gap light in the understory, while a GLI of 100 indicates a totally open site. We assumed  $P_{\text{diffuse}}$  and  $P_{\text{beam}}$  were equal to 0.5 (Machado and Reich 1999, Comeau *et al* 1998, Gendron *et al* 1998, Canham *et al* 1990) for an entire growing season. The use of GLI to estimate light transmittance in longleaf pine forests is an acceptable surrogate to continuous direct measurements of light availability (Chapter 3).

### *Spatial statistics*

Not only do studies of resource distribution in forested ecosystems need to consider the average levels, but also the variation, the frequency, and the spatial distribution of these resources (Nicoira *et al* 1999). The use of geostatistics, a branch of applied statistics that focuses on the detection, modeling, and estimation of spatial patterns, can aid in the characterization of understory light environments. The basic idea is that the closer two sampling points are to each other, the more likely it is that their values are similar. This assessment is typically performed by use of variograms and correlograms. Variograms model the average degree of similarity between the values as a

function of their separation distance. They provide a quantification of the degree of spatial continuity that includes any pattern due to changes in the local mean and variance. Correlograms are plots of lag correlation-coefficient values versus distance. They take account of and remove the effects of changing variances over the sampling space. These geostatistics indices have been widely used in characterizing spatial patterns of a spatial variable.

Accounting for changing means and variance throughout the sampling area is important when the data are extremely skewed or clustered. When changing means and variances are ignored, variograms are often inconsistent in the characterization of spatial continuity (Srivastava and Parker 1989). Thus, a cautious practice is to calculate the variogram in collaboration with the correlogram (Rossi et al 1992). Comparison of the results from both analyses will then reveal both the lag-to-lag spatial variability as well as any regional patterns due to local mean and variance changes.

#### *Data analysis*

Because each plot had a different distribution of OAI, we separated each point within a plot into five classes of OAI based on 20% intervals. Frequency percentages were calculated for each OAI class within a plot and were used as weighting factors. For each OAI class within a plot, the mean GLI was calculated. Weights were applied to the mean GLI for each class within a plot. The weighted values of GLI were summed to determine the total stand level mean GLI for each plot. Comparisons of average stand-level light availability based on gap light index were performed using the PROC GLM procedure in SAS (SAS Institute, V.8, Cary , NC). Treatment differences in stand-level light availability were determined using Duncan's multiple range test. For each treatment, the frequency percentage of GLI was determined to examine the spatial distribution of GLI within a treatment. GLI was separated into 10 classes of 5% intervals. Predicted seedling growth at each station was calculated using Palik et al (1997) equation (Equation 2) relating seedling growth to gap light index.

$$\text{Above-ground biomass (g)} = 1.64/(1-0.0098*\text{GLI}); r^2=0.39 \quad (2)$$

The predicted seedling growth for each station within a treatment was averaged and treatment differences were determined using Duncan's multiple range test.

A GIS (ARC-VIEW v. 3.2, ESRI) was used to map the distribution of light availability for each treatment based on the 25 stations per plot within a treatment. Using a nonlinear relationship between basal area and gap light index, an equation (Equation 3) was developed to determine the gap light index of each plot based on a 5-meter grid resolution.

$$\text{Predicted Gap Light Index} = 1/(0.0117 + 0.0005*\text{basal area}); r^2=0.58 \quad (3)$$

Semivariograms (GS+ geostatistical software Version 3.1a., Gamma Design Software, MI) and correlograms (Surfer version 7, Golden Software, CO) were calculated with 14 lag classes and a maximum lag of 130-150 m. To estimate ranges and nugget variances, spherical models were fit to semivariograms standardized by the standard deviation at each lag (Isaaks and Srivastava 1989). Nugget variance at lag distance zero is an estimate of the amount of non-structural variance. The lag distance in which the semivariogram or correlogram reaches an asymptote (range) is an estimate of patch size. The sill of the semivariogram is an indication of the variance. Structural variation was calculated by subtracting the semi-variogram nugget ( $C_0$ ) from the sill ( $C_0+C$ ) and dividing by the sill (Dent and Grimm 1999).

## RESULTS

### *Understory light environment*

Average stand-level GLI increased significantly with the harvest treatments ranging from 49% in the control treatment to 63% in the large-gap harvest treatment (Table 4.1). Although the harvest treatments had similar residual basal area, the single tree harvest had significantly lower stand-level light availability than the large-gap harvest treatment.

