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EFFECTS OF LIGHT REGIMES ON THE BIOMASS AND MORPHOLOGICAL CHARACTERISTICS OF 2-YEAR-OLD CHERRYBARK OAK SEEDLINGS

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Abstract—We used modified shadehouses to simulate the complex light conditions within forest openings and tested the effects of time of direct light exposure, the ratio of direct light to day length, and daily photosynthetically active radiation on aboveground biomass and morphological characteristics of 2-year-old cherrybark oak (*Quercus pagoda* Raf.) seedlings. The five treatments represented the time of exposure to direct sunlight: NO, NOON, MORNING, AFTERNOON, and FULL. At the end of the second growing season, aboveground biomass was not statistically different among the treatments receiving direct sunlight but was significantly lower for the NO treatment. The NO seedlings had the lowest foliage density (leaf number per unit of stem height), while the FULL seedlings had the greatest foliage density. The mean weight of individual leaves did not differ among the light regimes, but individual leaf area in the NO treatment was 65 percent greater than that in the FULL treatment. Results of this study indicate that cherrybark oak seedlings adapt their physiological and morphological features to the prevailing light regime.

INTRODUCTION

Oak seedlings are shade intolerant to intermediately intolerant (Smith 1992) and do not grow well under a closed forest canopy (Lorimer and others 1994). Once advanced oak reproduction is established, seedlings need adequate light to grow faster than competing vegetation (Bey 1964; Crow 1988; Johnson 1979; Minckler 1957; Sander 1972). Light conditions within a stand can be improved by creating openings or reducing stand density through natural disturbance or artificial removal of overstory and/or midstory trees. Considerable research has been conducted relating forest opening size or residual overstory basal area to oak seedling growth (Minckler and Woerheide 1965; Sander and Clark 1971; Smith 1980, 1981). However, quantifying the complex light conditions occurring within stands and relating them to seedling growth are difficult. Light conditions in the field can be complex; direct and partial sunlight may reach seedlings during certain times of a day, but seedlings may be fully shaded at other times. A complex light regime with fluctuating periods of direct and indirect sunlight is difficult to mimic but may strongly affect seedling establishment and growth.

Light is important for oak seedlings because it affects rates of photosynthesis. Under a closed canopy, Hanson (1986) found negative CO_2 assimilation for northern red oak seedlings. Lorimer and others (1994) found that 70 percent of planted white oak (*Quercus alba* L.) and northern red oak (*Q. rubra* L.) seedlings died within 5 years under a closed canopy, and the surviving seedlings showed a net decrease in total height. Oak seedlings do not grow well under full shade because they spend half of produced photosynthates for respiration (Dickson and others 1990). Northern red oak seedlings had similar daily CO_2 assimilation in both open areas and in sunflecks during clear days (Hanson 1986). Apparently, adequate amounts of direct sunlight exposure or photosynthetically active radiation (PAR) are important for oak seedling growth. Gardiner and Hodges (1998) reported approximately 6 times more biomass with 53 percent of the total available PAR than with 8 percent of total PAR for 2-year-old cherrybark oak (*Q. pagoda* Raf.) seedlings. On the other hand, during certain stages of seedling development, excessive exposure to sunlight may damage the photosynthetic apparatus thereby reducing or inhibiting photosynthesis (Powles 1984).

We hypothesized that timing and amount of daily direct sunlight exposure, amount of PAR, and ratio of direct sunlight to total sunlight would affect the growth and characteristics of cherrybark oak seedlings. To test the hypotheses, we used a nontraditional type of shadehouse to simulate the light conditions occurring within small forest openings. Each shadehouse had sections that had no shade cloth on top, which allowed direct sunlight to reach seedlings during different times of day. Applying methods of Marquis (1965) and Satterlund (1983), we calculated the length of time seedlings were exposed to direct sunlight and tested the effect of light regimes on aboveground biomass and morphological characteristics of 2-year-old cherrybark oak seedlings. The effect of light regimes on periodic height and diameter growth was reported earlier (Guo and others 2001).

METHODS

The study site was located in Drew County, Arkansas (91° 50' W and 33° 37' N) in the west Gulf Coastal Plain. The soil is an Amy silt loam (Typic Ochraquults). Site index for cherrybark oak is about 26 m at age 50. Before the study was established, the area was an open field, but the native vegetation of the site is classified as mixed pines and hardwoods (Larance and others 1976). Annual precipitation averages 134 cm, with most occurring in the winter and early spring.

