

RESPONSE OF SUN-GROWN AND SHADE-GROWN NORTHERN RED OAK SEEDLINGS TO OUTPLANTING IN CLEARCUTS AND SHELTERWOODS IN NORTH ALABAMA

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Abstract—The primary objective of this study was to determine if greenhouse light environment would affect outplanting success for northern red oak (*Quercus rubra* L.) in clearcuts and shelterwoods. In 2002, northern red oak seedlings were grown from acorns under full-ambient (sun) and half-ambient (shade) light conditions in a greenhouse. Seedlings grown under full sun conditions were significantly taller and had more leaves and more flushes than seedlings grown in shade. Root-collar diameter of sun-grown seedlings did not differ significantly from those of shade-grown seedlings. In February 2003, both sun-grown and shade-grown seedlings were outplanted in a clearcut and under an oak shelterwood. Three replicates of the oak shelterwood were created in November 2002 by using herbicide to selectively remove mid-canopy species; no gaps were created in the overstory canopy. Three clearcut plots were harvested in winter 2002. The clearcuts averaged 1 m²/ha residual basal area, 32 percent canopy cover, and photosynthetically active radiation was reduced to 30 percent less than above-canopy levels. Residual basal area for the shelterwood averaged 19 m²/ha, with 98 percent canopy cover and photosynthetically active radiation reduced by 86 percent. After one field growing season, sun seedlings outplanted in clearcuts had significantly greater basal diameter growth than either sun or shade seedlings planted in shelterwoods. Prior exposure to higher ambient light levels did not result in greater light use by outplanted seedlings.

INTRODUCTION

Uncertainties in regenerating oaks in southern Cumberland Plateau forests are similar to other oak-dominated regions. Favorable conditions for regenerating oak can be created by employing a specific shelterwood formula (Dey and Parker 1996, Hannah 1987, Johnson and others 1989, Loftis 1990). However, the shelterwood method requires the presence of naturally occurring oaks, whose growth is stimulated through canopy manipulations. This method does not work if adequate advanced oak reproduction is lacking.

An alternative is to couple the shelterwood method with oak planting. Experimental silvicultural prescriptions for this coupling have focused on appropriate levels of overstory tree density, seedling standards and nursery practices, and various outplanting cultural treatments (Buckley and others 1998, Dey and Parker 1997, Gottschalk and Marquis 1983, Johnson 1984, Spetich and others 2004, Weigel 1999).

Mattsson (1997) provides a thorough review of conifer seedling quality assessment methods for predicting field performance, and many of these methods can be applied to hardwood seedlings. Dey and Buchanan (1995) provide a synthesis of research pertaining to nursery production and direct seeding of oaks, with specific guidelines for the production of high-quality stock. Numerous studies have shown that hardwood (particularly *Quercus*) seedling survival and shoot growth after transplanting depends on root system form and ability of the seedling to produce new roots (Barden and Bowersox 1989, Burdett and others 1983, Farmer 1975, Kormanik and others 1988, Rietveld and van Sambeek 1989, Sutton 1980). The next challenge is to show how silvicultural treatments affect the seedling environment and subsequently seedling physiology and growth.

We hypothesized that the light environment under which seedlings develop influences seedling field performance in the first year after outplanting. To test this, we grew northern red oak (*Q. rubra* L.) seedlings from acorns under two light levels and outplanted them under two stand conditions that produced different light regimes.

METHODS

Northern red oak acorns were collected from the study sites in fall 2001. Collection amounts were low, and many acorns were small and visibly defective, so we discarded them and requested acorns from East Tennessee Nursery, Tennessee Department of Agriculture, Forestry Division. One thousand acorns from their wild seed collection were sent to us in January 2002 (courtesy of Paul Ensminger, Nursery Manager). Acorns were floated in water for 24 hours to increase their moisture content; floating and visibly unsound acorns were discarded. Sound acorns were stored in polyethylene bags at 3 °C for 30 to 45 days (Bonner and Vozzo 1987).

In February 2002, acorns were sown 4-cm deep, 1 acorn per pot, in 11-L pots filled with a 1:2:2 volume ratio of perlite, peat, and vermiculite. The resulting potted seedlings were grown in a greenhouse located on the Alabama Agricultural and Mechanical University campus, Normal, AL. Four hundred pots were sown to guarantee 150 seedlings for outplanting. Half of the pots were randomly selected and placed under black polypropylene shade fabric in the greenhouse (45 percent of full ambient sun = shade seedlings); the other half received full ambient greenhouse light (no supplemental light source used = sun seedlings). After germination, 150 sun seedlings and 150 shade seedlings were grown for 1 growing season. Pots were watered as needed to maintain ample soil moisture. Data loggers were placed under the shade fabric and

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on the open greenhouse table to record air temperature (°C), relative humidity (percent), and light intensity (lumens m⁻²).