### *Distribution of Gap Light Index within a treatment*

The light frequency distribution shows that the control treatment has a greater representation of shaded microsites than the harvest treatments. In the harvest treatments, as aggregation of the basal area increased, the range of light availability increased as well as the representation of brighter microsites. In the control and single tree harvest, 81-88% of GLI were between 45-60% (Figure 4.1a and b). However, the single tree harvest also had 18% of its microsites which received 65-80% GLI while the control had none at this level (Figure 4.1a and b). The small gap harvest and large gap had similar ranges, but the distribution of these ranges differed. Both the small and large gap had 50% of microsites that received 45-60% GLI (Figure 4.1c and d), however, the large gap had a shift in the distribution toward the higher values of GLI with 30% of GLI between 75-85% (Figure 4.1d).

Table 4.1: Average stand-level light availability (GLI) for each treatment (n=75 stations for each treatment). Letters indicate significant differences between treatments as calculated by the Duncan's multiple range test ( $\alpha=0.05$ ).

| TREATMENT   | AVERAGE GLI | STANDARD DEVIATION | SIGNIFICANT DIFFERENCE |
|-------------|-------------|--------------------|------------------------|
| CONTROL     | 49.29       | 6.09               | A                      |
| SINGLE-TREE | 56.18       | 8.16               | B                      |
| SMALL GAP   | 60.48       | 8.24               | BC                     |
| LARGE GAP   | 63.10       | 10.34              | C                      |

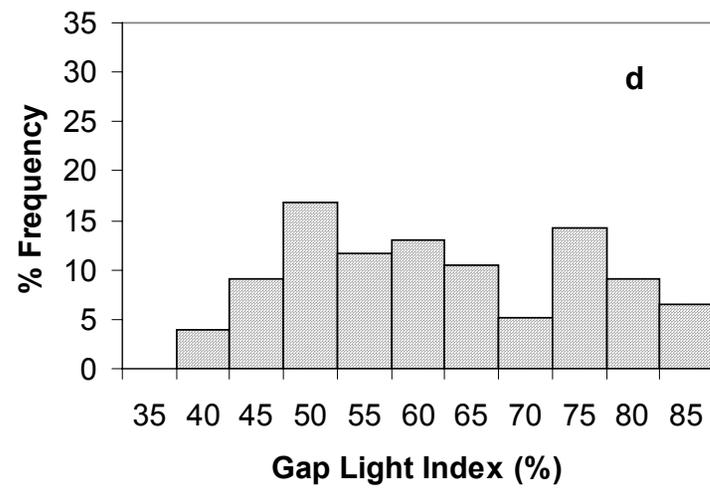
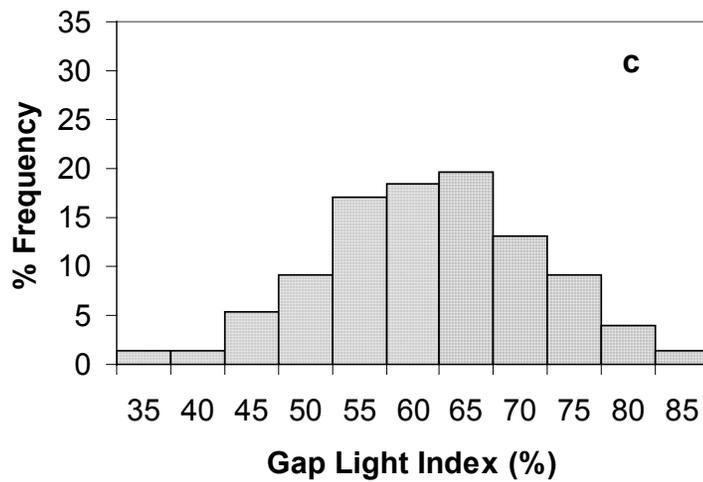
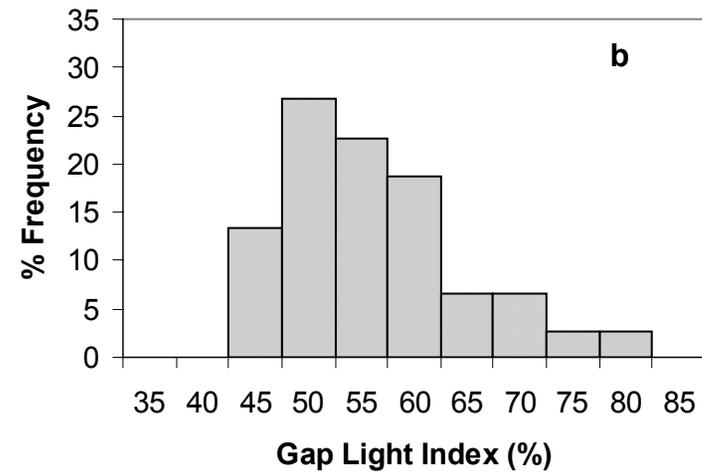
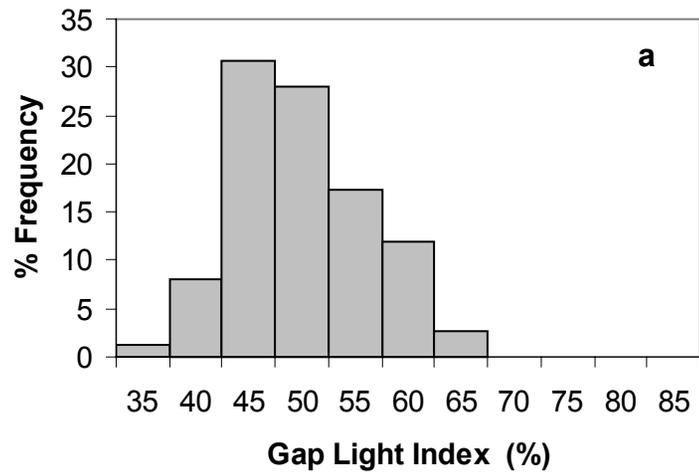


