EFFECTS OF SHADING ON GROWTH AND DEVELOPMENT OF NORTHERN RED OAK, BLACK OAK, BLACK CHERRY, AND RED MAPLE SEEDLINGS. I. HEIGHT, DIAMETER, AND ROOT/SHOOT RATIO[1]

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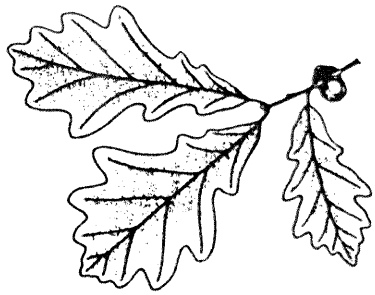

ABSTRACT.--Optimum light levels for shelterwood cutting to develop the large advance regeneration that oaks require were investigated using eight Saran[3] shade-cloth treatments. Seedlings of northern red oak, black oak, black cherry and red maple were grown under these light treatments for 2 years. Height and diameter were measured annually, and samples were harvested for dry weight and leaf area determination. All of the species grew the least at the lowest light level. Height and diameter growth for seedlings of black cherry, red maple, northern red oak, and black oak all reached a plateau at from 20% to 94% light. Second-year height and diameter (Y) responses to light level (X) were best described by $1/Y=b_0+b_1(1/X)$. Species rankings at all light levels were black cherry, northern red oak, black oak, and red maple (largest to smallest height and diameter). Root/shoot ratios were not affected by light levels during the first year. During the second year, root/shoot ratios were significantly affected only for black cherry, but a linear response to increasing light was evident for the other species.

INTRODUCTION

Successful regeneration of the mixed oak forest type requires an adequate number of large stems of advance regeneration in the understory before the overstory is harvested (Sander 1972, 1977; Sander et al. 1976, 1984). Of the numerous environmental and biotic factors that affect the development of advanced regeneration, light is one of the most important. Initial germination and growth of oak seedlings are often not limited by the low light levels found under hardwood canopies, but many seedlings fail to survive at these low light levels once cotyledonary reserves are exhausted (Tryon and Carvell 1958, Carvell and Tryon 1961). Increased light levels have resulted in increased height growth and usually in more root development and increased root/shoot ratios (McGee 1968, Musselman and Gatherum 1969, Phares 1971, Jarvis 1964, Loach 1970).

Shelterwood cutting should allow oak advance regeneration to grow large enough to survive after harvest. Identifying an optimal range of light levels for establishment and growth of oak regeneration will help to determine what level of overstory density should be retained in the overwood of the shelterwood system. On many good sites in the Allegheny Plateau region, harvested mixed oak stands are being regenerated to red maple or cherry-maple. In this area of transition, very little large oak advance regeneration is present in the stands. For oak to be successful on these sites, it must be able to compete with these other

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species. Therefore, the two major competitors of oaks on these transition sites (red maple and black cherry) were included in the study.

METHODS

Field and Laboratory

Twenty-four 8-foot-square plots were each covered with one of eight Saran shade-cloth screen treatments, providing three replications of each treatment. The screen tents were 6 feet tall, were covered on all four sides and the top, and transmitted 94%, 70%, 45%, 37%, 27%, 20%, and 8% of full sunlight. The plots were located inside a fenced field behind the Forestry Sciences Laboratory at Warren, PA. The area is an abandoned agricultural site on the flood plain of the Allegheny River. The plots were not watered nor fertilized. There were no major differences in soil moisture under the different shading treatments because there was frequent and abundant rainfall during the two growing seasons. The 8% treatment did have a higher soil moisture content, and algae and moss grew abundantly on the soil surface of those plots. Each plot was rototilled before planting and an aluminum flashing border, buried to a 6" depth, was installed to prevent rodent damage. Half-sib seeds from one tree each of northern red oak, black oak, and black cherry were sown in November 1980. Red maple half-sib seeds from one tree were collected and sown in June 1981. Each species was planted in row plots of five points with 1 foot spacing between and within rows (4'x5'). Northern red oak, black oak, and black cherry seed germinated in May and grew unshaded until June 15-17, 1981, when the shade-cloth tents were erected. Initial measurements of height, diameter at 2 cm above ground, and number of leaves were taken as soon as the shade-cloth tents were erected. Red maple seed did not germinate until after the tents were installed, so no initial measurements could be taken on them. Three seeds were sown at each point. Seedlings were thinned to one per point when the tents were installed. Red maple seeds germinated in mid- to late June and seedlings were thinned to one per point in early July. No mortality occurred in black cherry and northern red oak the first year, but one black oak seedling and 10 red maple seedlings died (no more than two seedlings from any one treatment plot). During the second year, one additional black oak seedling and three additional red maple seedlings died.