Following one greenhouse growing season, seedling height and basal diameter were measured using a tape measure (nearest cm) and digital caliper (nearest mm). The total numbers of leaves and stem flushes were also recorded. Seedlings were moved outside the greenhouse in November 2002. A shade house was constructed for the shade seedlings using similar shade fabric, while sun seedlings were placed adjacent to the shade house in an open area.

Seedlings were outplanted in February 2003 on a site located on the southern Cumberland Plateau in Jackson County, AL. The site encompasses strongly dissected margins and sides of the plateau (the escarpment). Soils are characterized as deep to very deep, loamy, well-drained, and moderately fertile. Slopes range from 15 to 30 percent. Upland oak site index is 22.9-24.3, and yellow-poplar site index is 30.5 [height, in meters, at base age 50 years, Smalley Landtype 16, pleateau escarpment and upper sandstone slopes and benches-north aspect (Smalley 1982)]. For a detailed description of the site, see Schweitzer (2004).

Seedlings were outplanted under two stand conditions, a clearcut and a midstory removal shelterwood. Treatment units were 4 ha in area and were replicated three times. Clearcut harvesting was completed in winter 2002. An imazapyr herbicide, which was applied by the hack-and-squirt method, was used to deaden the midstory in the shelterwood treatment. The herbicide treatment was completed in fall 2001, prior to leaf-fall.

Outplanted northern red oak seedlings were spaced 0.5 m apart; 12 sun and 12 shade seedlings were planted in each clearcut and shelterwood plot. Plots were fenced, and competing vegetation was controlled mechanically. Seedling growth (height and diameter), survival, and light response were measured in June 2003 and September 2003. Net photosynthesis (μmol m⁻²s⁻¹) of each sample leaf (four sample seedlings per light and outplanting treatment combination) was recorded at seven levels of photosynthetic photon flux density (PAR) (0, 50, 200, 400, 800, 1,200, and 1,600 μmol m⁻² s⁻¹) with a portable photosynthesis system. Ambient light levels in each plot were recorded. Sixty light measures were collected for each plot in each sample month. During the growing season, one canopy

cover measurement was made within five points in each plot using a handheld spherical densitometer.

Photosynthetic light response data were modeled using methods and equations outlined by Givnish (1988) and applied to outplanted oak seedlings by Gardiner and others (2001). Analysis of variance for a randomized block design was used to quantify treatment differences; t-tests and Duncan's new multiple range test were used to separate means at α = 0.05 (SAS Institute 1990).

RESULTS

Greenhouse Environment and Seedling Response

During the months of June, July, August, and September 2002, northern red oak seedlings in the greenhouse were exposed to temperatures, relative humidities, and diurnal light availabilities given in table 1. Shade seedlings received an average of 46 percent as much ambient light as sun seedlings.

Sun seedlings (mean height 28.8 cm) were significantly taller than shade seedlings (mean height 21.4 cm) (*p* < 0.001). There was no difference in basal diameter. By September, the average numbers of leaves and stem growth flushes were significantly greater for sun seedlings (eight leaves compared to five leaves per shade seedling; 1.7 flushes per sun seedling compared to 1.0 flush per shade seedling). Survival was 100 percent for all seedlings. No data on photosynthesis were collected for seedlings while the seedlings were in the greenhouse.

Outplanting Environment

Table 2 presents information about the conditions created by the shelterwood and clearcut treatments. Basal area of all trees ≥ 14.2-cm diameter at breast height was reduced more by clearcutting than by the shelterwood treatment. Herbicide was applied only in the shelterwood treatments, and most of the herbicide-treated trees were in the midstory. An average of 941 stems/ha were injected with herbicide, and the average tree diameter of treated trees was 7.5 cm. The 32 percent canopy cover recorded for the clearcuts resulted from stump-sprouting and rapid revegetation. This revegetation slightly reduced the amount of sunlight reaching the forest floor, but ambient light levels were significantly greater in the clearcuts than in the shelterwoods.

