PHOTOSYNTHESIS AND BIOMASS ALLOCATION IN OAK SEEDLINGS GROWN UNDER SHADE

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Abstract—Northern red oak (*Quercus rubra* L.) (NRO) and white oak (*Q. alba* L.) (WO) acorns were sown into wooden plots and grown under 30 percent shade screen (30 percent S) or 70 percent shade screen (70 percent S). Seedlings grown under full sun were the controls (C). At the end of the first year, the 30 percent S NRO had 30 percent greater seedling dry weight (DW) than C seedlings. No growth differences existed between these two treatments after 2 years. Compared to C, 70 percent S NRO had a 40 percent lower net photosynthetic rate (A), twofold less seedling DW and leaf number, and fourfold less lateral root DW after 2 years. Dry weight biomass allocation to lateral roots increased from 17 percent at the end of the first growing season to 22 percent after 2 years for both the C and 30 percent S NRO. The 70 percent S seedlings, however, allocated only 8 percent DW to lateral roots for both years. White oak seedlings responded similarly to shade as NRO seedlings. The 70 percent S WO had 30 percent lower A and fourfold less lateral root DW than the controls after 2 years. At the end of the second year, DW biomass allocation to lateral roots was 12, 7, and 5 percent, respectively, for C, 30 percent S, and 70 percent S WO seedlings. The impact of shade (reduced light intensity) on seedling growth of both oak species was discussed in terms of A, photoprotection, and DW biomass allocation.

INTRODUCTION

For the last three decades various silvicultural practices have been suggested to improve the success of natural and artificial regeneration of northern red oak (*Quercus rubra* L.) (NRO) on high-quality mesic sites. Several factors have been implicated in the less-than-satisfactory results of NRO regeneration. Competition for light between NRO seedlings and other hardwood species (such as *Acer saccharum* Marsh., *A. rubrum* L., and *Liriodendron tulipifera* L.) is the one most commonly mentioned in the literature (Barton and Gleeson 1996, Loftis and McGee 1993). Indeed, full-sun-grown NRO seedlings have higher net photosynthetic rates (A) than shaded seedlings (Crunkilton and others 1992, Kubiske and Pregitzer 1996, McGraw and others 1990). Yet, there still exist controversial results on the effects of shade on NRO growth. For example, Gottschalk (1985, 1987) reported that NRO seedlings receiving 70 percent of full sunlight grew better than seedlings receiving 8 to 57 percent or 94 percent of light. Similar contradictions exist for other *Quercus* species. Jarvis (1964) concluded that sessile oak [*Q. petraea* (Matt.) Liebl.] is intolerant to light intensity greater than 56 percent, whereas Gross and others (1996) reported that root collar diameters were smaller in sessile and pedunculate oak (*Q. robur* L.) seedlings grown under 50 percent shade for 3 years.

Even when oak seedlings are outplanted on clearcut sites, their poor initial growth results in their becoming overtopped by herbaceous vegetation and other faster growing hardwood species. Use of large size nursery stocks in the artificial regeneration practice has been suggested as a method of improving slow initial growth (Farmer 1975, Foster and Farmer 1970). Kormanik and others (1994) reported a nursery protocol that produced large-size oak seedlings as compared to seedlings used in various studies (Farmer 1979, Gottschalk 1985, Teclaw and Isebrands 1993). Nevertheless, shelterwood planting has been recommended as an alternative to outplanting oak seedlings on clearcut sites for various reasons (Loftis and McGee 1993, Teclaw and Isebrands 1993). However, these shaded oaks did not have fast growth even several years after release (Loftis and McGee 1993).