Figure 4.1: Percent frequency distribution of gap light index (GLI) for the control (a), single tree harvest (b), small gap harvest (c), and the large gap harvest (d).

*Heterogeneity of understory light environment (patterns of spatial dependence)*

Semivariogram relationships based on the GLI data showed distinct differences in spatial structure for the treatments (Table 4.2). The structural fraction (mean proportion of total variance accounted for by spatial dependence) increased as gap size increased. For example, spatial dependence explained 54% of the variation found in the control treatment, while for the large gap harvest it explained 100% of the variation.

For each treatment, semivariance increased with separation distance but leveled off at a different asymptote (Table 4.2). The control had the largest spatial autocorrelation with a patch size of 117 meters. The single-tree and large-gap harvest treatments showed much lower spatial autocorrelation of 56 m and 74 m, respectively. The small-gap harvest had the highest spatial autocorrelation of the harvest treatments with a patch size of 131 meters.

The use of correlograms allowed us to examine the spatial autocorrelation on a finer scale. All treatments showed a change in the spatial pattern of light over distance (Figure 4.2 a-d). The control and single-tree showed similar trends (Figure 4.2 a and b), with strong local autocorrelation patterns indicated by the small range (30-40 meters). The small gap harvest autocorrelation pattern had the largest scale >100 meters with the change more gradual than that of the large-gap harvest (Figure 4.2c). The large gap harvest autocorrelation pattern range was 80 meters with a more dramatic change in a short distance (Figure 4.2d).

Table 4.2: Semivariogram spherical model parameters for light availability across each treatment.  $C_0$ =nugget variance,  $C/(C_0+C)$ =structural variance C as a proportion of model sample variance ( $C_0+C$ ); range=distance (m) over which structural variance expressed autocorrelation. Lag class was separated into 15 classes of 10 meters with a maximum lag distance of 150 meters.

| TREATMENT   | $C_0$ | $C_0+C$ | RANGE (m) | STRUCTURAL VARIATION $C/(C_0+C)$ | $r^2$ |
|-------------|-------|---------|-----------|----------------------------------|-------|
| CONTROL     | 19.82 | 43.41   | 117.70    | 0.54                             | 0.53  |
| SINGLE TREE | 15.10 | 72.91   | 56.50     | 0.79                             | 0.77  |
| SMALL GAP   | 14.80 | 145.80  | 131.20    | 0.90                             | 0.74  |
| LARGE GAP   | 0.10  | 188.60  | 74.30     | 1.00                             | 0.84  |

