
Effects of Light Regimes on the Growth of Cherrybark Oak Seedlings

Yanfei Guo, Michael G. Shelton, and Brian R. Lockhart

ABSTRACT. Light regimes vary significantly within small forest openings, ranging from full sunlight to total shade, and they may affect the establishment and early growth of oak seedlings. We designed modified shadehouses to simulate the complex light conditions within forest openings and tested the effects of daily photosynthetically active radiation (PAR), time of direct light exposure, and the ratio of direct light to day length (direct-sunlight ratio) on height, diameter, and periodic growth of cherrybark oak (*Quercus pagoda* Raf.) seedlings through 2 yr. Five treatments representing the time of exposure to direct sunlight were created: NO, NOON, MORNING, AFTERNOON, and FULL. Treatments significantly affected both the height and root-collar diameter of seedlings, especially during the second growing season. The direct-sunlight ratio was linearly related to periodic height growth for the NOON treatment but not related to height growth for the other treatments. However, periodic height growth in the AFTERNOON and FULL treatments was highly correlated to mean daily PAR. Maximum periodic height growth occurred at moderate daily PAR levels. This research showed that light conditions for maximum growth of cherrybark oak seedlings change through time, with adequate shading being most favorable during the early stages of establishment. *FOR. SCI.* 47(2):270–277.

Key Words: Forest openings, periodic growth, *Quercus pagoda*, reproduction, shadehouses.

OBTAINING ADEQUATE OAK REGENERATION is a major concern in the United States (Loftis and McGee 1993). Extensive research has shown that advanced oak reproduction must be established before overstory removal for successful regeneration. Larger, well-established seedlings are more likely to grow into crop trees. Loftis (1990a) predicted that as basal diameter of northern red oak (*Quercus rubra* L.) seedlings increased at the time of overstory harvest, the probability of seedlings becoming future dominant or codominant trees increased.

Following acorn production and germination, successful oak seedling establishment is highly dependent on adequate light exposure. Oak seedlings are shade intolerant to intermediately intolerant (Smith 1992) and cannot grow well under a closed forest canopy. Lorimer et al. (1994) found that 70% of planted white oak (*Q. alba* L.) and northern red oak seedlings died within 5 yr under a closed canopy, and the surviving seedlings showed a net decrease in total height.

Oak seedlings often die back to the root collar and resprout (Crow 1988, Dickson 1991). If not released from intense shade, most oak seedlings will perish or remain small for years. Some seedlings, however, may eventually develop a large taproot (Merz and Boyce 1956). Oak seedlings may respond to improved light conditions resulting from reproduction cutting or understory/midstory removal. Lorimer et al. (1994) reported that understory removal resulted in 90% survival of northern red and white oak seedlings and 50–90% increases in height. Similar increases in survival and height growth were also observed after midstory removal by Janzen and Hodges (1987) and Lockhart et al. (2000) for cherrybark oak (*Q. pagoda* Raf.). Once released, oak seedlings may be able to compete with faster growing species (Minckler 1957, Bey 1964, Sander 1972, Johnson 1979).

Because of the clear importance of light to oak regeneration, reproduction methods have been developed that create adequate light regimes for oak seedlings, such as the

Yanfei Guo is Assistant Professor, School of Forest Resources, University of Arkansas at Monticello, P.O. Box 3468, Monticello, AR 71656—Phone: (870) 460-1692; Fax: (870) 460-1092; E-mail: guo@uamont.edu. Michael G. Shelton is Research Forester, Southern Research Station, USDA Forest Service, P.O. Box 3516, Monticello, AR 71656—Phone: (870) 367-3464; E-mail: mshelton@fs.fed.us. Brian R. Lockhart is Associate Professor, School of Forestry, Wildlife, and Fisheries, Louisiana State University, Baton Rouge, LA 70803—Phone (225) 388-4131; E-mail: blockh1@lsu.edu.

Acknowledgments: Publication of this manuscript was approved by the Director, Arkansas Agricultural Experiment Station, manuscript #99119. The authors appreciate the assistance of Suzanne Wiley in constructing the shadehouses, and Yujia Zhang and Mike Begier in taking periodic measurements. We thank Emile Gardiner, Alex Friend, three anonymous reviewers, and the associate editor for their helpful comments.

Manuscript received February 4, 2000. Accepted August 8, 2000.

Copyright © 2001 by the Society of American Foresters

shelterwood and group selection methods. Successes have been reported for regeneration of northern red oak in the southern Appalachians, but oak reproduction has not always been successful in the same area (Loftis 1990b). The lack of consistent success reflects the complexity of growth environments for oak seedlings. This complexity results from variation in light availability, species competition, and other environmental factors. Hodges (1989) reported that heavy shelterwood cuts encouraged development of the faster growing competitors of oaks. Brose and Van Lear (1998) found that burning in shelterwood stands increased oak seedling establishment. Burning controlled yellow poplar (*Liriodendron tulipifera* L.) and red maple (*Acer rubrum* L.), giving oak sprouts time to achieve a competitive advantage. If competing understory vegetation is controlled, light conditions resulting from the stand's canopy become the most critical factor for oak seedling growth. Gardiner and Hodges (1998) used shadehouses to study the effect of various light conditions on cherrybark oak seedlings and found that height of 2-yr-old seedlings was the greatest with 27% and 53% of full sunlight. Root-collar diameter showed a similar pattern, except that it was greater with 53% of full sunlight than with 27%. Full sunlight exposure and 8% of full sunlight resulted in much smaller seedlings. Similar results have been reported by others (Kolb and Steiner 1990a, 1990b, Shumway et al. 1993, Gottschalk 1994).