The study was a split plot with a completely randomized block layout and three replicates. The main plot was the regimes of direct sunlight, and subplot was parent trees. With the shadehouses oriented toward north, five light

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regimes were created based on when direct sunlight occurred: mostly in the morning (MORNING), around noon (NOON), mostly in the afternoon (AFTERNOON), all day (FULL), and at no time (NO). The treatments were intended to represent the light conditions occurring within a small forest opening: FULL at the center of a large opening, NO at the south end, MORNING at the western edge, AFTERNOON at the eastern edge, and NOON at the center and northern edge of smaller openings.

The dimensions of the shadehouses for the NOON treatment were 2.4 x 3.7 x 2.4 m, while the dimensions for the NO treatment were 2.4 x 2.4 x 2.4 m (Guo and others 2001). Shade for the MORNING and AFTERNOON treatments came from the vertical walls of the NOON treatment. All shade cloth provided 20 percent of full sunlight. The shadehouse for the NO treatment had shade cloth on the top and all sides except for the lower half of the north side. The NOON treatment only had vertically-oriented shade cloth on the north, east, and west side.

Acorns from four open-pollinated cherrybark oak trees in Drew County, AR were collected in November 1996, float tested, and stored in a refrigerator at 4 °C. Acorns were stratified for 60 days and sown in a soil-vermiculite mixture in February 1997. Seedlings were grown for 2 months in a greenhouse before field planting in April 1997. Six seedlings from each parent tree were planted in 0.9- x 1.5-m beds in each main-plot treatment. Seedlings were planted with a 0.3- x 0.3-m spacing and a 4 row x 6 column arrangement with parent trees randomized within a row. A total of 24 seedlings was planted in each plot for a total of 360 seedlings in the study. During the first month after planting, dead seedlings, averaging six seedlings per bed, were replaced by seedlings of the same parent tree. Replanting was mainly due to a severe storm in early May with high wind, which damaged shoots, and root damage caused by burrowing crawfish. Replanted seedlings did not differ ($P >$ 0.05) from non-replanted seedlings in height and root-collar diameter.

A mulch of foliar litter from a mixed hardwood stand was used to retard herbaceous plant competition within the beds, and beds were periodically hand-weeded. Herbaceous vegetation outside of the beds was periodically controlled with a foliar-applied herbicide. Seedling beds were irrigated to field capacity during periods of low summer rainfall.

For the partially shaded treatments, the length of time each planting space was in direct sunlight at ground level was calculated for each day by tracking the shadows cast by the shadehouse's walls. Solar declination was calculated from formula given by Satterlund (1983), and shadow lengths during each day were calculated from formula provided by Marquis (1965) and Satterlund (1983). Day lengths, the time between sunrise and sunset, were obtained from the Time Service Department (U.S. Naval Observatory, Washington, DC) for each day of the second growing season. The ratio of direct sunlight to day length (the direct-sunlight ratio) was calculated for each day of a measurement period and then averaged for the second growing season. A LI-190SA quantum sensor (LI-COR, Inc. Lincoln, Nebraska, USA) was installed in each treatment of one shadehouse. The calibrated sensors allowed determining mean PAR for each treatment. PAR was automatically recorded by a LI-1000 (LI-COR, Inc. Lincoln, Nebraska, USA) data logger at a 15 minute interval for 2 days a week during the second growing season.

On November 5 and 6, 1998, foliage, branches, and stems of seedlings were harvested by parent trees within a plot after counting the number of surviving seedlings. We randomly collected a subsample of 20 leaves from each parent to determine leaf area using a LI-COR 3100 Area Meter (LI-COR Inc. Nebraska, USA). Biomass samples were dried in a force-draft oven at 75 °C until constant weights were obtained. The 20-leaf subsamples were dried and weighed separately.

The average number of leaves for the seedlings of a parent tree was calculated by dividing foliar biomass (corrected for the 20-leaf subsample) by the average weight of individual leaves determined from the subsample. To obtain an expression of seedling morphology, we calculated foliage density (leaf number m^{-1}) as the ratio of leaf number to seedling height. A similar expression was calculated for foliage area density ($m^2\ m^{-1}$), which was the ratio of leaf area of seedlings to their height. All seedling characteristics were analyzed by General Linear Procedure of SAS (1990). Means were separated by the Ryan-Einot-Gabriel-Welsch multiple range test at $\alpha = 0.05$. Regression was used to relate foliage density or foliage area density to seasonal mean daily PAR or direct sunlight ratio using a simple linear model. All reported regression coefficients differed from zero at $\alpha \leq 0.05$.

