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Overhead shading and growth of young longleaf pine

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A study to determine the effects of environmental conditions on the growth of longleaf pine (*Pinus palustris* Mill.) was initiated in 1969 on the Escambia Experimental Forest near Brewton, Alabama, USA. This study sample consisted of forty young naturally regenerated, even aged longleaf pine seedlings evenly divided between two soil types. At the beginning of the study, the seedlings were 14 years from seed and ranged in height from 0.8 to 1.5 m. From 1969 to 1970, height and diameter measurements were recorded once to four times weekly during the growing seasons and once a month during the dormant seasons. To test the effects of shading on growth, cheesecloth was suspended over 10 randomly selected seedlings from each soil type only during the first growing season, from March 28 to September 24, 1969. This study provides data from the only known in-field shading experiment with longleaf pine seedlings of this size. The effects of the shading treatment and soil type were evaluated for height and diameter growth. The shading treatment did not have a significant effect on either height or diameter growth, but soil type had a significant effect on diameter growth.

Key words: *Pinus palustris*, longleaf pine, shade, soil type, shade intolerance.

INTRODUCTION

Trees, like all terrestrial plants, are dependent on sunlight, carbon dioxide, oxygen, water, and nutrients to survive and grow. Growth on the most basic scale can be defined as an irreversible increase in the size or number of cells (Kramer and Boyer, 1995). Growth and maintenance are the main purposes of a tree's metabolism and essential to a tree's survival (Kramer and Boyer, 1995). However, growth is not achieved without resistance from environmental stresses. Changes in the environment result in changes in a tree's internal physiological processes like photosynthesis, respiration, and absorption of water and minerals, which in turn affect growth (Kozlowski and Pallardy, 1997). At the genetic level, these changes or stresses in the environment can cause plants to modify morphology and physiology over time through phenotypic plasticity, which has many implications for forest management (Bradshaw, 1965; Schlichting, 1986; Chambel et al., 2005). The desire to identify and understand the many relationships that exist between the environment and tree growth has influenced numerous research efforts, but often the answers found lead to more questions.

The first European settlers in what is now the southeastern United States were confronted with an upland forest that was dominated by this one tree species-longleaf pine *(Pinus palustris Mill.)*. Stretching from the coastal plains of Virginia across a broad belt of the South Atlantic and Gulf Coasts into eastern Texas, longleaf historically occurred on over 36 million hectares and is thought to have been predominant on over 24 million hectares, but the ecosystem now only occupies fragments of the range (Frost, 1993). From southeastern Virginia to eastern Texas, it historically dominated the Coastal Plain but also extended into the Cumberland Plateau,

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Ridge and Valley, Blue Ridge, and Piedmont physiographic provinces (Boyer 1990). Throughout the literature, longleaf pine is referred to as an intolerant species (Schwarz, 1907; Wahlenberg, 1946; Boyer, 1990). From observations of virgin stands of longleaf pine, Schwarz (1907) believed that light was the most critical factor in the development of longleaf pine regeneration. He believed light determined not only the time and place, but also the manner in which succession occurred. The light required for a new generation of trees was admitted through openings in the crown cover. Small openings were caused by the fall of one or several large trees as a result of old age, disease, lightning, insects or windstorms. Larger openings were similarly caused by hurricanes and severe storms. Schwarz (1907) noted smaller openings in the forest would be filled by a dense grove of young trees, locally known as "sapling thickets." If the opening did not fill with longleaf pine then oaks and other species would take over. Longleaf pine has a grass-stage, a unique growth phase where there is no above-ground height growth, but the seedling is putting on root and ground-line diameter growth (Chapman, 1932; Wahlenberg, 1946; Brown, 1964; Boyer, 1990). Seed-lings will remain in this grass stage until a sufficient root system has developed, and height growth is initiated (Wahlenberg, 1946; Boyer, 1990; Outcalt, 2000). With the commencement of height growth, a seedling can grow about 30.5 to 100 cm a year (Wahlenberg, 1946). Long-leaf pine's adaptations as a climax species to fire like the grass stage, timing of height growth initiation, needle architecture, and branching structure makes it unique among the other southern pines and tree species around the world (Chapman, 1932).

Researchers in the 1930's began to look at how the growth of longleaf pine was related to environmental variations. Lodewick (1930) found positive correlations between diameter growth and precipitation. Diameter growth was found to be positively correlated with precipitation and negatively related to temperature (Coile 1936). Pessin (1938) using field studies showed tree stocking levels and ground cover plants had negative effects on seedling growth and noted the importance of light inten-sity for longleaf pine seedlings. Niinemets and Valladares (2006) found an inverse relationship between tolerances for shade and drought for a range of species, which shows tolerances can change depending on the existing factors. Manipulating light availability is very important since longleaf pine is commonly considered shade intolerant (Schwarz, 1907; Wahlenberg, 1946; Boyer, 1990). McGuire et al. (2001) found a positive correlation bet-ween the amount of light available and longleaf pine seedling growth in an in-field experiment with seedlings that had not initiated height growth. Barnett (1989) found significant differences between the shading treatments and a full sunlight control in a nursery setting. However, he did not see significant differences between the 30 and 50% shading treatments. Palik et al. (1997) found an upward curvilinear relationship between the growth rates of the selected trees and the variations in nitrogen and sunlight levels from 40 to 80% of full sunlight. Jose et al. (2003) evaluated the effects of light, water, and nitrogen on grass stage longleaf pine seedling growth. They concluded that seedling growth in a greenhouse with a shade treatment seemed to be more influenced by water and nitrogen than light, but they did find a significant response in root and stem biomass with interactions bet-ween light and soil resources (Jose et al., 2003). Climent et al. (2006) also found significant effects in biomass with reductions in light for Canary Island pine (*Pinus canariensis)* seedlings. They also found that light and water effects were significant and created an interaction where shoot elongation almost stopped. Variations might be related to the in-field conditions in comparison with controlled greenhouse studies, but variations might also be related to an age and growing conditions of microsites. Cavender-Bares and Bazzaz (2000) found environmental components and ontogenetic components played an equal role in photosynthetic capacity if water was not a limiting factor between red oak (*Quercus rubra*) seed-lings and mature trees.