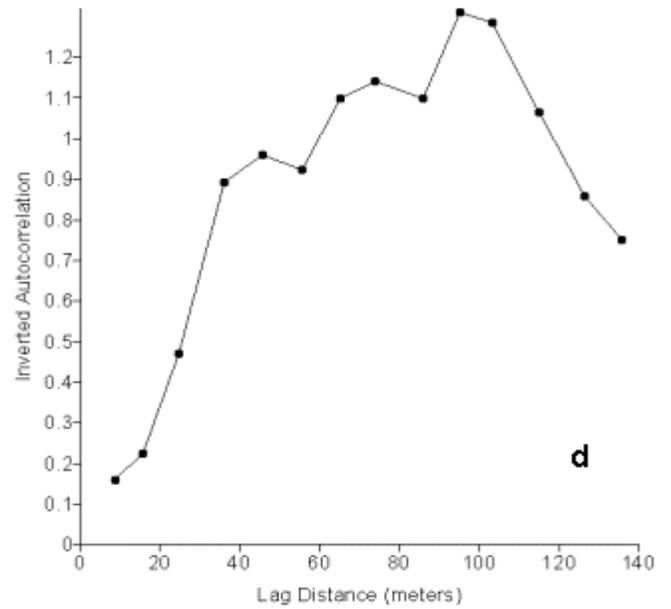
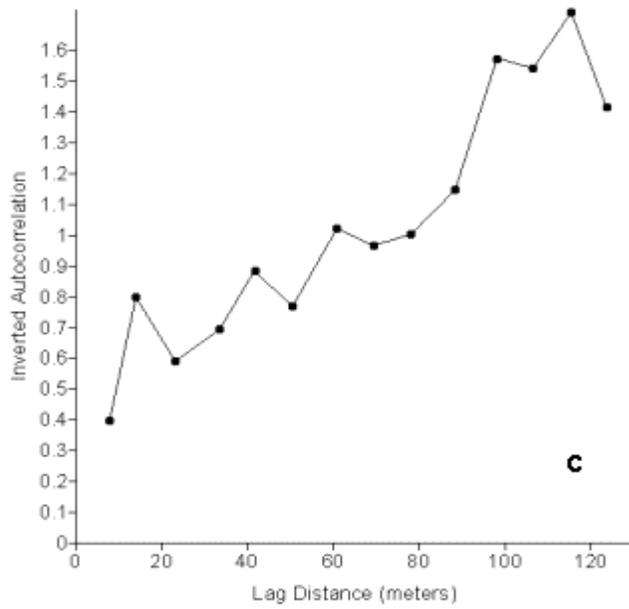
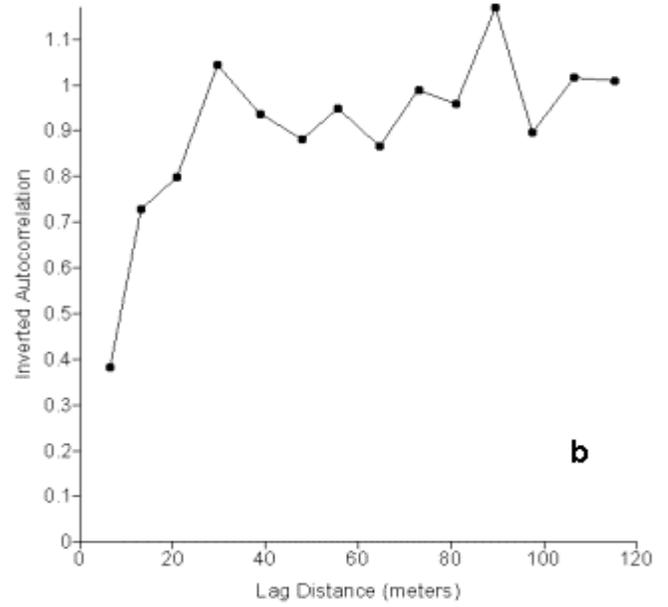
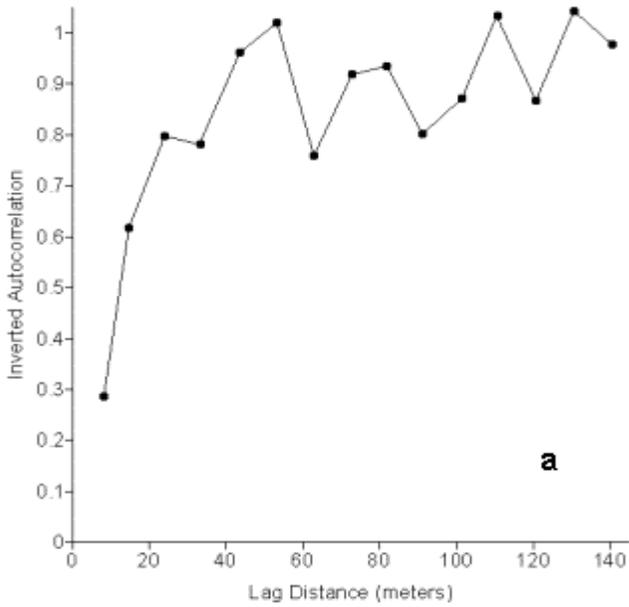