Field studies relating quantified light conditions with oak establishment and growth had been rare until Buckley et al. (1998, 1999) reported photosynthetically active radiation (PAR) in pine and oak stands in northern Michigan and related it to early northern red oak establishment and growth. Most studies, however, related forest opening size or residual overstory basal area to oak seedling growth. For instance, Minckler and Woerheide (1965), Sander and Clark (1971), and Smith (1980, 1981) reported that oak seedling growth in the center of forest openings with diameters as small as one or two times the height of surrounding trees was similar to that in clearcuts. In the field, however, quantifying the light regime of seedlings is difficult. Direct sunlight may reach seedlings during certain times of the 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.

Quantifying the sunlight received at any spot within forest openings is crucial to evaluating the effect of that light regime on the growth of oak seedlings. Marquis (1965) proposed a method to predict light conditions in small forest openings, making it possible to compute daily and seasonal light conditions. Similar research was also conducted by Satterlund (1983) and Dai (1996).

We hypothesized that timing and amount of direct sunlight exposure and daily PAR affect the growth of cherrybark oak seedlings. To test these hypotheses, we built 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 the methods of Marquis (1965) and Satterlund (1983), we calculated the length of time seedlings were exposed to direct sunlight and tested the hypothesis that the ratio of direct sunlight to total sunlight affected oak seedling growth. In addition, since small forest openings result in a complex light regime, we tested the hypothesis that exposure of oak seedlings to direct sunlight during different times of day would affect seedling growth. Cherrybark oak was used in this study because of its importance in the regional forest ecosystem and economy.

Materials and 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 native vegetation is classified as mixed pines and hardwoods (Larance et al. 1976). Annual precipitation averages 134 cm, with most occurring in the winter and early spring.

The statistical design 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 long axis of the shadehouses oriented toward north, the main plot was divided into five treatments 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 × 3.7 × 2.4 m, while the dimensions for the NO treatment were 2.4 × 2.4 × 2.4 m (Figure 1). Shade for the MORNING and AFTERNOON treatments came from the vertical walls of the NOON treatment. All shade cloth provided 20% of full sunlight, which is equivalent to the light transmittance in an oak stand with a basal area of 21 m²ha⁻¹ based on equations of Buckley et al. (1999). 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 sides.

Acorns from four open-pollinated cherrybark oak trees in Drew County, AR, were collected in November 1995, float tested, and stored in a refrigerator at 4°C. Acorns were stratified for 60 days and sowed in a peat-vermiculite mixture in February 1996. Seedlings were allowed to grow for 2 months in a greenhouse before planting in the soil in April 1997. Six seedlings from each parent tree were planted in 0.9 × 1.5 m beds in each main-plot treatment (Figure 1). Seedlings were planted with a 0.3 × 0.3 m spacing and a 4 row by 6 column arrangement with parent trees randomized within a row. A total of 24 seedlings were planted in each plot for a total of 360 seedlings in the study. During the first month after

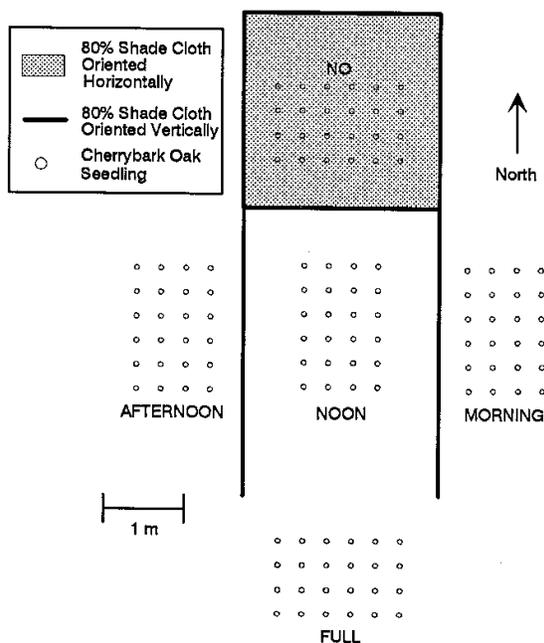


Figure 1. Design and layout of a shadehouse and the associated seedbeds. Treatment names reflect when direct sunlight occurred.

the planting, dead or damaged seedlings, averaging six seedlings per bed, were replaced by seedlings of the same parent tree. Replanting was necessary due to a severe storm in early May, which caused shoot damage and damage to roots by burrowing crawfish.

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 weekly during periods of low summer rainfall.