In 1969, the U.S. Forest Service, studied a young longleaf pine stand in southern Alabama, USA to explore the relationships between the growth of young longleaf pine that had initiated height growth and the surrounding environment including an in-field shading treatment. This study was a follow-up to work done with loblolly pine in North Carolina (Boyer, 1970, 1976). Due to time and money constraints, the data were never analyzed until work began on it in 2003 as part of a master's thesis (Gilbert, 2007). This article focuses on the study of the in- field shading treatment.

METHODS

This project was installed on the Escambia Experimental Forest near Brewton, Alabama, USA in 1969. Data from a weather station located near the study site showed average precipitation which was 176.78 cm in 1969 and 195.83 cm in 1970. The average maximum temperature was 25°C and the average minimum temperature was 11°C for both years. The study sample consisted of young naturally regenerated, even aged longleaf pines, which were a product of the 1955 seed crop. All of the overstory had been removed prior to the study, which eliminated all overhead competition. Forty longleaf pine seedlings ranging from 0.8 to 1.5 m in height were selected for the study. Twenty were selected on each of the 2 distinct soil types that were present in the stand.

The two soil types that separated the seedlings were Lucy loamy sand (Lucy site) and Wagram loamy sand (Wagram site). The taxonomic class for both soils is: loamy, kaolinitic, thermic Arenic Kandiudults (Soil Survey Division, NRCS, 2003). The seedlings on the Lucy site were located on the crest of a ridge, and the seedlings on the W agram site were located on a slope at the base of the ridge. Mattox et al. (1975) reported soil composition, average site index and depths of the A-horizon for both soil types. The soils are very similar with an average site index of 20.4 m (base age 50). The depth of the A-horizon for the Lucy soil varies from 55.88 to 101.6 cm, while the depth of the A-horizon varies from 50.8 to 68.58 cm for Wagram soils. The Lucy loamy sand also has higher clay content at shallower depths than the Wagram loamy sand. Soil samples were taken for this study in coordination with the collection of soil moisture at neutron probe tubes across the study site.

Shading treatment

Half of the seedlings in each of the two soil types were randomly selected for artificial shading. These seedlings were shaded with cheesecloth for six months during the growing season of the first year of the study. The shading treatment was installed on March 28, 1969 and removed September 24, 1969. The cheesecloth was stretched across a one-meter-square frame that was structured to keep the cheesecloth at least one meter above the growing tip of the seedling. The structures were periodically checked, adjusted, and maintained at one meter above the growing tip. The cheese cloth prevented the growing tips of the shaded seedlings from receiving direct sunlight during the peak of the diurnal cycle. A pyrheliograph was used to measure solar radiation in langleys(cal/cm^3) for both shaded and unshaded areas. The mean percent difference in solar radiation between non-shaded and shaded seedlings was 38.5%.

Growth measurements

Initial heights were measured from the ground level to the base of the bud on the terminal growing shoot of each seedling on January 27, 1969. The length of the terminal bud was also measured. Separate records were maintained for each new leader. Terminal shoots were measured from 2 to 4 times weekly from March to October of 1969 and 1970. During the dormant season of both years, heights were measured every two weeks or at least once a month.

Monthly growth intervals covered 22 months from March 1969 through December 1970. Each monthly interval was 28 ± 1 day. The biweekly intervals included 22 measurements in 1969 ranging from March to December and 24 measurements in 1970 ranging from January to December. Biweekly growth intervals were 14 ± 1 day in length. Weekly intervals included 34 measurements in 1969 ranging from March to October and 38 measurements in 1970 ranging from March to November. The weekly intervals were 7 ± 1 day in length.

Diameters of each seedling were measured in centimeters at 10 cm above the ground line with the use of dendrometer bands. The 10 cm height was set because all the seedlings had not reached dbh (diameter at breast height of 1.37 m). Diameter measurements were taken weekly from March to October of 1969 and 1970. From the end of October to March, measurements were taken every two weeks to a month during 1969 and 1970. These measurements can again be divided into monthly, biweekly, and weekly growth intervals using the same interval lengths and durations as outlined for height growth.

Statistical procedures

Statistical procedures were executed in Statistical Analysis System (SAS) software version 9.1 (SAS, 2003). All analyses were conducted at the 0.05 level of significance. Analyses of variances were conducted to test for the effects of shade treatments and location over various growth rates using PROC GLM and PROC MIXED in SAS (SAS 2003). PROC MIXED was used to conduct a repeated measures analysis using seedling as the random factor (SAS, 2003). The repeated measures analyses were conducted with the measurements from each interval and with consecutive growth from the initial measurement. PROC MIXED was chosen because it allows for missing data and an unbalanced data structure (Littell et al., 1996). Interactions were tested further using Tukey's Studentized Range (HSD) and least significant difference (LSD) multiple comparison procedures and within group t-tests (Ramsey and Schafer, 2002; SAS, 2003).

All statistical tests were evaluated to confirm any potential violations from assumptions. To evaluate normality of residuals, a normal probability plot or a normal QQ plot was used from PROC UNIVARIATE (Neter et al., 1996; Ramsey and Schafer, 2002; SAS, 2000-2004). The Anderson-Darling test from PROC UNIVARIATE was also used to determine normality of the residuals (SAS, 2000-2004). Results from the QQ plot and from PROC UNIVARIATE were compared to determine if normality was suspected. Unless other-wise stated, the assumptions were not violated.