Figure 4.2: Correlograms for the control (a), single tree harvest (b), small gap harvest (c), and the large gap harvest (d). Maximum lag distance=140 meters for the control, single, and large gap harvest. Maximum lag distance=130 meters for small gap.

## DISCUSSION

The use of the variable retention harvest system allows the forest manager to distribute the residual basal area in a way that can maximize seedling growth while maintaining a structurally complex forest. Our results demonstrated that increasing the aggregation of residual basal area increases the average stand level light availability in the understory. Aggregation also increases the variation of light resulting in more heterogeneous understory light environments. This heterogeneity of light was related to the spatial pattern of the residual overstory trees and these patterns differed among the treatment.

It is well known that basal area has a negative relationship to understory light availability. Thus, it was no surprise when our results demonstrated that the lowest average stand level light availability was observed in the uncut control treatment. Although the harvest treatments had a 22% reduction in total basal area, the single tree harvest only had a 12% increase in stand level light availability. In contrast, both the small and large gap harvests had approximately a 20% increase in light availability. These results indicate that reducing basal area in a stand will not simply increase light availability proportional to the reduction and that the spatial arrangement of the residual basal area plays an important role.

Different spatial arrangements of residual basal area lead to different distributions of light availability within a stand. In this study, there were few microsites in the control that exceeded  $GLI > 60\%$  and a low percentage (18%) of microsites in the single-tree harvest which had higher light ( $GLI 65-80\%$ ). In contrast, the small and large gap had much lower percentage of microsites (50%) receiving intermediate light levels ( $GLI 45-60\%$ ) with much higher frequency of microsites with higher light levels. In the small gap harvest, 47% of the microsites received 65-80% of available light. The shift toward higher light levels was even greater in the large gap harvest that showed 30% of microsites receiving high light ( $GLI 75-85\%$ ). These results indicate that explanation of the effects of different spatial arrangements of residual overstory on light availability may be best interpreted by examining the frequency distributions rather than the mean light

availability (Logan and Peterson 1964, Chazdon and Fetcher 1984, Baldocchi and Collineau 1994, Brown and Parker 1994, Nicotra et al 1999).

Examination of the distribution and variation of total light availability in combination allows the characterization of gap openings for the different treatments. Semi-variogram analysis indicated that as residual basal area became more aggregated, the total variation of light availability substantially increased. The combination of the lower variation and more frequent microsites at the intermediate light level suggests that the single tree harvest had more, but smaller, canopy openings than the small and large gap harvest (Figure 4.3). Furthermore, the small gap harvest had a slightly higher variance, with an increase in brighter microsites indicating that this harvest had a wide range of gap openings (Figure 4.3). The substantial increase in variation and the uniform distribution of light availability in the large gap harvest indicates this stand had a number of small canopy openings and large canopy openings, with fewer medium sized openings (Figure 4.3). These differences in the distribution of canopy opening aids in the explanation of the difference in mean stand level light availability and distribution of light within a stand.

#### *Spatial dependence*

The recognition of the scale of spatial dependence of light availability is an important factor to consider when developing spatially explicit models that predict forest dynamics. This recognition allows the investigator to study at the appropriate spatial scale to achieve an unbiased evaluation. Based on our semi-variogram analysis, we confirmed that light was not distributed independently among microsites, rather the light availability (GLI) has a high degree of spatial dependence at different scales with harvest treatments. We found that patch size was 50% higher for the control and small gap treatments than for the single tree and large gap treatments. When the trends in the local means and variance were removed, results for the control treatment changed. In the control, spatial autocorrelation greatly decreased (~40 meters) indicating strong local patterns. Harvest treatments showed coarse patterns. The small gap still showed 50% higher patch sizes than the other harvest treatments confirming that this treatment had a