Chlorophyll bleaching has been reported to occur in shade leaves as well as in sun leaves formed from shade buds in the released understory plants. In other words, the sudden improvement of light intensity and quality resulting from overstory canopy removal actually imposes damage to the released plants. During the last decade, it has been well documented that under conditions when absorbed light energy cannot be fully utilized for photochemical reactions in photosynthesis, the xanthophyll cycle-dependent and pH-dependent dissipation of excessive energy prevents photo-oxidative damage to chlorophyll, chloroplasts, and cells. Of the three carotenoid pigments in the xanthophyll cycle, zeaxanthin (Z) and antheraxanthin (An) can dissipate excess energy but violaxanthin (V) cannot. Under light conditions, the de-epoxidation of V to Z via the intermediate An is catalyzed by de-epoxidase in the presence of ascorbate and low thylakoid lumen pH. Thus, the xanthophyll pool size and the ratio between Z+An and Z+An+V have been used to describe a leaf's photoprotection capacity (Demig-Adams and Adams 1996). Indeed, several reports showed that shaded leaves have lower levels of xanthophyll cycle pigments and smaller ratio of Z+An to Z+An+V as compared to sun leaves (Demig-Adams and Adams 1996, Faria and others 1996). The objectives of this study are to use the protocol of Kormanik and others (1994) to grow NRO and white oak (*Q. alba* L.) (WO) seedlings under different shade conditions and to evaluate the effects of shade on photosynthesis and biomass allocation.

MATERIALS AND METHODS

Seedling Growth and Harvest

In January 1993, 16 acorns of NRO or WO were sown into 1 meter by 1 meter by 0.6 meter wooden plots at a depth

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of 1 centimeter below soil surface. Seedlings began to emerge by mid-March. The study was a complete random design with three treatments and two replications. A total of 12 plots were used for each species. In early April, a layer of neutral density screen was draped over a wooden frame 3.3 meters in height. Four plots were enclosed in each frame with a 0.6-meter distance between plots and a 0.8-meter distance between plots and the screen. The extent of shade was created by screens of different densities. Maximal photosynthetic active radiation, measured by a LiCor quantum sensor, for 30 percent shade (30 percent S) and 70 percent shade (70 percent S) treatments was 1100 $\mu E/m^2.s$ and 550 $\mu E/m^2.s$, respectively. The full sun control (C) had greater than 1800 $\mu E/m^2.s$. A gap of 0.3 meters was left between the ground and the lower edge of the screen to help air circulation. Seedlings were watered and fertilized according to the protocol of Kormanik and others (1994). The screen was lifted after leaf abscission in December 1993 and placed back in early April 1994.

In early December of 1993, seedlings were harvested from two of four plots for each species in each treatment. Care was taken to minimize root loss during harvest. Seedlings were separated into stems (with branches), leaves, taproots, and lateral roots. Each seedling component was oven dried at 95 °C until constant weight was obtained. Leaf area was measured with a portable CID Leaf Area Meter. The rest of the seedlings were grown for another year and harvested in December 1994. Dry weight for each seedling component was obtained.

Photosynthesis and Leaf Pigments

A portable LiCor 6200 Infrared gas analyzer was used to measure net photosynthetic rate (A) from recently mature leaves still attached to seedlings. In early September 1994, developing leaves of elongating flushes and mature leaves of the latest mature flushes from NRO seedlings grown under full sun were harvested throughout a day and immediately frozen in liquid N_2. Procedures for leaf pigment extraction and analysis were modified from the method by Gilmore and Yamamoto (1991). Ethanol (95 percent) and $CaHCO_3$ were used to extract pigments. A Dionex Al- 450 High Performance Liquid Chromatograph with a 4.5 millimeter by 25 centimeter Zorbax non-endcapped C18 column was used. The gradient system used was as followed: 0 to 6 minutes, eluent A (acetonitrile : methanol, 80 percent : 20 percent); 6 to 9 minutes, eluent A to eluent B (methanol : ethyl acetate, 68 percent : 32 percent); 9 to 15 minutes, eluent B. Flow rate was 2 milliliters per minute for both eluents. Pigments were detected at 445 nanometers. Retention times (in minutes) are: neoxanthin 2.4, violaxanthin 2.8, antheraxanthin 3.7, lutein 4.7, zeaxanthin 5.0, chlorophyll b 9.4, chlorophyll a 11.0, α-carotene 13.9, and β-carotene 14.1.