RESULTS

Height growth: 1969 to 1970

Evaluating differences in height growth over the different intervals is necessary to see if the recorded environmental conditions and treatments affect height growth. Each interval (monthly, biweekly, and weekly) covers different portions of the growing seasons. Patterns of growth over the growing seasons show that seedlings do not grow at the same rates during the entire growing season. Figure 1 displays average monthly height measurements illustrating how patterns of growth changed over the study period. Growth rate tends to vary over the growing sea-son which could raise questions about how relationships between growth and the environment change over the same period. Figure 2 displays initial height measurements. Initial height measurements ranged from 0.8 to 1.5 m. The measurements were tested to look for any significant differences before the treatments were app-lied. Initial heights were not significantly different for site, shading treatments, or an interaction for the site and shading treatment combinations.

Table 1 shows mean height growth for 1969 and 1970 individually. Overall height growth was first tested over the entire monthly interval. There were no significant differences between shade treatments or site location, but there was a significant interaction between the site and shade variables. Within group comparisons were then used to evaluate the significant interaction. Monthly height growth was also explored for potential significant differences using the repeated measurements design. Only time related variables and the shade/site interaction were significantly different. Testing the biweekly interval for height growth resulted in no significant differences between shade treatments or site location, but the shade/site interaction was significant as for monthly intervals. Biweekly intervals were also tested using repeated measures. Again, only time related variables and the shade/site interaction were significantly different. Weekly intervals were tested for both 1969 and 1970 because the measurements were not consecutive. Only the time variable was significantly different in 1969, and no significant differences were observed in 1970 except the shade/site interaction and time related variables. This shows that the soil/shade interaction occurred in the 1970 growth period, as shown in Table 1.

Neither the shade treatment nor site location was statistically significant with respect to height growth over

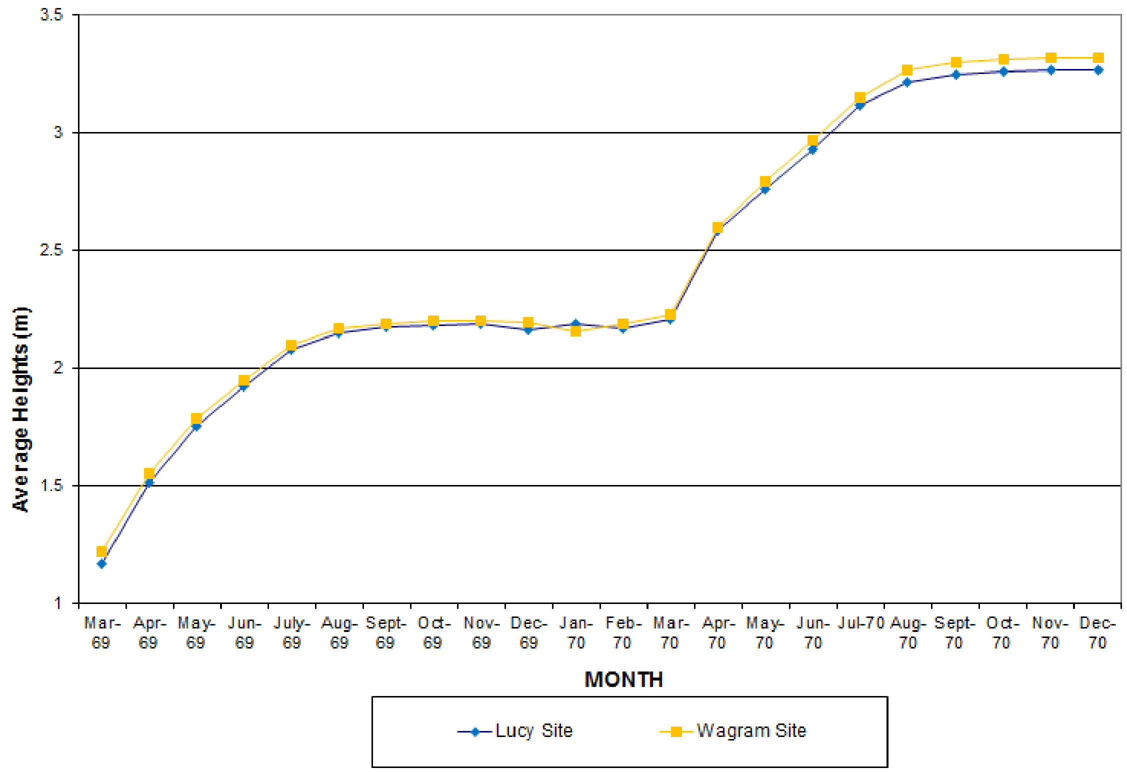

Figure 1. Average monthly height measurements illustrating a similar pattern of height growth on the Lucy and W agram sites for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