In mid-October 1981, the height and diameter of all seedlings were measured. In addition, one seedling from each species-light-replication combination was randomly selected for harvest. These seedlings were excavated by hand to recover as many roots as possible. The harvested seedlings were partitioned into stem, leaves, and roots, dried at 75 C, and weighed to the nearest 0.001 g. The leaves were photocopied before they were dried, and leaf areas were measured with an integrating planimeter. The shade-cloth tents were taken down in November after leaf-fall was complete.

The shade-cloth tents were erected again in April 1982 before budbreak. In late September-early October 1982, the height and diameter of all seedlings were measured. Since some black cherry seedlings had reached the top of the tents, the study was terminated. All of the seedlings were harvested in the same way as in the first year, except that branches were partitioned into a separate category and leaf area was measured with a LiCor Leaf Area Meter.

Data Analysis

The study design was a split plot with randomized blocks. However, the differences in the means between species were large, and the variances were heterogeneous. The data were analyzed by species. Height, diameter, and root/shoot ratio were averaged for each plot and the plot averages used in analysis of covariance, with initial seedling height and diameter as covariates. If the analysis of covariance showed that the covariate was significant and there were significant differences attributable to levels of light, treatment means were adjusted by the covariate and Tukey's HSD procedure was used to separate the adjusted means. If the covariate was not significant and there were statistically significant differences attributable to levels of light, the statistical analysis was redone without the covariate. The actual means were then separated using Tukey's HSD procedure. The 0.05 level of probability was accepted as significant.

More detailed analyses were done on the second-year data. Since the seedlings in the 8% treatment grew less than those in the other treatments, the hypothesis that the other seven treatment effects were the same was tested using a series of six contrasts. Also nine models were fitted to the data using least squares regression in an effort to describe the relationships between seedling growth and light level (X). The models that were fitted for Y= second-year height, diameter, and root/shoot ratio are:

(1) $Y=b_0+b_1X$

(2) $Y=b_0+b_1(1/X)$

(3) $Y=b_0+b_1X+b_2X^2$

(4) $\ln Y=b_0+b_1X^2$

(5) $\ln Y=b_0+b_1X$

(6) $\ln Y=b_0+b_1(\ln X)$

(7) $\ln Y=b_0+b_1(\ln X)+b_2X$

(8) $1/Y=b_0+b_1(1/X)$

(9) $Y=b_0+b_1(\ln X)$

RESULTS

First Year

HEIGHT.--First-year height was not affected by shading (Tables 1, 2). Red oak and black oak had completed most of their height growth before the shading treatments were applied. Red maple seedlings grew under the shading treatments, but because of their late germination, small growth, and large variation, they did not show any significant differences. However, red maple seedlings in the 8% treatment were half the size of those in the other treatments. Black cherry, an indeterminate species, was the tallest species at the end of the first year, because it continued to grow after the treatments were installed. The light level treatment effect for black cherry failed to meet the probability criterion for significance by only 0.003, so differences in first-year height were almost significant. Seedlings in the 8% treatment were considerably shorter than those in the other treatments.

DIAMETER.--However, first-year diameter growth did respond to the shading treatments. First-year diameter of all four species had a significant response to shading (Table 1). Seedlings in the 8% treatment had the smallest diameters and there were no significant differences between the other treatments (Table 2).