RESULTS AND DISCUSSION

Light Regimes

Seasonal mean daily PAR (mol m^{-2} per day) was computed by adding all the measurements for a day and calculating the mean daily PAR. Mean daily PAR varied among the light regimes, ranging from 6.6-10.9 mol m^{-2} per day for NO, 20.0-24.3 mol m^{-2} per day for NOON, 25.2-34.7 mol m^{-2} per day for MORNING, 28.2-37.1 mol m^{-2} per day for AFTERNOON, and 36.3-45.8 mol m^{-2} per day for FULL. Direct sunlight exposure at ground level in the NOON treatment ranged from 3.6 hours per day in May to 2.7 hours per day in October. MORNING and AFTERNOON treatments averaged 8.5 hours per day in May and 6.9 hours per day in October. For the FULL treatment, day length varied from 13.6 hours in May to 11.2 hours in October. Exposure to direct sunlight increased as seedlings grew taller because the distance between the top of the shadehouse and the seedling's height diminished. In May for example, direct sunlight in the NOON treatment increased from 3.6 hours per day at ground level to 7.3 hours per day at 1.5 m above ground. Direct sunlight in the MORNING treatment increased from 8.5 hours per day at ground level to 10.3 hours per day at 1.5 m above ground in May. The pattern in the AFTERNOON treatment was similar to that of the MORNING treatment.

Aboveground Biomass

Mean foliar biomass of the NO seedlings was significantly smaller than that of the other treatments, and there was no statistical difference among the remaining treatments (fig. 1).

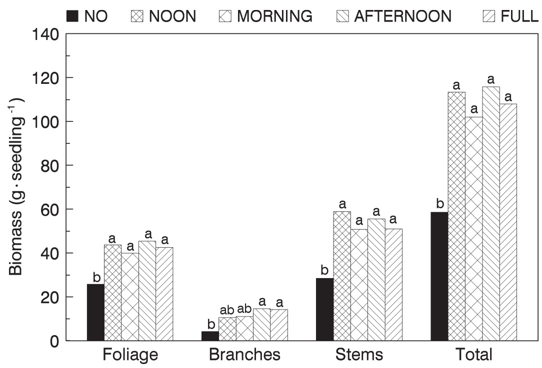

Figure 1—Effect of light regimes on foliage, branch, stem, and total aboveground biomass of cherrybark oak seedlings at the end of the second growing season. Bars with the same letter in the same cluster are not significantly different at $\alpha = 0.05$.

The mean foliar biomass for the NO seedlings was 26 g, compared to 40-46 g for seedlings in the other treatments. Mean branch and stem biomass had similar patterns to that of foliage, except that mean branch biomass of the NO seedlings did not differ from those with the NOON and MORNING treatments. However, mean branch biomass in the NOON and MORNING treatments was more than twice the biomass of the NO seedlings (11 versus 4 g). Total biomass was similarly affected by light regimes. The mean total biomass of the NO seedlings was 59 g, which was significantly smaller than that of other treatments (102-116 g) (fig. 1). Significant variation occurred among seedlings from the parent trees, but parent trees did not significantly interact with light regimes. Seedlings with the greatest total biomass (Parent 4) exceeded those with the least (Parent 2) by 63 percent.

The percentage of total biomass in stems did not differ among treatments. Although the NO treatment had both the lowest foliage and total biomass, the percentage of total biomass in foliage for the NO treatment was significantly greater than the percentage for other treatments (fig. 2). No difference was found among the treatments receiving direct sunlight. In contrast, the percentage of total biomass in branches for the NO treatment was the lowest observed and was significantly different from the FULL treatment but not the NOON, MORNING, and AFTERNOON treatments. This difference in biomass allocation appeared to be an adaptation to the shade. Smith (2000) stated that shade avoidance is a developmental response, which collectively allows plants to maintain photosynthetic structure in limited light conditions.

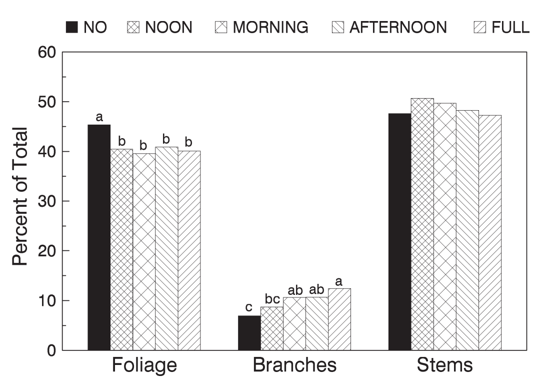

Figure 2—Effect of light regimes on the percentage distribution of total α aboveground biomass among foliage, branches, and stems of cherrybark oak seedlings at the end of the second growing season. Bars with the same letter or no letter in the same cluster are not significantly different at $\alpha = 0.05$.