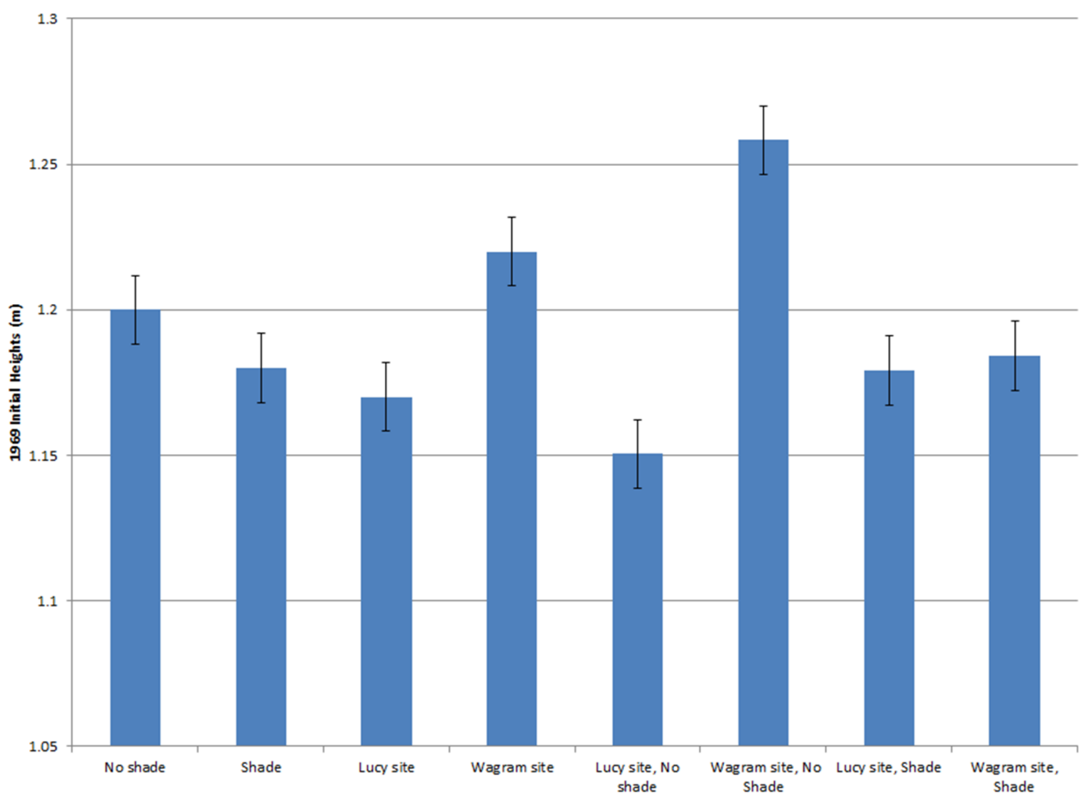

Figure 2. Average initial heights (m) in for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

Table 1. Test of average height growth and within group comparisons during the 1969 and 1970 intervals for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

Year	Site type	Average height growth (m)
1969	Lucy	1.01a
	Wagram	0.99a
1970	Lucy	1.09b
	Wagram	1.12b
Year	**Shade treatment**	**Average height growth (m)**
1969	Not Shaded	0.99c
	Shaded	1.01c
1970	Not Shaded	1.09d
	Shaded	1.12d
Year	**Shade/site combination**	**Average height growth (m)**
1969	NW (Not Shaded, Wagram)	1.02e
	SL (Shaded, Lucy)	1.06e
	SW (Shaded, Wagram)	0.96e
	NL (Not Shaded, Lucy)	0.97e
1970	NW (Not Shaded, Wagram)	1.20f
	SL (Shaded, Lucy)	1.20f
	SW (Shaded, Wagram)	1.04fg
	NL (Not Shaded, Lucy)	0.98g

Means with the same letter are not significantly different (α = 0.05); NL = no shade, Lucy site; NW = no shade, Wagram site; SL = shade, Lucysite; SW = shade, Wagram site.

the intervals, in overall tests, or in years evaluated. An interaction between the shade treatment and site location was significant. The interaction was not significant for the 1969 growth interval, but it was for 1970. When isolating 1970 growth, the same general interactions occurred, but mean height growth for seedlings on the Lucy site with no shade treatment was significantly lower than on the Wagram site with no shade treatment and seedlings on the Lucy site with the shade treatment. The significant interaction for the total growth over the 2 years showed that mean height growth for seedlings on the Wagram site with no shade and seedlings on the Lucy site with the shade treatment was significantly greater than mean height growth for seedlings on the Wagram site with the shading treatment. The within group interactions for 1970 and overall height growth were significant for LSD means but not for HSD means. Figure 3 displays mean height growth over the two year measurement period from March of 1969 through December 1970 for the shade treatment, site and shade/site combinations, which illustrates the findings from the statistical examinations.

Diameter growth: 1969 to 1970

Patterns of growth over the growing seasons show that seedlings diameters do not grow at the same rates during the entire growing season. Figure 4 displays average monthly diameter measurements illustrating how patterns of growth changed over the study period. There was a loss of diameter growth as shown in Figure 4 during January and February of 1970, which were the coldest months of the study with average minimum temperatures of 1 and 0°C, respectively. The initial diameter measurements ranged from 2.97 to 4.64 cm and were not significantly different for site location or shade treatment at the beginning of the study. There was a significant shade/site interaction. For site locations, Levene's test for homogeneity of variance was significant, but Barlett's was not. Testing within group interactions for initial diameters showed that diameters between shade treatments on the Wagram site were significant for LSD means but not for HSD. Figure 5 displays average initial diameters for shade treatments, site locations and shade/site locations at the beginning of the study.

Monthly diameters were measured from March 5 to December 24, 1969. When testing overall diameter growth for 1969, a significant difference of mean diameter growth between seedlings on the Lucy site and the Wagram site was observed (Table 2). Diameters were measured from January to December 1970 (Table 2). Testing within group differences, site location was significant, and mean diameter growth was non-significantly larger for the seedlings