ROOT/SHOOT RATIO.--First year RSR was not affected by shading (Table 1). Black cherry and red maple seedlings maintained an overall balance between the dry weights of their above- and below-ground portions, while northern red oak and black oak maintained about twice as much dry weight in their roots as in their shoots (Table 3).

Second Year

HEIGHT.--There were significant differences in seedling height during the second year for all four species (Table 1). Northern red oak and black oak had significant differences between the smallest heights (8%) and largest heights (20%); black oak had no other differences but red oak did (Table 4). Black cherry and red maple also had significant differences between the smallest heights (8%) and the largest heights (37% and 57%) (Table 4). The contrasts between pairs of the 20% to 94% treatments showed that for red maple and black cherry there were no significant differences between these seven treatments. However, northern red oak and black oak had several significant differences, so their second-year height was affected more by these treatments than that of red maple and black cherry. Conversely, when models were fitted to all eight treatments, model 8 best described the seedling heights of all four species (Table 5). Model 8, which fits a hyperbolic curve, described only a small portion of the total variation in three of the species and 58% of the variation for red maple.

DIAMETER.--As in the first year, second-year diameter was significantly affected by shading for all four species (Table 1). Seedlings in the 8%

TABLE 1.--Analysis of covariance (or variance) for height, diameter, and root/shoot ratio (RSR) of seedlings of four tree species grown under different light levels.

Species	Source of variation	First year			Second year		
		Height	Diameter	RSR	Height	Diameter	RSR
Red maple	Light level	ns[a]	*	ns	*	**	ns
	Covariate[b]	-	-	-	-	-	-
Red oak	Light level	ns	*	ns	**	**	ns
	Covariate	ns	ns	-	ns	ns	-
Black oak	Light level	*	**	ns	*	*	ns
	Covariate	**	**	-	ns	ns	-
Black cherry	Light level	ns	*	ns	*	*	**
	Covariate	*	ns	-	ns	ns	-

[a]ns = Not significant at 0.05 level.
* = Significant at 0.05 level.
** = Significant at 0.01 level.

[b]Covariate is either initial height or diameter of seedlings. Initial height and diameter were not measured on red maple since it germinated under the shading treatments.

TABLE 2.--Height (cm) and diameter (cm) of seedlings of four tree species after one growing season under different light levels.

Light level	Red maple		Red oak		Black oak		Black cherry	
	Height	Diameter	Height	Diameter	Height	Diameter	Height	Diameter
8[a]	2.8[b]	0.08b[c]	18.0	0.33b	11.8a[d]	0.23b[d]	18.4	0.25b
20	4.8	0.12ab	24.3	0.39ab	15.6a	0.28ab	40.0	0.41ab
27	5.4	0.14ab	18.0	0.38ab	13.0a	0.31ab	33.7	0.38ab
37	6.0	0.15ab	18.6	0.42ab	14.3a	0.32a	41.5	0.45ab
45	7.0	0.13ab	14.4	0.37ab	13.2a	0.29ab	38.9	0.43ab
57	7.2	0.18a	16.0	0.37ab	11.0a	0.28ab	29.7	0.41ab
70	5.1	0.14ab	19.3	0.45a	11.1a	0.30ab	53.4	0.57a
94	7.3	0.16a	16.1	0.36ab	10.0a	0.28ab	41.8	0.49ab
Overall mean	5.7	0.14	18.1	0.38	12.5	0.29	37.2	0.42

[a]Percentage of full sunlight.

[b]Means in columns without letters have no significant differences.

[c]Means within a column followed by the same letter were not significantly different at 0.05 level according to Tukey's HSD test.

[d]Means in this column were adjusted by analysis of covariance using initial seedling height or diameter as a covariate. Means within this column followed by the same letter were not significantly different at 0.05 level according to Tukey's HSD test.

TABLE 3.--Root/shoot ratio (RSR) of seedlings of four tree species grown under different light levels.