Morphological Characteristics

The low foliar biomass of the NO treatment was due to fewer leaves on the seedlings, because no significant differences occurred among light regimes for the mean weight of individual leaves (table 1). Leaf weights only ranged between 0.56 to 0.63 g leaf^{-1}. In contrast, leaf area varied significantly among the treatments and strongly reflected the amount of direct sunlight a treatment received. Leaves in the NO treatment had 65 percent more area per leaf than those in the FULL treatment. Specific leaf area ranged from a minimum of 96 cm^2 g^{-1} in the FULL treatment to a maximum of 142 cm^2 g^{-1} in the NO treatment; these values and the pattern of variation were consistent with those compiled for a wide variety of different tree species by Shelton and Switzer (1984). In addition, shade leaves usually develop bigger chloroplast and are richer in chlorophyll content than sun leaves (Boardman 1977).

Foliage density averaged 39, 52, 57, 61, and 69 leaves m^{-1} in NO, NOON, MORNING, AFTERNOON, and FULL treatments, respectively. Foliage density was linearly related to seasonal mean daily PAR ($r = +0.81$) and to seasonal mean direct sunlight ratio ($r = +0.79$) (fig. 3). On the other hand, foliage area density was not significantly affected by light regimes, with values only ranging from 0.34 to 0.36 m^2 m^{-1}. This phenomenon was likely caused by an increase in individual leaf area as shading increased.

CONCLUSIONS

Light conditions were important for the early growth of cherrybark oak seedlings. A daily direct sunlight exposure of 3-4 hours on the forest floor and 20 percent of the full sunlight in the remaining time resulted in the same aboveground biomass as longer exposures. Without any direct sunlight and about 23 percent of the total daily PAR, biomass was significantly reduced. Some exposure to direct

Table 1—Effect of light regime on the mean properties of individual leaves of cherrybark oak seedlings at the end of the second growing season

Light regimes	Wgt.	Area	Specific leaf area
	g	*cm²*	*cm² g⁻¹*
No	0.63[a]	89a	142a
Noon	0.60	68b	116b
Morning	0.58	60bc	103c
Afternoon	0.59	63bc	106c
Full	0.56	54c	96c

Means are based on four subsamples of 20 randomly selected leaves within each bed.

[a] Means of a column with the same letter or no letter are not significantly different at α = 0.05.

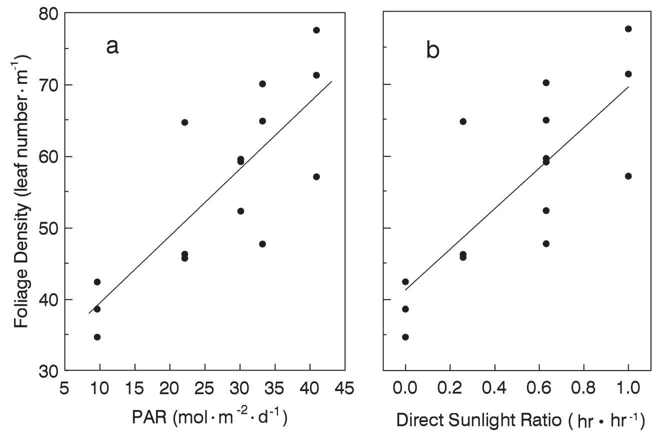

Figure 3—Relationship between foliage density of cherrybark seedlings at the end of second growing season and (a) the seasonal mean daily PAR and (b) the mean direct sunlight ratio. For mean seasonal daily PAR: Y = 30.07 + 0.935X; r^2 = 0.66. For direct sunlight ratio: Y = 41.22 + 28.26X; r^2 = 0.62.

sunlight seemed to be important for maximum seedling development. The implication of this finding is that if competition is controlled, proper size of forest openings or overstory coverage is important for adequate direct sunlight exposure of the seedlings. In response to different light regimes, seedlings developed different foliar densities and morphologies. Foliage density was significantly greater for the FULL seedlings than for the NO and NOON seedlings. There was a positive linear relationship between foliage density and direct sunlight ratio and PAR. High foliage density would have provided more mutual shading for seedlings in the FULL treatment, which might have been beneficial in avoiding excess light. However, foliage area distribution did not differ greatly among the treatments because of the increased area of individual leaves as shading increased. Finally, selection of maternal trees for acorn collection is important for producing seedlings for planting. Results from our study showed a difference in biomass of up to 63 percent resulted from seedlings that originated from different parent trees.

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Station ID: GTR-SRS-071

Description: Ninety-two papers and thirty-six poster summaries address a range of issues affecting southern forests. Papers are grouped in 15 sessions that include wildlife ecology; fire ecology; natural pine management; forest health; growth and yield; upland hardwoods - natural regeneration; hardwood intermediate treatments; longleaf pine; pine plantation silviculture; site amelioration and productivity; pine nutrition; pine planting, stocking, spacing; ecophysiology; bottomland hardwoods - natural regeneration; and bottomland hardwoods—artificial regeneration.