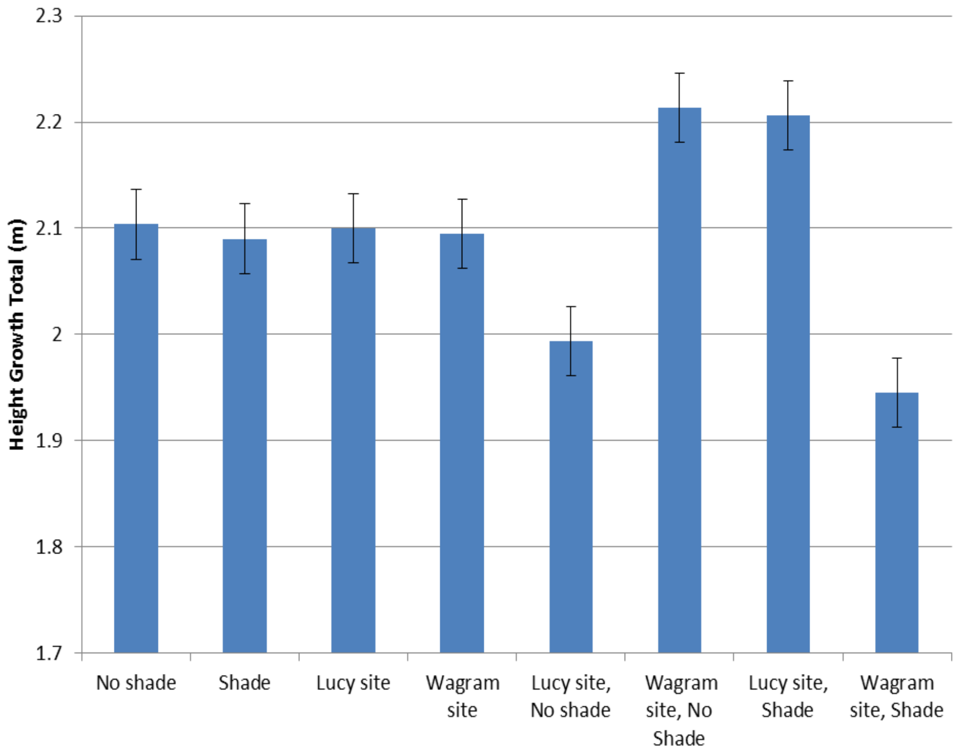

Figure 3. Average height growth and within group comparisons during the 1969 and 1970 interval from March 1969 to December 1970 for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

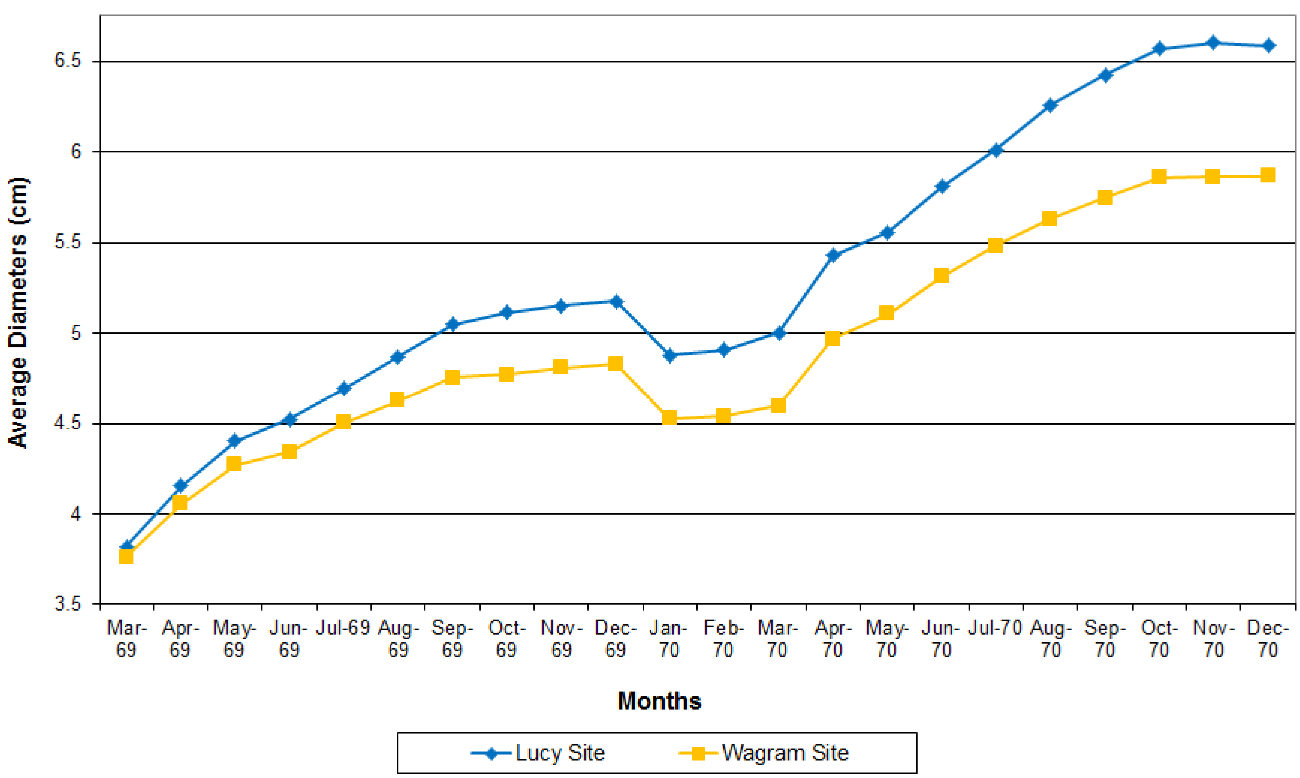

Figure 4. Average monthly diameter measurements illustrating greater diameter growth on the Lucy site for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