Light level	Red maple		Red oak		Black oak		Black cherry	
	First year	Second year	First year	Second year	First year	Second year	First year	Second year
8[a]	1.13[b]	0.64	1.24	0.86	1.09	1.12	0.77	0.50b[c]
20	0.99	0.75	1.47	0.50	1.28	0.93	0.98	0.61b
27	0.74	0.84	1.11	0.85	1.94	1.16	0.80	0.63ab
37	0.58	0.94	1.90	1.06	2.17	1.24	1.01	0.71ab
45	1.66	0.74	1.83	0.91	2.05	1.26	1.32	0.74ab
57	0.86	1.00	1.54	1.32	2.84	1.72	1.36	0.93a
70	0.79	1.11	1.74	1.09	2.80	1.53	1.02	0.75ab
94	1.22	1.13	2.95	1.28	2.76	1.73	1.10	0.78ab
Overall mean	1.00	0.89	1.72	0.98	2.12	1.33	1.04	0.70

[a]Percentage of full sunlight.

[b]Means in columns without letters have no significant differences.

[c]Means within a column followed by the same letter were not significantly different at 0.05 level according to Tukey's HSD test.

TABLE 4.--Height (cm) and diameter (cm) of seedlings of four tree species after two growing seasons under different light levels.

Light level	Red maple		Red oak		Black oak		Black cherry	
	Height	Diameter	Height	Diameter	Height	Diameter	Height	Diameter
8[a]	9.3b[b]	0.17b	37.0c	0.41b	21.3b	0.28b	57.7b	0.47b
20	26.3ab	0.32ab	78.7a	0.78a	38.3a	0.50ab	105.7ab	0.95ab
27	28.7ab	0.33ab	62.0abc	0.81a	37.3ab	0.56ab	114.3ab	1.01ab
37	25.0ab	0.33ab	69.7ab	0.86a	35.0ab	0.62a	133.0a	1.19ab
45	27.0ab	0.25ab	55.7abc	0.70ab	24.3ab	0.48ab	118.7ab	1.13ab
57	33.7a	0.42a	45.3bc	0.68ab	31.7ab	0.56ab	81.0ab	0.87ab
70	22.7ab	0.32ab	64.7abc	0.81a	29.3ab	0.63a	123.7ab	1.39a
94	24.0ab	0.44a	58.7abc	0.74a	31.0ab	0.61a	100.0ab	1.07ab
Overall mean	24.6	0.32	59.0	0.72	31.0	0.53	104.2	1.01

[a]Percentage of full sunlight.

[b]Means within a column followed by the same letter were not significantly different at 0.05 level according to Tukey's HSD test.

treatment had the smallest diameters and there were no significant differences between the other treatments (Table 4). The contrasts between pairs of the 20% to 94% treatments for all four species confirmed that these treatments had no differences, so the 8% treatment was providing most of the treatment-effect significance in the analysis of variance. Because of this, fitting curves to all eight treatments resulted in a hyperbolic curve, as given by model 8, which explained about half of the variation present (Table 5).

ROOT/SHOOT RATIO.--Second-year RSR was significantly affected by shading only for black cherry (Tables 1, 3). Lower light levels tended to decrease RSR in the other species, as evidenced by the linear model that provided the best fit to the data (Table 5). Black cherry was best described by a hyperbolic curve that implies a response plateau at higher light levels. RSR decreased from the first to the second year, but the oaks still partitioned more dry weight into their root systems than black cherry and red maple did.

DISCUSSION

The literature on the effects of shading on height growth of tree seedlings is inconclusive--in some cases height growth decreases with increasing shade (Jarvis 1964, Yakshina 1978, Stutz and Frey 1980, Reed et al. 1983, McGee 1968, Ashby 1976), in some cases it increases (Musselman and Gatherum 1969, Shirley 1929a), in some cases there was no effect (Kappel and Flore 1983, McGee 1975, Farmer 1975), and in some cases there was a peak at intermediate light levels with decreases in both directions (Phares 1971, Gatherum et al. 1963, Withers 1979, Blair 1982, Shirley 1929b). One of the major reasons there is so much variation in response may be the tolerance of the species involved (Loach 1967, 1970). The more tolerant species are more likely to increase in height or to exhibit nonsignificant shade effects. Species intermediate in tolerance are more likely to follow the maximum or peak response at intermediate light levels or plateau levels. Finally, the intolerant species are more likely to show a decrease in height with increasing shade. Species used in this study were primarily intermediate in tolerance, so the height patterns found were similar to those of other intermediate-tolerance species.