Seedling height (m) and root-collar diameter (mm) were measured four times in 1997 and seven times in 1998. Because of minor variation in the length of measurement periods, periodic diameter and height growth were standardized to a 30 day basis. For the partially shaded treatments, the length of time (hr) each planting space was in direct sunlight at ground level was calculated for each day of a measurement period by tracking the shadows cast by the shadehouse's walls. Solar declination was calculated from formulas given by Satterlund (1983), and shadow lengths during each day were calculated from formulas provided by Marquis (1965) and Satterlund (1983). Day lengths (hr), 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. A 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 period. A LI-190SA quantum sensor (LI-COR, Inc., Lincoln, Nebraska) was installed in each treatment of one shadehouse. The calibrated sensors allowed determination of mean PAR ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) for each treatment. PAR was

automatically recorded by a LI-1000 (LI-COR, Inc., Lincoln, Nebraska) data logger at a 15 min. interval for 2 days a week during the growing season. The average PAR at each interval during a measurement period was calculated, and total daily PAR ($\text{mol} \cdot \text{m}^{-2}$) was computed by adding all the measurements for a day and calculating the mean total daily PAR.

Mean height, root-collar diameter, periodic height and diameter growth, and percentage mortality of each parent in a plot were analyzed by General Linear Models Procedure of SAS (SAS 1990). We used the following model:

$$Y_{ijk} = \mu + \rho_i + \alpha_j + \gamma_{ij} + \beta_k + (\alpha\beta)_{jk} + \varepsilon_{ijk} \quad (1)$$

where Y_{ijk} = mean response variable for each parent tree in a plot; μ = overall mean; ρ_i = block ($i = 1-3$); α_j = light regime ($j = 1-5$); γ_{ij} = block \times light regime; β_k = parent trees ($k = 1-4$); $(\alpha\beta)_{jk}$ = light regime \times parent trees; ε_{ijk} = error term. To test the effect of replanting, mean height and diameter of each replanting class (replanted and nonreplanted) in a plot were analyzed by Model 1, except β_k = replant ($k = 1-2$). Means were separated by the Ryan-Einot-Gabriel-Welsch multiple range test at $P = 0.05$. Regression was used to relate periodic height and diameter growth in 1998 to the following environmental variables: average daily PAR, hours of direct sunlight, and direct-sunlight ratio. There were 18 observations for each regression (six periods with three replicates). We used the following model:

$$Y_i = b_0 + b_1 X_i + b_2 X_i^2 + \varepsilon_i \quad (2)$$

where Y_i = mean periodic height or diameter growth of a light regime treatment in a block; X_i = the specified environmental variable; b_0 , b_1 , and b_2 = coefficients determined by least squares regression (SAS 1990); ε_i = error term. Terms were dropped from the full model if their coefficients did not differ from zero at $P \leq 0.05$.

Results

Environmental Conditions

Daily direct sunlight, direct-sunlight ratio, and average daily PAR were all affected by the light regime treatments. Direct sunlight exposure at ground level in the NOON treat-

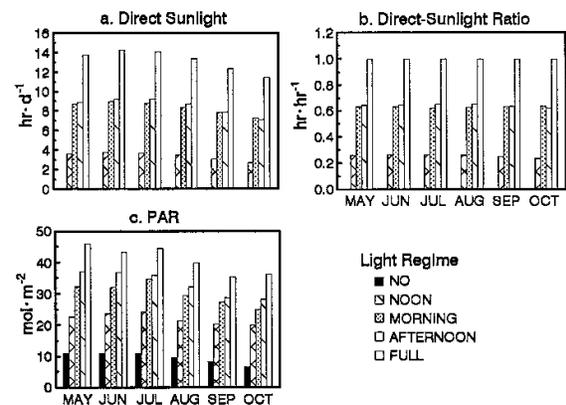


Figure 2. Effects of light regimes on (a) direct sunlight, (b) direct-sunlight ratio, and (c) daily PAR.

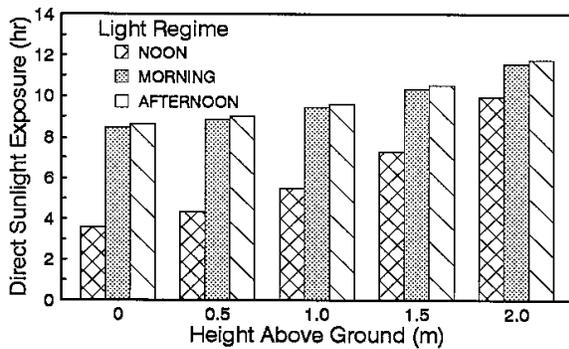


Figure 3. Direct light exposure in the NOON, MORNING, and AFTERNOON treatments as related to height above ground.

ment ranged from 3.6 hr-day⁻¹ in May to 2.7 hr-day⁻¹ in October (Figure 2a). MORNING and AFTERNOON treatments received more direct sunlight than those in NOON treatment, averaging 8.5 hr-day⁻¹ in May and 6.9 hr-day⁻¹ in October. Day length, which was represented by the direct light exposure of the FULL treatment, varied from 13.6 hr in May to 11.2 hr in October (Figure 2a). Direct-sunlight ratio ranged from zero for the NO treatment to one for the FULL treatment, and this ratio appeared to be a good relative expression of a seedling's light regime (Figure 2b). Direct-sunlight ratio for the NOON treatment ranged from 0.23 to 0.26 during the second growing season, while the ratios for the MORNING and AFTERNOON treatments ranged from 0.63 to 0.65. For a specific treatment, the slight variation in the ratio during the growing season reflected seasonal changes in solar position. Average daily PAR also varied greatly, ranging from: 6.6–10.9 mol·m⁻² for NO, 20.0–24.3 mol·m⁻² for NOON, 25.2–34.7 mol·m⁻² for MORNING, 28.2–37.1 mol·m⁻² for AFTERNOON, and 36.3–45.8 mol·m⁻² for FULL (Figure 2c).