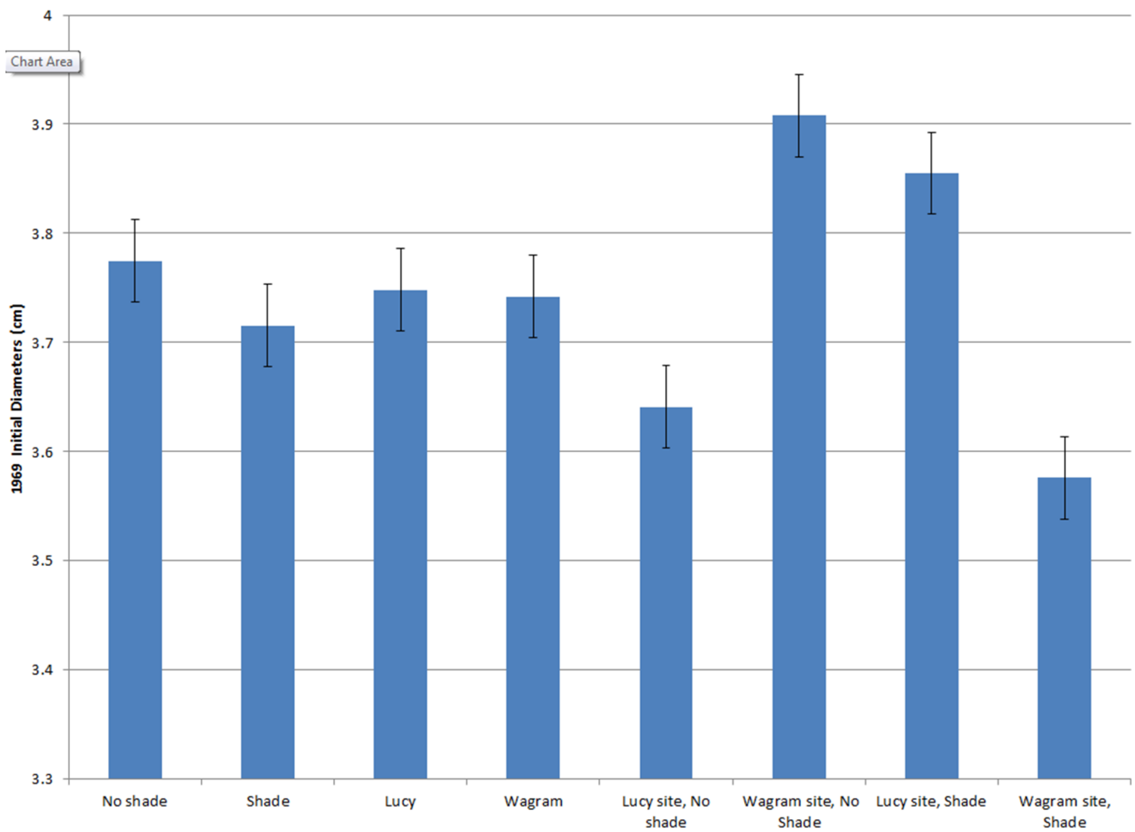

Figure 5. Average initial diameters (cm) in for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

with the shade treatment on both sites. A significant difference between seedlings on Lucy site and the Wagram site was observed for overall growth during the 1970 monthly interval and total growth over the two year period. Figure 6 displays mean diameter growth over the two year measurement period from March of 1969 to December 1970 for the shade treatment, site and shade / site combinations, which illustrates the findings from the statistical examinations.

Monthly diameter growth was also explored for potential significant differences using the repeated measures design. The results of the monthly measures analysis over both years showed a significant difference for site location, shade treatment and significant interactions between time and shade and time and site. Repeated measures analyses also showed a significant shade treatment for diameter growth over the monthly interval in 1970 and the weekly intervals in 1969 and 1970. The weekly analyses showed significant interactions between soil conditions and time and the shade treatment and time, but there was no significant interaction between the site location and shade treatment. However, adjusting weekly interval tests for autocorrelation did affect the analyses, and the normality assumption was suspect for the weekly 1970 test. Calculating the overall means for each year, the shade treatment was not significant, but testing growth within each site location during 1969 showed that shaded seedlings grew less than the non-shaded seedlings. The opposite was seen in 1970. The biweekly intervals from 1969 and 1970 were also tested, but there were no significant differences or interactions in diameter growth with respect to site location or shade treatment for the 1969 interval. The 1970 biweekly interval showed a significant shade/site interaction, but neither the shade treatment nor site location was statistically significant.

DISCUSSION

The desire to identify and develop a better understanding on the many relationships that exist between the environment and seedling growth was the main purpose of this research work. To determine this, height and diameter growth were evaluated over numerous intervals during various periods of the growing and dormant seasons. It was necessary to examine seasonal patterns of growth to understand how seedlings grow before attempting to determine what is affecting growth. Figures 1 and 4 show average monthly height and diameter measurements over the two year measurement period, which displays the seasonal patterns of growth for the sampled longleaf pine seedlings. The six month shade treatment was installed

Table 2. Test of average diameter growth and within group comparisons during the 1969 and 1970 intervals for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

Treatment and site		Average diameter growth (cm)	
		1969	1970
No shade		1.31a	1.49a
Shade		1.21a	1.56a
Lucy		1.43b	1.71b
Wagram		1.09c	1.34c
Shade/site combination			
NL		1.50d	1.67d
SL		1.36de	1.76d
NW		1.11fe	1.30e
SW		1.06f	1.38e
Analysis of variance	**DF**	**Probability > F-value**	
Site	1	0.0004*	<0.0001*
Shade	1	0.2674	0.3359
Site-Shade interaction	1	0.5903	0.9436
Error means square	36		

Means with the same letter are not significantly different (α=0.05); df – degrees of freedom; NW = no shade, Wagram site; SW = shade, Wagram site; NL = no shade, Lucy site; and SL = shade, Lucy site.