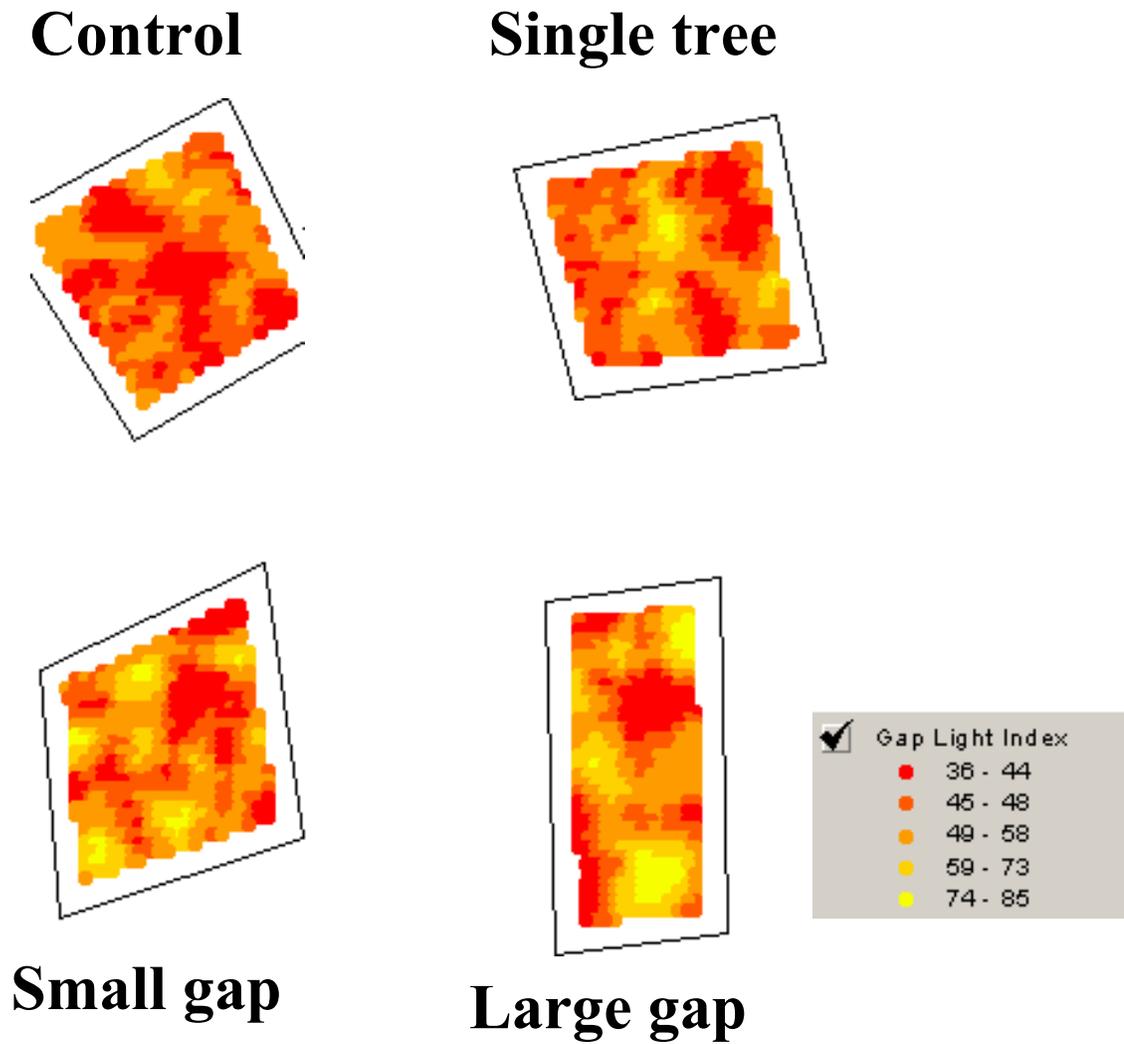


Figure 4.3. GIS representation of the spatial distribution of gap light index (5 meter resolution) within each treatment based on the relationship of basal area to gap light index. Equation: Predicted gap light index =  $1/0.0117 + 0.0005 * \text{Basal area (m}^2/\text{ha)}$ .

wider range of gap openings in the canopy. The strong spatial autocorrelation of light availability in all the treatments suggests that seedling growth and survival responses to light may result in spatially distinct structures of future forests under various harvests.