Exposure to direct sunlight increased as seedlings grew taller because the distance between the top of the shadehouse and the seedling's height diminished. For instance, direct sunlight in the NOON treatment increased from 3.6 hr-day⁻¹ at ground level to 4.4 hr-day⁻¹ at 0.5 m in May, or an increase of 0.8 hr-day⁻¹. At 1.5 m above ground, the direct sunlight was 7.3 hr-day⁻¹ (Figure 3). Increases in the MORNING and AFTERNOON treatments were not as pronounced as in the NOON treatment. At ground level, direct sunlight in the MORNING treatment was 8.5 hr-day⁻¹ and 10.3 hr-day⁻¹ at 1.5 m above ground in May. The increase of 1.9 hr-day⁻¹ was half of the increase in the NOON treatment. The pattern in the AFTERNOON treatment was similar to that of the MORNING treatment (Figure 3).

Seedling Survival and Mean Size

Seedling survival averaged 91.4%, and most mortality occurred during the first growing season. There was no significant treatment effect for mortality ($P = 0.71$). Replanted seedlings did not differ in height ($P = 0.86$) and diameter ($P = 0.60$) from the nonreplanted seedlings in September 1997 and in following measurements (P ranged from 0.44 to 0.86).

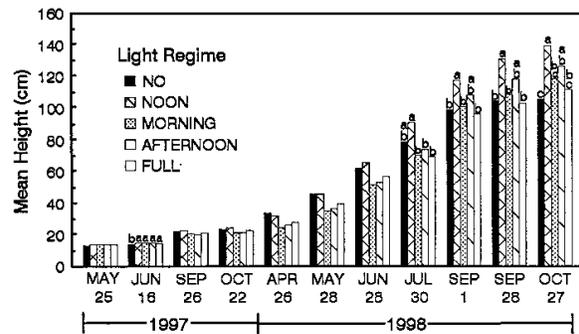


Figure 4. Effects of light regime on mean height of cherrybark oak seedlings during the first (1997) and second (1998) growing seasons. Bars with same letter or no letter in the same cluster are not significantly different at $P = 0.05$.

At the end of the second growing season, mean height of cherrybark oak seedlings in the NOON treatment was significantly taller than seedlings in other treatments except the AFTERNOON treatment (Figure 4). Mean height for the NO treatment was significantly the shortest, but there was no significant difference among the MORNING, AFTERNOON, and FULL treatments. Seedlings in the NOON treatment averaged 34, 28, and 21 cm taller than seedlings in NO, FULL, and MORNING treatments, respectively. Mean root-collar diameter in the NO treatment was also smaller than those with the other treatments at the end of the second growing season, but no significant differences occurred among the other treatments (Figure 5).

Parent trees affected the height and root-collar diameter of seedlings significantly, but did not interact with light regime. At the end of the second growing season, seedlings from Parent Tree 2 were significantly smaller in both height and root-collar diameter than those from the other three parents. The difference was over 20 cm for height and 2.2 mm for diameter. No difference was found for root-collar diameter among the other three parent trees, but height varied significantly. Height of seedlings from Parent Tree 1 averaged 141 cm, compared to 124 cm for Parent 4, 119 cm for Parent 3, and 99 cm for Parent 2.

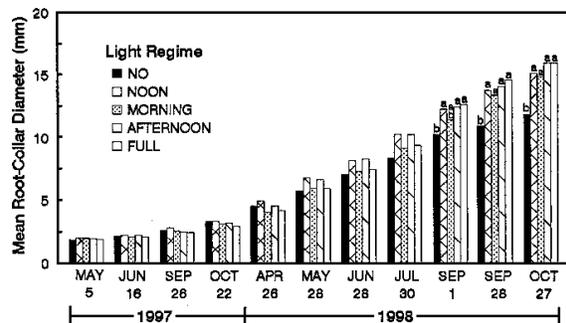


Figure 5. Effects of light regime on mean root-collar diameter of cherrybark oak seedlings during the first (1997) and second (1998) growing seasons. Bars with same letter or no letter in the same cluster are not significantly different at $P = 0.05$.

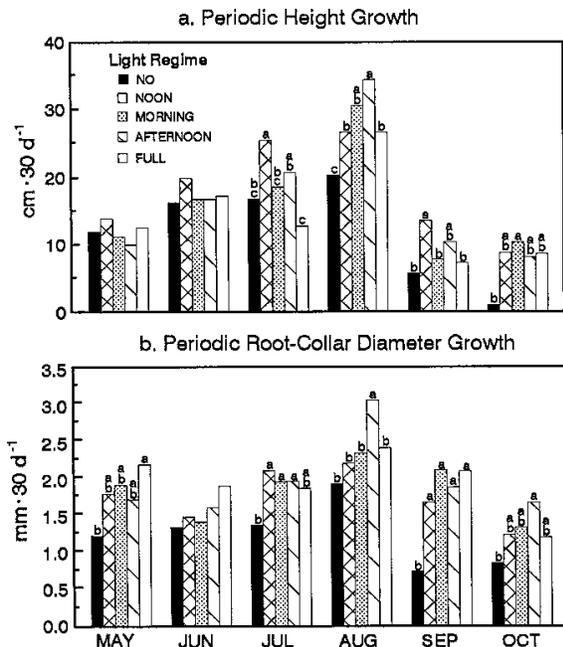


Figure 6. Effects of light regime on periodic height and root-collar diameter growth of cherrybark oak seedlings during the second growing season (1998). Bars with same letter or no letter in the same cluster are not significantly different at $P = 0.05$.