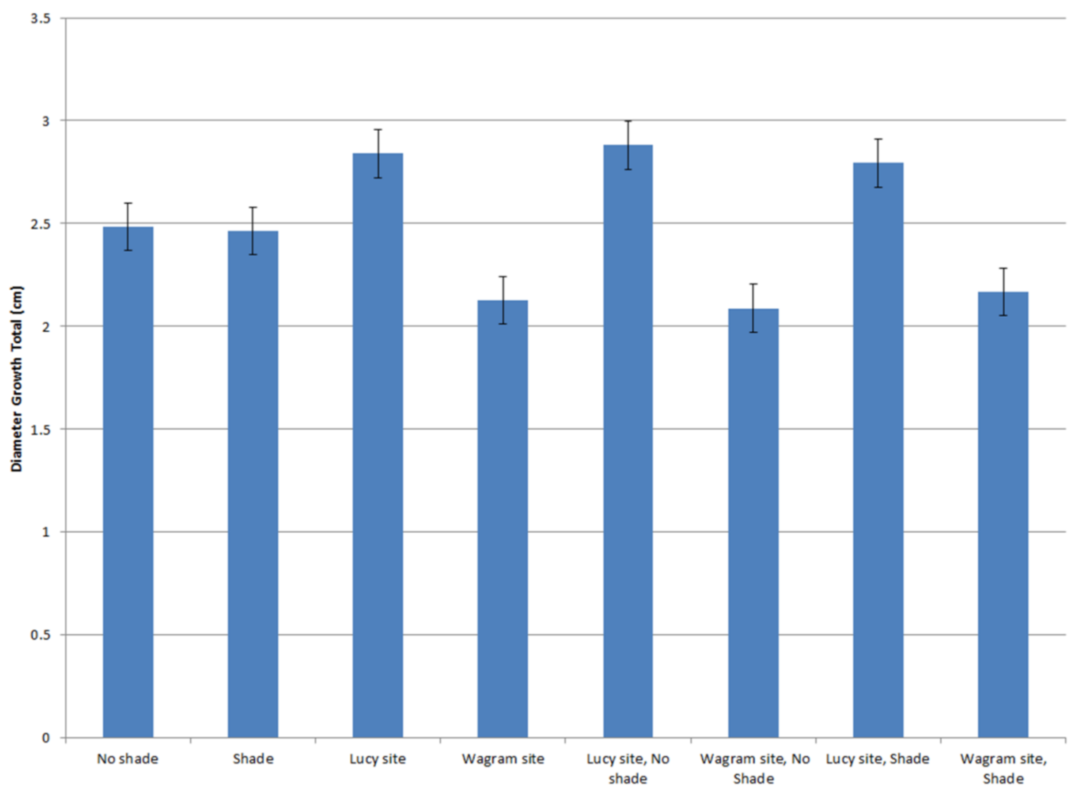

Figure 6. Average diameter growth and within group comparisons during the 1969 and 1970 interval from March 1969 to December 1970 for seedlings sampled on the Escambia Experimental Forest, near Brewton, Alabama, USA.

during the peak of the growing season.

Longleaf pine is commonly known to be very shade intolerant and drought resistant. To determine how much light intensity affects the growth of longleaf pine seedlings, a shading treatment was randomly installed to half of the sampled seedlings. Six months of shading caused a percent difference in direct solar radiation of about 38% during the 1969 growing season. The treatment seemed to have no significant effect on height growth of young longleaf pine over any of the intervals analyzed except for a larger average height growth for seedlings on the Wagram site when looking at growth over the two-year period. For the Lucy site there was an opposite trend for 1970 growth where shaded seedlings on average grew significantly better than non-shaded seedlings (Table 1). This could be a residual effect from the shading treatment because weekly diameter growth of both 1969 and 1970 was significant with respect to the shade treatment. In this study, the shade treatment did not affect diameter growth in either year. Mean diameter growth was also lower, however not significant, for shaded seedlings on both sites, and it was not significant on an annual basis.

The lack of an overall effect on height growth potentially occurred because of several reasons. One reason might be the percent of shading caused by the cheesecloth, or the height it was placed. The cheesecloth was suspended and maintained at 1 m above the terminal bud, which allowed the seedling to receive lateral rays of sunlight during the early morning and late afternoon. Schwarz (1907) notes that areas of dense seedlings and saplings were able to survive in virgin stands by receiving light during the morning and afternoon from certain angles where light entered low in the forest. Duration is another key factor. The treatment was only applied in the 1969 growing season. It may take a longer duration of shading to see an effect on growth. This along with the low percent of sunlight reduced by the cheesecloth did not seem to change the growth rates of the shaded seedlings in comparison with those that were not shaded at all, although overhead shade levels of 50% reduced diameter growth of 20-week-old longleaf pine seedlings growing in a trusshouse with shade cloth (Barnett, 1989). In contrast, a greenhouse study with 16 months of continuous shade of over 60% did not have a significant effect on height growth or root collar diameter of longleaf pine seedlings growing in a greenhouse, but they did find a significant response in root and stem biomass with interactions between light and soil resources (Jose et al., 2003). Climent et al. (2006) also found significant effects in biomass with reductions in light for Canary Island pine seedlings. Testing for significant effects of shade and site on above and below ground biomass for different age classes of seedlings might provide interesting results for the different stages of longleaf pine growth.

Longleaf pine is commonly thought of as a species that is intolerant to shade. This concept may not be completely understood. This study provides data from the only known in-field shading experiment with longleaf pine seedlings that had initiated height growth and were initially up to 1.5 m tall, which are very different from grass stage seedlings or controlled studies. Cavender-Bares and Bazzaz (2000) found that age classes and environmental components played any equal role in photosynthetic capacity if water was not a limiting factor between red oak seedlings and mature trees. The intolerance of longleaf pine to shade may depend more on the age class or stage of growth like grass stage or after height growth is initiated, location of the tree in the stand, and the duration of the shading.

Site location was another key factor that needed to be evaluated in determining a possible influence on growth. Seedlings were on different sites and the two measures of growth were affected in different ways. Site location did not seem to have a significant effect on seedling height growth, but it did for diameter growth. Site location significantly affected diameter growth over all measurement periods during the two-year study including the dormant season measurements. Diameter growth for seedlings on the Lucy site was significantly greater than diameter growth for seedlings on the Wagram site across all intervals except for the biweekly datasets. Diameter growth varied by location in both years as seen in Table 2. Figure 4 shows average monthly diameter measurements over the two year measurements, which displays greater diameter growth on the Lucy site for seedlings sampled. The difference in growth seemed to increase as the seedlings got older. One explanation could be that longleaf pine grows better on drier ridge top site with Lucy soils due to potentially less ground layer competition than Wagram soil on the lower side slope site. If the root systems were deep enough to reach the B-horizon, there might be a moisture gradient caused by the higher clay content at shallower depths than at the bottom of the ridge. The significant differences in diameter growth by site location may also be due to competition of surroundding seedlings or other vegetation instead of soil differences, but without more detailed data about surrounding seedlings and vegetation this concept cannot be further explored. Another explanation might be due to different levels of non-pine competition. Longleaf pine often grows slower on sites with more ground-layer competition (Pessin, 1938) and it is possible that competition was greater at the Wagram site. The growth difference may also be due to differences in soil characteristics. Without more detailed data on surrounding seedlings and vegetation, we can only consider the primary cause of better diameter growth on the Lucy site.