When diameter growth is considered, there is a consensus: diameter growth decreases with increasing shade (Kappel and Flore 1983, Gatherum et al. 1963, Stutz and Frey 1980, Reed et al. 1983). Diameter growth is considered more sensitive to stress and limiting factors than height growth. It is also sensitive to photosynthate supply. For these reasons, diameter growth is limited as shading decreases the photosynthates available for growth. The small diameter growth at 8% light is probably a result of decreased photosynthate supply at this low light level.

RSR commonly decreases with increasing shade (Loach 1970, Phares 1971, Musselman and Gatherum 1969, Jarvis 1964). This result is generally a redistribution of dry weight from roots to leaves, which is probably an adaptation to maximize light interception under low light conditions.

The interpretation of these results requires a little caution. The uniform shade provided under these shade-cloth tents is a poor representation of the light levels in shelterwoods because of the sunflecks and other irregularities in the quantity and quality of light reaching the understory. Marquis (1973) grew black cherry seedlings under similar shade-cloth tents and found a hyperbolic light response curve that is almost exactly the same

TABLE 5.--Relationships of light level treatments to seedling growth characteristics of four tree species after two growing seasons under different light level treatments.

Species	Model parameters	Height	Diameter	RSR[a]
Red maple	Model[b]	8	8	1
	R^2	0.58	0.55	0.33
	b_0'	0.023**[c]	2.29**	0.64**
	b_1'	0.706**	31.95**	0.006**
Red oak	Model	8	8	1
	R^2	0.19	0.54	0.28
	b_0'	0.016**	1.13**	0.66**
	b_1'	0.072*	9.45**	0.007**
Black oak	Model	8	8	1
	R^2	0.12	0.53	0.38
	b_0'	0.030**	1.44**	0.92**
	b_1'	0.132*	16.96**	0.009**
Black cherry	Model	8	8	8
	R^2	0.16	0.50	0.50
	b_0'	0.009**	0.75**	1.22**
	b_1'	0.062*	10.46**	7.10**

[a]RSR = root/shoot ratio.

[b]Model = number of model equation in text.
R^2 = adjusted R^2 value of the regression.
b_0' = estimate of intercept parameter of model.
b_1' = estimate of slope parameter of model.

[c]Significance of parameter estimates.
* = significant at 0.05 probability level.
** = significant at 0.01 probability level.

as my curve for black cherry. However, he also measured natural seedlings in the field under different light levels and found a different curve--an exponential curve where black cherry seedling height increased exponentially with increasing light levels up to full sunlight. The following conclusion can be drawn from these results: seedlings of all four species grow poorly under 8% light (similar to uncut stands); increasing light to levels above 20% will increase seedling growth.

This conclusion supports the use of the shelterwood system in regenerating northern red oak, black oak, red maple, and black cherry. Shelterwood cutting which increases light levels above the 5% to 10% of the light available in uncut stands should result in increased growth of the seedlings present in the stand. Although there were few differences between 20% and 94% light, the general trend toward an increase in root growth at higher light levels supports maintaining as high a light level as possible without greatly reducing the benefits of shelterwood cutting or increasing the growth of woody and herbaceous competitors. Since cutting 40% of the stand basal area would increase light to only 20% of full light, cutting 60% of the stand basal area would increase light to only 38%, and cutting 80% of the stand basal area would increase light to only 64% of full light, the practical light range for shelterwoods is 20% to 60% of full sunlight (Marquis 1973). The use of shelterwood cutting to

favor oaks over black cherry and red maple does not look promising because of the favorable responses of these two competitors to the light levels that would be created. Some form of competition control would be required to favor the oaks.