RESULTS AND DISCUSSION

Seedling Growth

Growth parameters of NRO and WO seedlings grown under different shades were presented in tables 1 to 4. Regardless of treatments, mean seedling size and weight for both species in this study are much greater than those reported in the literature (Farmer 1975, 1979; Gottschalk 1985, 1987; Teclaw and Isebrands 1993). The NRO seedlings were similar in size to the "1-0 large" seedlings classified by Johnson and others (1984). Because this study was designed for 2 years, the planting density used was about one-fourth of the prescribed density by Kormanik and others (1994).

The screen used in this study only decreased light intensity but did not change light quality. The 30 percent S grown NRO were significantly greater in total leaf area per seedling, total seedling dry weight (DW), and stem plus branch DW than the controls in 1993 (table 1). Although not statistically

Table 1—Effects of shade on first-year growth of northern red oak seedlings

Variable measured	Full sun	30% shade	70% shade	p-Value
Height (cm)	100.7a[a]	139.5a	100.8a	.0513
Groundline diameter (mm)	14.5a	16.4a	11.7b	.0063
FOLR number[b]	16.4a	17.8a	13.8a	.4209
Taproot DW[c] (g)	62.6a	70.1a	38.9b	.0077
Lateral root DW (g)	28.5a	34.2a	9.4a	.0671
Leaf DW (g)	34.9a	38.5a	23.2a	.0403
Leaf number	53.2a	50.1a	34.5a	.1925
Leaf area (cm^2)	3237.0b	4590.0a	3381.0b	.0016
Average leaf area (cm^2)	66.3a	93.2a	98.8a	.0795
Stem and branch DW (g)	48.1b	85.2a	34.5b	.0009
Seedling DW (g)	174.1b	228.0a	105.9c	.0029

[a] Least-square means for a given variable are not significantly different at the 0.05 experimentwise level using the Bonferroni approach when each pairwise contrast is tested at the 0.05/3 = 0.0167 level.
[b] First-order lateral root.
[c] Dry weight.

significant, these 30 percent S seedlings were generally larger in each growth parameter than C except for leaf number. This trend was less obvious for the second year (table 2). The 30 percent shade screen probably provided a cooling effect on the oaks during hot weather of the 1993 summer, thus resulted in more growth than controls. Northern red oak grown at 23 °C/23 °C (day/night) for 4 months had 60 percent greater seedling DW than those grown at 29 °C/23 °C (Farmer 1975). Hodges and Gardiner (1993) also reported that full-sun-grown *Q. pagoda* Raf. seedlings were smaller than those under 53 percent sun, but larger than seedlings grown under 27 and 8 percent sun.

Northern red oak seedlings of 70 percent S were consistently smaller in taproot and total seedling DW than controls for both years. At the end of the second year, effects of 70 percent shade on decreasing DW growth were significant in all seedling components with the exception of average individual leaf DW (table 2). Fewer leaves and larger individual leaf were observed in 70 percent S seedlings as compared to C and 30 percent S seedlings. Similar effects of shade on leaf number and area were reported with pedunculate oak (Ziegenhagen and Kausch 1995). The specific leaf weight for C, 30 percent S, and 70 percent S seedlings were 10.8, 8.4, and 6.9 mg/cm^2, respectively. Greater average leaf area, smaller specific leaf weight, and thinner leaf have been observed in several oak species grown under shade (Ashton and Berlyn 1994, Carpenter and Smith 1981, Farmer 1975).