Conclusions

This study provides an interesting look at the growth of longleaf pine over two years and provides insight about the question of the shade tolerance of longleaf pine. This concept may not be completely understood and needs to be explored in detail. With the resurgence of interest in longleaf pine and restoration, shade tolerance plays a large role in the stand dynamics of restoration and conservation efforts. This study provides data from the only known in-field shading experiment with longleaf pine seedlings that had initiated height growth and were initially up to 1.5 m tall at 14 years from seed, which are very different from grass stage seedlings or controlled studies. This makes the results difficult to compare with other studies. The intolerance of longleaf pine to shade may depend more on the stage of growth like grass stage or after height growth is initiated, location of the tree in the stand, and the duration of the shading. There are still many unanswered questions about influences of the environment on the growth of young longleaf pine seedlings. Future field based studies can build upon this research and explore the shade tolerance, environmental interactions, and phenotypic plasticity for seedlings of this size and utilize current technology to help answer more questions. More understanding about relationships between seedling growth and the environment is very important in elucidating patterns of seedling growth.

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REFERENCES

Barnett JP (1989). Shading reduces growth of longleaf and loblolly pine seedlings in containers. Tree Planter. Notes. Winter: 23-26.

Boyer WD (1970). Shoot growth patterns of young loblolly pine. For. Sci. 16(4): 472-482.

Boyer WD (1976). Thermal efficiency: a possible determinant of height growth potential in young loblolly pine. For. Sci. 22(3): 279-282.

Boyer WD (1990). Longleaf pine. In: Burns, RM, Honkala, BH (tech coord) Silvics of North America, Volume I Conifers. USDA For. Serv. Ag Handbook 654, pp.405-412.

Bradshaw AD (1965). Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13: 115-155.

Brown CL (1964). The seedling habit of longleaf pine. Georgia Forest Research Council. Report No. 10: 68p.

Cavender-Bares J, Bazzaz FA (2000). Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling seedlings to mature trees. Oecologia 124: 8-18.

Chambel, MR, Climent J, Alía R, Valladares F (2005). Phenotypic plasticity: a useful framework for understanding adaptation in forest species. Invest Agrar: Sist Recur Fore 14(3): 334-344.

Chapman HH (1932). Is the longleaf type a climax? Ecology 13: 328– 334.

Climent JM, Aranda I, Alonso J, Pardos J A, Gil L (2006). Developmental constraints limit the response of Canary Island pine seedlings to combined shade and drought. For. Ecol. Manage. 231(1-3): 164-168.

Coile TS (1936). The effect of rainfall and temperature on the annual radial growth of pine in the southern United States. Ecol.Mono. 6:533-562.

Frost CC (1993). Four centuries of changing landscape patterns in the longleaf pine ecosystem. In: Hermann, S.H., editor. Proceedings of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration, and manage-ment; 1991 May 30 – June 2; Tallahassee, FL. Tallahassee(FL): Tall Timbers Research Station 18: 139-158.

Gilbert JC (2007). Environmental effects on the growth of young longleaf pine. Thesis, Auburn University, AL. p.102.

Jose S, Merritt S, Ramsey CL (2003). Growth, nutrition, photosynthesis, and transpiration responses of longleaf pine seedlings to light, water, and nitrogen. For. Ecol. Manage. 180: 335-344.

Kozlowski TT, Pallardy SG (1997). Physiology of woody plants second edition. San Diego, CA: Academic Press, Inc.

Kramer PJ, Boyer JS (1995). Water relations of plants and soils. San Diego, CA:Academic Press, Inc.

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996). SAS System for Mixed Models. SAS Inst Inc., Cary, NC.

Lodewick JE (1930) Effect of certain climatic factors on the diameter growth of longleaf pine in western Florida. J. Ag. Res. 41: 349-363.

Mattox MG, Duncan LA, Neal HB, Parker WB, Walkup TA (1975). Soil survey of Escambia County, Alabama. USDA SCS and For Serv, in cooperation with the Ala Dept Ag and Ind, and Ala Ag Exp Stn.

McGuire JP, Mitchell RJ, Moser EB, Pecot SD, Gjerstad DH, Hedman CW (2001). Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can. J. For. Res. 31: 765-778.

Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996). Applied linear statistical models 4th ed McGraw-Hill, Boston, MA.

Niinemets Ü, Valladares F (2006). Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76(4): 521-547.

Outcalt KW (2000). The longleaf pine ecosystem of the south. Native Plants J. 1: 43-44,47-53.

Palik, BJ, Mitchell, RJ, Houseal, G, Pederson N (1997). Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Can. J. For. Res. 27: 1458-1464.

Pessin LJ (1938). The effect of vegetation on the growth of longleaf pine seedlings. Ecol. Monogr. 18(1): 115-149

Ramsey FL, Schafer DW (2002). The statistical sleuth a course in methods of data analysis 2nd ed Duxbury, Pacific Grove, CA.

SAS Institute Inc. (2000-2004). SAS 9.1.3 Help and Documentation, SAS Inst Inc, Cary, NC.

SAS Institute Inc. (2003). Version 9.1, SAS Inst Inc, Cary, NC.

Schlichting CD (1986). The evolution of phenotypic plasticity in plants. Annu. Rev. Ecol. Syst. 17: 667-93.

Schwarz GF (1907). The longleaf pine in virgin forest: a silvical study. John Wiley & Sons, New York.

Soil Survey Division, NRCS (2003). USDA Official Soil Series Descriptions. http://ortho.ftw.nrcs.usda.gov/osd/. Accessed 27 Oct 2003.

Wahlenberg WG (1946). Longleaf pine: its use, ecology, regeneration, protection, growth, and management. Charles Lathrop Pack Forestry Foundation, Washington, DC.