#### *Implications for longleaf pine seedling growth*

The response of the shade intolerant longleaf pine to differences in canopy openings and the subsequent distribution of light availability are likely to be important to seedling growth. Palik et al (1997) suggested stand-wide growth of regeneration could be maximized by manipulating the spatial arrangement of residual overstory toward a more aggregated distribution thus increasing the proportion of the area in a stand that has light availability >70%. In our study, as the residual overstory became more aggregated, the proportion of light availability >70% increased from 12% in the single tree treatment to 35% in the large gap treatment. Based on the curvilinear relationship between seedling biomass increment and gap light index reported in Palik et al (1997), maximum average seedling growth would occur in the large gap treatment (Table 4.3). In fact, by aggregating the residual basal area, the large gap treatment would have a substantially higher (25%) stand level seedling growth than the single tree treatment (Table 4.3) and small gap treatment (13%).

The scenario above does not consider the competitive interactions between longleaf pine seedlings and other vegetation growing alongside it. The understory of a longleaf pine forest is dominated by C<sub>4</sub> graminoids that respond positively to high light environments (McPherson and Weltzin 1998) and have better water use efficiency (Mitchell et al 1999). In areas of low residual basal area, more direct light can reach the understory, which in turn will increase evapotranspiration and thus lower soil moisture. In addition, increases in nitrogen occur with a decrease in overstory basal area (Palik et al 1997, McGuire et al 2000). Therefore, the combination of higher light and nitrogen availability and lower soil moisture in areas of low residual basal area may actually give C<sub>4</sub> plants a competitive advantage over longleaf pine seedlings.

Table 4.3: The predicted average seedling growth for each treatment based on the relationship between gap light index and seedling growth reported in Palik et al (1997). Equation: Seedling growth (g)= 1.64/(1-0.0098\*GLI);  $r^2=0.39$  . Letters indicate significant differences between treatments as calculated by the Duncan's multiple range test ( $\alpha=0.05$ ).

| TREATMENT   | AVERAGE SEEDLING GROWTH (g) | STANDARD DEVIATION | SIGNIFICANT DIFFERENCES |
|-------------|-----------------------------|--------------------|-------------------------|
| CONTROL     | 3.22                        | 0.397              | A                       |
| SINGLE-TREE | 3.81                        | 0.434              | AB                      |
| SMALL GAP   | 4.34                        | 0.648              | B                       |
| LARGE GAP   | 5.03                        | 0.956              | C                       |

McGuire et al (2000) reported that light was probably not a factor in the competition between longleaf pine seedlings and graminoids in large open areas. Since the limiting resource for  $C_4$  plants is light, in situations where herbicide is not applied, managers should attempt to alter the residual basal area that inhibits  $C_4$  carbon gain while allowing longleaf pine seedlings to maximize carbon gain. However, the lack of data describing the photosynthetic response of longleaf pine and other competitors in this system to different light levels inhibits our ability to precisely predict competitive outcomes. Therefore, further investigations will need to address the competitive ability of longleaf pine seedlings under various abiotic and biotic interactions.

## **CONCLUSIONS**

The use of the variable retention harvest system has been proposed as a management tool for the longleaf pine ecosystem. With this technique, residual basal area can be arranged differently to obtain various levels of competitive neighborhoods. Although stands may have similar residual basal, the spatial arrangement of the residuals has been shown to alter characteristics of light availability. In this study, we showed that average stand level light availability was increased 20% by aggregating residual trees to form various sized gap openings. Our results indicated that the average light levels among different harvest treatments might conceal biologically important environmental variability.

The spatial pattern of the light distribution differed according to the degree of aggregation. As residual basal area became more aggregated, larger amounts of the variation in light availability was explained by the spatial pattern of the canopy structure. Different methods of determining autocorrelation allowed discernment of strong local patterns in the treatments. The control treatment showed a strong local pattern of light, indicating that light is patchier in this treatment. Autocorrelations for the harvest treatments were similar for both analyses indicating that local means and variance were constant. Patch size of light availability was twice as large in the small gap harvest than the single tree and large gap harvests. Thus, seedling response to these differences in

spatial patterns of light may differ between these different harvests. However, the seedling response to the difference in spatial patterns of light availability has yet to be determined.

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## VITA

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