LITERATURE CITED

ASHBY, W. C. 1976. Basswood seedlings outgrow red and bur oak in full light or heavy shade. Tree Planter's Notes 27(3):24-26, 34.

BLAIR, R. M. 1982. Growth and nonstructural carbohydrate content of southern browse species as influenced by light intensity. J. Range Manage. 35:756-760.

CARVELL, K. L., and E. H. TRYON. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. For. Sci. 7:98-105.

FARMER, R. E., Jr. 1975. Growth and assimilation rate of juvenile northern red oak: effects of light and temperature. For. Sci. 21:373-381.

GATHERUM, G. E., A. L. MCCOMB, and W. E. LOOMIS. 1963. Effects of light and soil moisture on forest tree seedling establishment. Iowa Agric. Exp. Sta. Res. Bull. 513:776-792.

JARVIS, P. G. 1964. The adaptability to light intensity of seedlings of Quercus petraea (Matt.) Liebl. J. Ecol. 52:545-571.

KAPPEL, F., and J. A. FLORE. 1983. Effect of shade on photosynthesis, specific leaf weight, leaf chlorophyll content, and morphology of young peach trees. J. Am. Soc. Hort. Sci. 108:541-544.

LOACH, K. 1967. Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytol. 66:607-621.

LOACH, K. 1970. Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. New Phytol. 69:273-286.

MCGEE, C. E. 1968. Northern red oak seedling growth varies by light intensity and seed source. USDA For. Serv. Res. Note SE-90. 4 p.

MCGEE, C. E. 1975. Change in forest canopy affects phenology and development of northern red and scarlet oak seedlings. For. Sci. 21:175-179.

MARQUIS, D. A. 1973. The effect of environmental factors on advance regeneration of Allegheny hardwoods. Ph.D. Dissertation. Yale University. 147 p.

MUSSELMAN, R. C. and G. E. GATHERUM. 1969. Effects of light and moisture on red oak seedlings. Iowa State J. Sci. 43:273-284.

PHARES, R. E. 1971. Growth of red oak (Quercus rubra L.) seedlings in relation to light and nutrients. Ecology 52:669-672.

REED, K. L., J. S. SHUMWAY, R. B. WALKER, and C. S. BLEDSOE. 1983. Evaluation of the interaction of two environmental factors affecting Douglas-fir seedling growth: light and nitrogen. For. Sci. 29:193-203.

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. 1977. Manager's handbook for oaks in the North Central States. USDA For. Serv. Gen. Tech. Rep. NC-37. 35 p.

SANDER, I. L., P. S. JOHNSON, and R. F. WATT. 1976. A guide for evaluating the adequacy of oak advance reproduction. USDA For. Serv. Gen. Tech. Rep. NC-23. 7 p.

SANDER, I.L,, P.S. JOHNSON, and R. ROGERS. 1984. Evaluating oak advance reproduction in the Missouri Ozarks. USDA For. Serv. Res. Pap. NC-251. 16 p.

SHIRLEY, H. L. 1929a. The influence of light intensity and light quality upon the growth of plants. Am. J. Bot. 16:354-390.

SHIRLEY, H. L. 1929b. Light requirements and silvicultural practice. J. For. 27:535-538.

STUTZ, J. C. and D. R. FREY. 1980. Altered light levels on growth, fruiting, and leaf characteristics of natural stands of Ilex opaca. HortScience 15:94-96.

TRYON, E. H. and K. L. CARVELL. 1958. Regeneration under oak stands. W. Va. Agric. Exp. Sta. Bull. 424T. 22 p.

WITHERS, J. R. 1979. Studies on the status of unburnt Eucalyptus woodland at Ocean Grove, Victoria. IV. The effect of shading on seedling establishment. Aust. J. Bot. 27:47-66.

YAKSHINA, A. M. 1978. Rate of respiration of the root system in maple under different shading conditions. Sov. Plant Physiol. 25:46-50.