Periodic Growth

Periodic height growth in the NO treatment was significantly lower than in the other treatments for August and October (Figure 6a). In contrast, seedlings in the NOON treatment usually had the greatest periodic height growth during the second growing season, except for August when seedlings in the MORNING and AFTERNOON treatments had greater growth. Although periodic height growth in the AFTERNOON and MORNING treatments occasionally surpassed the NOON treatment, seedling height at the end of the second growing season was best for the NOON treatment. Seedlings in the MORNING, AFTERNOON, and FULL treatments had similar rates of periodic height growth.

The smaller root-collar diameter of seedlings in the NO treatment reflected a decrease in periodic diameter growth during the second growing season (Figure 6b). At the end of the first growing season, root-collar diameter in the NO treatment was not different from the other treatments (Figure 5). However, during the second growing season, periodic diameter growth in the NO treatment was frequently lower than that in the other treatments. Periodic diameter growth in the other treatments was similar during most of the second growing season, except in August when growth in the AFTERNOON treatment was greater than the other treatments.

Periodic height growth in the NOON treatment was linearly related to the direct-sunlight ratio with an adjusted coefficient of determination of 0.53 (Figure 7). Periodic root-collar diameter growth in the NOON treatment and diameter and height growth in the MORNING and AFTERNOON treatments were not significantly (P ranged from 0.21 to 0.29) related to the direct-sunlight ratio. Regressions for the

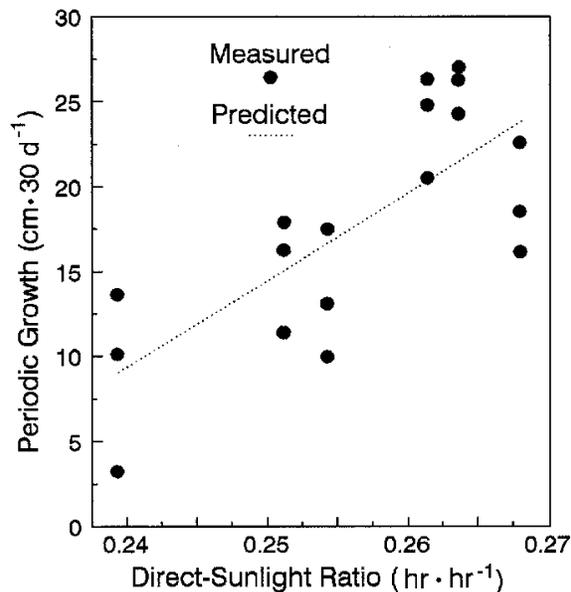


Figure 7. Relationships between periodic height growth and direct-sunlight ratio for cherrybark seedlings in the NOON treatment during the second growing season (1998). $Y = -114.2 + 514.74X$, adjusted $R^2 = 0.53$.

FULL and NO treatments could not be conducted because the direct-sunlight ratio was always 1 for the FULL treatment and always 0 for the NO treatment. Although periodic height and diameter growth in the AFTERNOON treatment was not related to the direct-sunlight ratio, strong relationships occurred for mean periodic PAR with adjusted coefficients of determination of 0.89 and 0.70, respectively (Figures 8d and 9d). Periodic height growth in the NO and FULL treatments

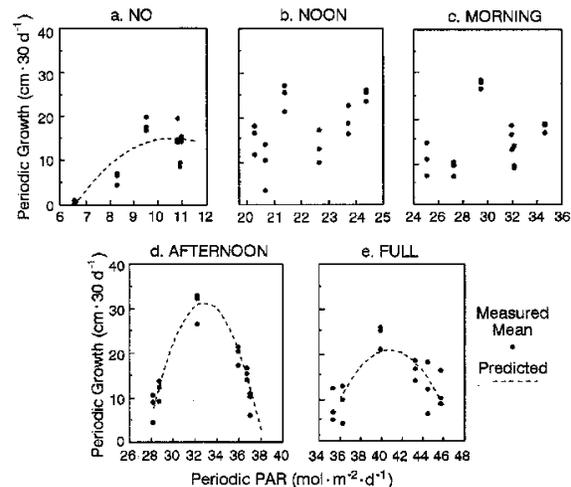


Figure 8. Relationships between periodic height growth of the cherrybark oak seedlings and mean periodic daily PAR during the second growing season (1998) for the tested light regimes. Regression models were: (1) for the FULL treatment, $Y = -781.48 + 39.31X - 0.48X^2$, adjusted $R^2 = 0.55$; (2) for the AFTERNOON treatment, $Y = -1146.57 + 71.81X - 1.09X^2$, adjusted $R^2 = 0.89$; and (3) for the NO treatment: $Y = -94.47 + 20.85X - 0.99X^2$, adjusted $R^2 = 0.68$.