Unlike NRO seedlings, the 30 percent S treatment did not increase WO growth over that of C (tables 3, 4). Lateral

Table 2—Effects of shade on growth of northern red oak seedlings for 2 years

Variable measured	Full sun	30% shade	70% shade	p-Value
Height (cm)	142.7a[a]	171.5a	160.6a	.3566
Groundline diameter (mm)	23.1a	22.9a	17.8a	.0281
Taproot DW[b] (g)	195.2a	186.6a	92.6b	.0176
Lateral root DW (g)	120.6a	122.0a	23.8b	.0053
Leaf DW (g)	52.3a	56.9a	38.5b	.0145
Leaf number	157.3a	140.8a	74.3b	.0019
Average leaf DW (g)	0.34a	0.42a	0.53a	.0171
Stem and branch DW (g)	154.5ab	177.0a	114.2b	.0275
Seedling DW (g)	522.6a	542.5a	269.1b	.0063

[a] Least square means for a given variable are not significantly different at the 0.05 experimentwise level using the Bonferroni approach when each pairwise contrast is tested at the 0.05/3 = 0.0167 level.
[b] Dry weight.

Table 3—Effects of shade on first-year growth of white oak seedlings

Variable measured	Full sun	30% shade	70% shade	p-Value
Height (cm)	36.9a[a]	45.7a	37.5a	.2657
Groundline diameter (mm)	9.3a	9.9a	7.4b	.0133
FOLR number[b]	10.0a	9.4a	7.8a	.1649
Taproot DW[c] (g)	33.9a	37.1a	19.5a	.0619
Lateral root DW (g)	3.1a	2.7ab	1.5b	.0280
Leaf DW (g)	8.6ab	10.2a	6.4b	.0264
Leaf number	45.0a	53.8a	42.1a	.0811
Leaf area (cm^2)	965.0a	1309.0a	893.0a	.0573
Average leaf area (cm^2)	21.0a	24.9a	21.3a	.3242
Stem and branch DW (g)	11.3ab	14.9a	7.1b	.0278
Seedling DW (g)	56.9a	64.8a	34.4a	.0353

[a] Least-square means for a given variable are not significantly different at the 0.05 experimentwise level using the Bonferroni approach when each pairwise contrast is tested at the 0.05/3 = 0.0167 level.
[b] First-order lateral root.
[c] Dry weight.

Table 4—Effects of shade on growth of white oak seedlings for 2 years

Variable measured	Full sun	30% shade	70% shade	p-Value
Height (cm)	95.0a[a]	98.6a	101.0a	.9420
Groundline diameter (mm)	18.1a	17.3a	14.0a	.1235
Taproot DW[b] (g)	120.3a	108.6a	62.4a	.0734
Lateral root DW (g)	36.3a	30.2ab	7.6b	.0215
Total leaf DW (g)	25.2a	24.3a	13.3a	.1352
Regular leaf DW (g)	15.1a	19.4a	8.4a	.0567
Recurrent leaf DW (g)	10.1a	4.9a	4.9a	.3454
Total leaf number	149.8a	154.7a	72.4a	.1268
Regular leaf number	131.0a	144.0a	60.7a	.0964
Recurrent leaf number	18.8a	10.7a	11.7a	.9233
Avg regular leaf DW (g)	0.11a	0.14a	0.14a	.0513
Avg recurrent leaf DW (g)	0.54a	0.46a	0.42a	.2837
Stem and branch DW (g)	80.0a	90.7a	52.7a	.2701
Seedling DW (g)	261.8a	253.8a	136.0a	.1095

[a] Least square means for a given variable are not significantly different at the 0.05 experimentwise level using the Bonferroni approach when each pairwise contrast is tested at the 0.05/3 = 0.0167 level.
[b] Dry weight.

Root DW growth was consistently less in 70 percent S seedlings than C for both years (tables 3, 4). In 1994, we noticed that some WO recurrent flushes had individual leaves with much greater area than most leaves. These extra large-area leaves (recurrent leaves) were threefold to fivefold greater in DW than the regular leaves (table 4). Control seedlings seemed to have more recurrent leaves than shaded seedlings. The specific leaf weights for C, 30 percent S, and 70 percent S seedlings in 1993 were 8.9, 7.3 and 7.2 mg cm^2, respectively. Similar to NRO, WO seedlings grown under shade had fewer leaves, smaller individual leaf DW, and less total leaf area (tables 3, 4).