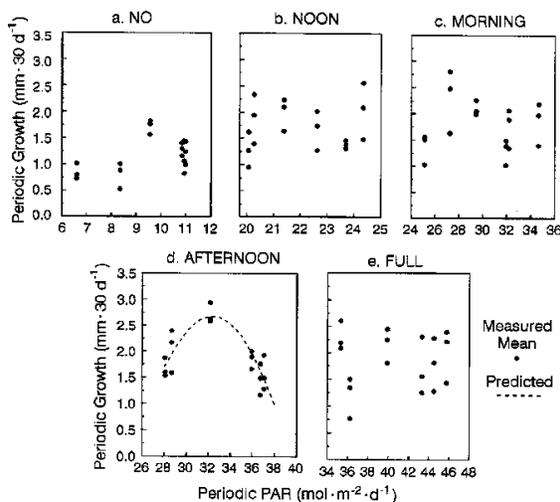


Figure 9. Relationships between periodic root-collar diameter growth of the cherrybark oak seedlings and mean periodic daily PAR during the second growing season (1998) for the tested light regimes. Regression model for the AFTERNOON treatment was: $Y = -54.86 + 3.56X - 0.055X^2$, adjusted $R^2 = 0.70$.

was also related to mean periodic PAR with adjusted coefficients of determination of 0.68 and 0.55, respectively (Figures 8a and 8e). These relationships showed that periodic height growth maximized at moderate levels of mean daily PAR, except for the NO treatment because its maximum mean daily PAR was below the minimums of other treatments. As indicated by periodic growth, the optimum PAR occurred in August when day length averaged 13.4 hr compared to 14.3 hr in June and 14.2 hr in July.

Discussion

In our study, we attempted to simulate the light conditions in different locations within forest openings. The NO treatment represented light conditions under the crowns of bordering trees along the southern edge of openings. The lower half of the northern side of the NO treatment, which did not have shade cloth, allowed additional diffuse light to reach seedlings, and this would simulate the light transmission between the bottom of trees' crown and the ground. The NOON treatment simulated light conditions of center and northern edge of smaller forest openings. At the beginning of the study, the NOON treatment simulated the 9.1 m area in the center and northern part of small rectangular openings with a width of 24.4 m and with surrounding trees as tall as the opening's width. MORNING and AFTERNOON treatments simulated light conditions of western and eastern edges of openings. The FULL treatment represents seedlings growing without any shade, which would only occur in clearcuts. However, oak seedling growth in the center of forest openings with diameters as small as one or two times the height of surrounding trees was reported to be similar to that in clearcuts (Minckler and Woerheide 1965, Sander and Clark 1971, Smith 1980 and 1981).

The treatments of our study only partially simulate the complex light conditions in forest openings. Tree crowns do

not transmit light in a constant rate, such as 20% of full sunlight provided by the shade cloth used in this study. Seedlings in the NO treatment did not have underground competition from overstory trees, which is common in field conditions. Additionally, environmental variables other than light may also be affected by the shadehouses, such as wind and temperature. These factors are moderated by the more protected locations represented by the NO and NOON treatments, and they probably vary within small forest openings in a similar manner. Another issue is that partially shaded seedlings in this study received extra sunlight as their height increased in proportion to the vertical walls of the shadehouses. Despite these shortcomings, shadehouses provide a simplified way of studying the complex light regimes occurring in stands.

Height and diameter growth during the first growing season was low, and there was only a minor effect of the different light regimes. Because seedlings were transplanted and in an establishment stage, this slow growth is understandable and seems to be a characteristic of cherrybark oak (Gardiner and Hodges 1998). Light regimes during the first growing season affected seedlings differently than in the second. During the first growing season, seedlings in the NO treatment did not differ in height and diameter compared to the NOON treatment. Although not significantly different, seedling height in the NOON and NO treatments was greater than that in other treatments throughout most of the first growing season. Crow (1988) indicated that northern red oak seedlings need protection from direct sunlight for optimum establishment, but need more light for maximum growth once established. The growth pattern of the first growing season in this study seemed to confirm that observation. During the first growing season, the NOON and NO treatments provided more protection for seedlings from excessive direct sunlight than other treatments. However, when more light was needed in the second growing season, sunlight within the NO treatment was too low to support growth at its full potential. At the end of the second growing season, for example, average daily PAR of the NO treatment dropped to less than $7 \text{ mol}\cdot\text{m}^{-2}$, while other treatments had daily PAR of $20 \text{ mol}\cdot\text{m}^{-2}$ or above. At $7 \text{ mol}\cdot\text{m}^{-2}$ daily PAR, seedlings grew little in height in the NO treatment, but seedlings in the other treatments grew $10 \text{ cm}\cdot 30 \text{ days}^{-1}$ or more in height. Seedlings in the NO treatment apparently needed a daily PAR of $9 \text{ mol}\cdot\text{m}^{-2}$ or greater to support good height growth, but reduced day length and light intensity late in the growing season did not satisfy this requirement. Consequently, the effective growing season for the NO treatment was shortened. Moreover, light intensity for the NO treatment never seemed to be enough to support growth at its full potential, and both height and diameter growth always lagged behind that in the other treatments during the second growing season. In contrast, the optimum light conditions were provided by the NOON treatment, which ranged in direct-sunlight ratio of 0.23 to 0.26 or about 50% daily PAR of the FULL treatment at ground level (exposure of seedlings to direct sunlight increased with time because they were taller and, thus, in the shadows of the shadehouse for less time). When