There were great variations in seedling size even within a wooden plot. The effects of shading on growth can be masked by these variations. When percents of DW allocated to each seedling component were examined, it was clear that DW allocation to lateral roots was affected the most by shading with both oak species in both years (table 5). It has been reported that shading decreased oak DW allocation to root system (Gottschalk 1987, Hodges and Gardiner 1993, Ziegenhagen and Kausch 1995). Our study probably is the first to show that shading decreased DW allocation to lateral roots but not taproots in oaks. Messier and Puttonen (1995) reported shading decreased DW allocation to fine-root biomass in *Betula pubescens* Ehrh. and *B. pendula* Roth

Table 5—Effects of shade on percent dry weight biomass allocation within oak seedlings

	Full sun		30% shade		70% shade	
Variable measured	1 year	2 year	1 year	2 year	1 year	2 year
Northern red oak						
Lateral root	16.9	22.0	14.9	20.5	8.3	8.3
Taproot	37.2	39.9	32.1	38.1	38.5	37.3
Stem and branch	27.0	27.9	36.2	30.5	31.0	39.8
Leaf	18.9	10.2	16.8	10.9	22.2	14.6
White oak						
Lateral root	5.2	11.7	4.3	10.7	4.5	4.9
Taproot	61.1	50.1	57.4	46.8	57.4	50.9
Stem and branch	19.2	28.3	22.0	32.5	19.5	35.3
Leaf	14.5	9.9	16.3	10.0	18.6	8.9

grown under pine stands of different light availability. Thus, the underplanted oak seedlings with decreased lateral root growth would probably become less and less competitive for water and nutrient with established trees in the stands. High mortality of outplanted oaks in mixed hardwood stands as compared to that of pine stands and clearcut site planting has been observed by Kormanik and others (in press).

Photosynthesis

In this study, NRO A was not affected by the 30 percent shade treatment in either year (table 6). However, there was at least 30 percent decrease in A in 70 percent S NRO seedlings as compared to the controls. Effect of shade on decreasing A was more obvious with WO seedlings. Decreased oak A by shading, with or without change in light quality, has been reported in many studies (Crunkilton and others 1992, Kormanik and others (in press), Kubiske and Pregitzer 1996, McGraw and others 1990).

If leaf number and area were taken into consideration, the estimated A for 70 percent S NRO and WO seedlings were about 70 and 30 percent, respectively, of the controls for 1994 (table 6). These estimated A values are close to the value of 50 percent less seedling DW for both species grown under 70 percent S (tables 2, 4). Although WO has similar A to that of NRO, the slower growth by WO seedlings can be explained by the fact that WO seedlings have fewer leaves and smaller individual leaf area than NRO (table 6). Similar A's for WO and NRO were reported by Barton and Gleeson (1996) and Sung and others (1995).

Photoprotection

Levels of pigments in developing and mature leaves from full sun-grown NRO seedlings are presented in table 7. Mature leaves had twice as much chlorophyll a plus chlorophyll b (Chl a+b) as developing leaves. No significant differences in the levels in all the carotenoid pigments, expressed on the mol Chl a+b basis, were observed between developing and mature leaves (table 7). Only the xanthophyll cycle pigments exhibited diurnal patterns in both types of leaves. The Z+An to Z+An+V ratio was low in the dark and very high around noon. Values presented in table 7 were comparable to those found with cork oak leaves (Faria and others 1996). Judged from the xanthophyll pool size (Z+An+V) and the ratio between Z+An and Z+An+V, it is obvious that the photoprotection mechanism is more active in developing leaves than in mature leaves. Similarly, sun cork oak leaves are more photoprotective than shade leaves (Faria and others 1996). The effects of shading on the xanthophyll pool sizes and the diurnal patterns of Z+An to Z+An+V ratio will be examined for NRO and WO seedlings grown under different types of stands in the future.

CONCLUSIONS

Northern red oak and white oak seedlings grown under 70 percent shade had lower net photosynthetic rate, fewer leaves, and less specific leaf weight, seedling dry weight, and dry weight allocation to lateral roots as compared to those grown with full sun. Like most plants, developing and mature northern red oak leaves exhibit diurnal xanthophyll cycle for photoprotection. Greater dry weight growth with northern red oak seedlings than white oak is associated with the former having more and larger leaves. With the presence of large leaves on some of the recurrent flushes in white oak seedlings, dry weight growth can be increased because recurrent leaves have a higher

Table 6—Effects of shade on oak net photosynthetic rate (A)

Light level	1993		1994		
	Average A[a] μmol/m^2.s	Estimated A[b] μmmol/seedling.h	Average A μmol/m^2.s		Estimated A μmmol/seedling.h
Northern red oak					
Full sun	10.1	11.76	10.5		18.34[c]
30% shade	10.3	17.02	10.4		25.40
70% shade	6.6	8.03	6.3		12.72
White oak:			(Regular)	(Recurrent)	
Full sun	10.2	11.89	11.5	15.1	13.40[d]
30% shade	8.9	14.71	9.7	10.7	11.11
70% shade	6.5	7.91	5.7	6.8	4.16

[a] Average of photosynthetic rates measured between June and October.
[b] Derived from average A x leaf area per seedling.
[c] Leaf area per seedling was calculated using the same specific leaf weight (g/cm^2) obtained from seedlings harvested in 1993.
[d] Derived from sum of estimated A for regular leaf and for recurrent leaf.

Table 7—Levels of chlorophyll and carotenoids in developing and mature leaves from northern red oak seedlings grown under full sun

	Time of day					
Pigment	5 am	9 am	11 am	2 pm	5 pm	9 pm
Developing leaf[a]						
Chl a+b, mol/m^2	174.3	143.4	168.1	163.1	147.2	165.1
Zeaxanthin (Z)[b]	5.1	21.8	33.8	33.8	41.7	8.5
Antheraxanthin (An)	4.8	17.0	17.8	22.8	26.8	8.4
Violaxanthin (V)	78.1	35.6	14.3	27.1	21.3	82.3
Z+An+V	88.0	74.4	65.9	83.7	89.8	99.2
Lutein	122.9	116.0	115.0	130.3	122.2	124.6
Neoxanthin	58.5	60.5	57.8	56.0	57.9	54.4
α-Carotene	1.8	2.4	2.3	2.6	2.2	1.6
β-Carotene	50.8	49.6	47.7	48.7	49.2	47.8
Total Carotenoid	322.1	302.9	288.7	321.3	321.3	327.6
Z+An/Z+An+V ratio	0.11	0.52	0.78	0.68	0.76	0.17
Mature leaf[c]:						
Chl a+b, mol/m^2	394.3	336.4	363.7	354.8	363.4	360.2
Zeaxanthin (Z)	4.6	8.3	12.5	29.1	16.8	6.7
Antheraxanthin (An)	4.8	8.8	8.2	11.4	9.3	5.9
Violaxanthin (V)	52.7	50.7	25.2	19.4	14.9	50.7
Z+An+V	62.1	67.8	65.9	59.9	51.0	63.3
Lutein	92.7	94.7	84.4	99.4	84.3	94.4
Neoxanthin	57.0	56.1	53.1	60.7	50.1	57.8
α-Carotene	1.1	1.1	1.4	1.4	1.1	1.1
β-Carotene	56.5	56.7	53.1	61.5	50.9	57.4
Total Carotenoid	269.4	276.3	258.0	282.8	237.5	273.9
Z+An/Z+An+V ratio	0.15	0.25	0.62	0.68	0.71	0.20

[a] Average of four developing leaves from an elongating flush. Flushes of similar developmental stages were used for analysis throughout the day. All leaves were between 5 and 20 percent of average mature leaf size.
[b] All carotenoid pigments are in mmol/mol Chl a+b.
[c] Average of three mature leaves from the latest mature flush; different sets of leaves were used throughout the day.

net photosynthetic rate than regular leaves. Use of large-size planting stock and outplanting these seedlings on clearcut sites should improve success of artificial regeneration of oak species.

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