the direct-sunlight ratio increased to 0.63–0.65 or daily PAR of 75–80% of the FULL treatment, height growth was reduced in the MORNING and AFTERNOON treatments. This phenomenon indicates that moderate light conditions may be important for maximum height growth of cherrybark oak seedlings during their first few growing seasons, whether by sunlight alone or in combination with associated factors. Gardiner and Hodges (1998) also reported that moderate light regimes promote the best early growth in oak seedlings for cherrybark oak.

The tallest seedlings in this study were 31 cm taller than those in a Mississippi study (Gardiner and Hodges 1998), although root-collar diameter was similar. In both studies, seedling height maximized at a similar percentage of full sunlight at ground level—the NOON treatment in this study and at 53% of full sunlight in the Mississippi study. If genotype and/or site conditions did not account for the difference between the studies, the partial exposure to direct sunlight provided by the NOON treatment of our study might have stimulated the extra growth when compared to the more constant shade levels provided by traditional shadehouses. On the other hand, because seedlings in field openings are not likely to receive the extra light as the seedlings with the same height in this study, height growth of field seedlings may have different patterns from this study.

Cherrybark oak is characterized as intolerant of shade, and seedlings supposedly need full sunlight for optimum development (Belanger and Krinard 1990). However, full light exposure of the cherrybark oak seedlings in the Mississippi study (Gardiner and Hodges 1998) drastically reduced height and diameter growth. This reduction was attributed to increased moisture stress and higher vapor pressure deficit. In this study, seedlings in the FULL treatment had one of the greatest root-collar diameters but were about 30 cm shorter than seedlings in the NOON treatment. More carbohydrates might have been allocated to diameter or root growth, as evidenced by the greater root-collar diameter growth in the FULL treatment. These results suggest that under similar environmental and site conditions, seedlings on eastern and western edges of forest openings may display higher rates of height growth than those in the middle of large openings. Cherrybark oak seedlings may initially have greater height growth in the center of the smaller forest openings, which would receive direct sunlight similar to that of NOON treatment in our study.

An interesting finding was the linear relationship between periodic height growth and direct-sunlight ratio in the NOON treatment. Daily PAR was not related to periodic height growth in the NOON treatment, but daily PAR was strongly related to periodic growth of the AFTERNOON and FULL treatments. Apparently, a majority of the daily PAR was contributed by direct sunlight in these treatments. Direct sunlight in the NOON treatment seemed never to exceed a level that would restrict seedling height growth. Direct sunlight in the MORNING, AFTERNOON, and FULL treatments must have been over the optimum level since height growth was less than that in the NOON treatment, except in August for the AFTERNOON treat-

ment. The reason that direct sunlight in the NOON treatment was not related to periodic height growth was due to the relatively long direct sunlight exposure in May but the associated low growth. When adjusted by day length, however, direct-sunlight ratio showed a better fit for periodic height growth. Environmental factors, such as temperature, PAR, and soil moisture are likely related to direct sunlight and day length, especially under the controlled conditions in this study.

In summary, light conditions were important for the early growth of cherrybark oak seedlings, although seedling survival was not affected. A daily direct sunlight exposure of 3–4 hr at ground level and 20% of the full sunlight in the remaining time resulted in the greatest height growth through 2 yr. Increasing direct sunlight exposure to 8–9 hr-day⁻¹ or to full sunlight reduced height growth. Without any direct sunlight and about 23% of the total daily PAR, both total height and diameter were significantly reduced compared to the NOON treatment. A limited but sufficient direct sunlight exposure seemed to be important for seedling growth of cherrybark oak. The implication of this finding is that if understory competition is controlled, proper size of forest canopy openings is important for adequate direct sunlight exposure of seedlings. Finally, selection of trees for acorn collection or retention of seedtrees is also important for producing seedlings with a high growth potential. Results from our study showed that a difference of as much as 40% in height growth over 2 yr could result from different parent trees.

Literature Cited

- BEY, C.F. 1964. Advanced oak reproduction grows fast after clearcutting. *J. For.* 62:339–340.
- BELANGER, R.P., AND R.M. KRINARD. 1990. Cherrybark oak. P. 644–649 in *Silvics of North America*. Vol. 2, Hardwoods. Burns, R.M., and B.H. Honkala (tech. coords.). USDA For. Serv. Agric. Handb. 654.
- BROSE, P.H., AND D.H. VAN LEAR. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Can. J. For. Res.* 28:331–339.
- BUCKLEY, D.S., T.L. SHARIK, AND J.G. ISEBRANDS. 1998. Regeneration of northern red oak: Positive and negative effects of competitor removal. *Ecology* 79:65–78.
- BUCKLEY, D.S., J.G. ISEBRANDS, AND T.L. SHARIK. 1999. Practical field methods of estimating canopy cover, PAR, and LAI in Michigan oak and pine stands. *North. J. Appl. For.* 16:25–32.
- CROW, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. *For. Sci.* 34:19–40.
- DAI, X. 1996. Influence of light conditions in canopy gaps on forest regeneration: A new light index and its application in a boreal forest in east-central Sweden. *For. Ecol. Manage.* 84:187–197.
- DICKSON, R.E. 1991. Episodic growth and carbon physiology in northern red oak. P. 117–124 in *The oak resources in the upper Midwest: Implication for management*, Laursen, S.B., and J.F. DeBoe (eds.). Publ. No. NR-BU-5663-5. Minn. Ext. Serv., Univ. Minn., St. Paul, MN.
- GARDINER, E.S., AND J.D. HODGES. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. *For. Ecol. Manage.* 108:127–134.
- GOTTSCHALK, K.W. 1994. Shade, leaf growth and crown development of *Quercus rubra*, *Quercus velutina*, *Prunus serotina* and *Acer rubrum* seedlings. *Tree Physiol.* 14:735–749.

- HODGES, J.D. 1989. Regeneration of bottomland oaks. *For. Farmer* 49(1):10-11.
- JANZEN, G.C., AND J.D. HODGES. 1985. Influence of midstory and understory vegetation removal on the establishment and development of oak regeneration. P. 273-278 in *Proc. of the third bienn. south. silvic. res. conf.*, Shoulders, E. (ed.). USDA For. Serv. Gen. Tech. Rep. 54.
- JOHNSON, R.L. 1979. Adequate oak regeneration—a problem without a solution. P. 59-65 in *Management and utilization of oak*. Proc. of the seventh annu. hardwood symp. of the hardw. res. council. Hardw. Res. Council., Asheville, NC.
- KOLB, T.E., AND K.C. STEINER. 1990a. Growth and biomass partitioning of northern red oak and yellow poplar seedlings: effects of shading and grass root competition. *For. Sci.* 36:34-44.
- KOLB, T.E., AND K.C. STEINER. 1990b. Growth and biomass partitioning response of northern red oak genotypes to shading and grass root competition. *For. Sci.* 36:293-303.
- LARANCE, F.C., H.V. GILL, AND C.L. FULTZ. 1976. Soil survey of Drew County, Arkansas. USDA Soil Conserv. Serv. 86 p.
- LOCKHART, B.R., J.D. HODGES, AND E.S. GARDINER. 2000. Response of advanced oak reproduction to midstory removal and shoot clipping. *South. J. Appl. For.* 24:45-50.
- LOFTIS, D.L. 1990a. Predicting post-harvest performance of advanced red oak reproduction in the southern Appalachians. *For. Sci.* 36:908-916.
- LOFTIS, D.L. 1990b. A shelterwood method for regenerating red oak in the southern Appalachians. *For. Sci.* 36:917-929.
- LOFTIS, D.L., AND C.E. MCGEE (EDS.). 1993. Oak regeneration: Serious problems, practical recommendations. USDA For. Serv. Gen. Tech. Rep. SE-84. 319 p.
- LORIMER, C.G., J.W. CHAPMAN, AND W.D. LAMBERT. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* 82:227-237.
- MARQUIS, D.M. 1965. Controlling light in small clearcuttings. USDA For. Serv. Res. Pap. NE-39. 16 p.
- MERZ, R.W., AND S.G. BOYCE. 1956. Age of oak "seedlings." *J. For.* 54:774-775.
- MINCKLER, L.S. 1957. Response of pole-sized white oak trees to release. *J. For.* 55:814-815.
- MICKLER, L.S., AND J.D. WOERHEIDE. 1965. Reproduction of hardwoods 10 years after cutting as affected by site and opening size. *J. For.* 63:103-107.
- SANDER, I.L. 1972. Size of oak advance reproduction: key to growth following harvest cutting. USDA For. Serv. Res. Pap. NC-79. 6 p.
- SANDER, I.L., AND F.B. CLARK. 1971. Reproduction of upland hardwood forests in the Central States. USDA Agric. Handb. 405. 25 p.
- SAS INSTITUTE, INC. 1990. SAS user's guide. Vol. 2, version 6, 4th ed. SAS Institute, Inc., Cary, NC. 846 p.
- SATTERLUND, D.R. 1983. Forest shadows: How much shelter in a shelterwood? *For. Ecol. Manage.* 5:27-37.
- SHUMWAY, D.L., K.C. STEINER, AND T.E. KOLB. 1993. Variation in seedling hydraulic architecture as a function of species and environment. *Tree Physiol.* 12:41-54.
- SMITH, H.C. 1980. An evaluation of four uneven-age cutting practices in Central Appalachian hardwoods. *South. J. Appl. For.* 4:193-200.
- SMITH, H.C. 1981. Diameters of clearcut openings influence Appalachian hardwood stem development—a 10-year study. USDA For. Serv. Res. Pap. NE-476. 8 p.
- SMITH, D.W. 1992. Oak regeneration: The scope of the problem. P. 40-53 in *Oak regeneration: Serious problem, practical recommendations*, Loftis, D.L., and C.E. McGee. (eds.). USDA For. Serv. Gen. Tech. Rep. SE-84.