Table 1—Temperature, relative humidity, and mean diurnal light availability (lumens m⁻²) for sun (full ambient light) and shade (45 percent ambient light) northern red oak seedlings grown in a greenhouse at Alabama Agricultural and Mechanical University, Normal, AL

Environmental variable	Light treatment	Month			
		June	July	August	September
Temperature (°C)	Sun	25.9	27.2	25.8	23.9
	Shade	25.2	26.8	25.9	23.8
Relative humidity (%)	Sun	27.9	27.1	28.6	27.0
	Shade	50.7	47.9	31.5	32.3
Light	Sun	179.5	208.9	131.6	119.0
	Shade	89.5	108.2	91.4	59.7

Table 2—Stand conditions for outplanting plots, Jackson County, AL

Variable	Shelterwood	Clearcut
Pretreat BA/ha ^a (m ⁻²)	27	25
Posttreat BA/ha (m ⁻²)	19	1
BA retained (%)	70	5
Canopy cover (%)	98	32
Full sunlight at 1.37 m (%)	14	69
Light intensity average (μmol m ⁻² s ⁻¹)	128	1096
Light intensity range (μmol m ⁻² s ⁻¹)	19 – 1057	123 – 1827

BA = basal area.

^a BA = basal area of all trees ≥ 14.2 cm at 1.37 m aboveground.

Response of Outplanted Seedlings

Following one growing season in the greenhouse, seedlings were outplanted in the field in the winter of 2003. Table 3 details the survival and growth of outplanted seedlings. Survival was high for all outplanted seedlings; competition was controlled mechanically and the outplanting site fenced. After one field-growing season, sun seedlings outplanted in clearcuts had significantly greater basal diameter growth than both sun and shade seedlings planted in shelterwoods. There were no treatment-to-treatment differences in height growth.

Photosynthetic Response to Light

Full leaf-out for all seedlings was completed by mid-April 2003. In mid-June, photosynthetic light response of northern red oak leaves was similar for all seedlings, regardless of greenhouse light environment or outplanting condition (fig. 1). Dark respiration rates were 33 percent greater for clearcut sun and shade seedlings than for shelterwood sun and shade seedlings; no other light responses differed from treatment to treatment in mid-June (table 3).

There were two distinct light response curves for photosynthesis in September (fig. 2). At PAR of 800 and above, photosynthetic rates for seedlings in clearcuts were significantly

greater than those for shelterwood seedlings. Dark respiration was the only light response variable that did not differ significantly from treatment to treatment (table 4). Clearcut shade seedlings had significantly greater gross photosynthetic rate at light saturation, greater PAR required for half gross photosynthetic rate at light saturation, greater light compensation point, and greater quantum yield than shade shelterwood seedlings. Sun seedlings in clearcuts had significantly greater gross and net photosynthetic rate than sun shelterwood seedlings. In clearcuts, sun seedlings had a significantly greater light compensation point than shade seedlings; in shelterwoods, sun seedlings had significantly lower gross photosynthetic rate and higher quantum yield than shade seedlings.

DISCUSSION

Prior exposure to higher ambient light levels (sun seedlings) did not result in greater light use for outplanted seedlings in the following growing season. Outplanting light conditions significantly affected physiological response, as net photosynthetic rate was greater for clearcut than shelterwood seedlings. Light saturation and light compensation point were significantly less for shelterwood seedlings. Mean ambient light intensity (128 μmol m⁻²s⁻¹) under shelterwoods was below

Table 3—Survival, growth, and photosynthetic characteristics of northern red oak seedlings measured on sun and shade seedlings outplanted on shelterwood and clearcut plots, June 2003, Jackson County, AL

Variable	Clearcut		Shelterwood	
	Sun seedlings	Shade seedlings	Sun seedlings	Shade seedlings
Survival (%)	97a	92a	97a	100a
Diameter growth (mm)	3a	2ab	2b	1c
Height growth (cm)	1a	1a	1a	1a
P _{g-sat} (μmol m ⁻² s ⁻¹)	6.95a	6.71a	5.86a	5.67a
P _{n-sat} (μmol m ⁻² s ⁻¹)	3.72a	3.74a	3.94a	4.04a
R _d (μmol m ⁻² s ⁻¹)	2.81a	2.66a	1.11b	1.25b
Q ^a	0.03a	0.04a	0.04a	0.04a
LCP (μmol m ⁻² s ⁻¹)	80.4a	50.5a	50.1a	25.5a
K (μmol m ⁻² s ⁻¹)	99.9a	75.7a	286.4a	133.4a

P_{g-sat} = gross photosynthesis at light saturation; P_{n-sat} = net photosynthesis at light saturation; R_d = dark respiration rate; Q = quantum yield; LCP = light compensation point; K = light needed to attain one-half of P_{g-sat}.

Means in a row followed by the same letter do not differ at the 0.05 probability level.

^a (μmol CO₂ m⁻²s⁻¹/μmol photon m⁻²s⁻¹).

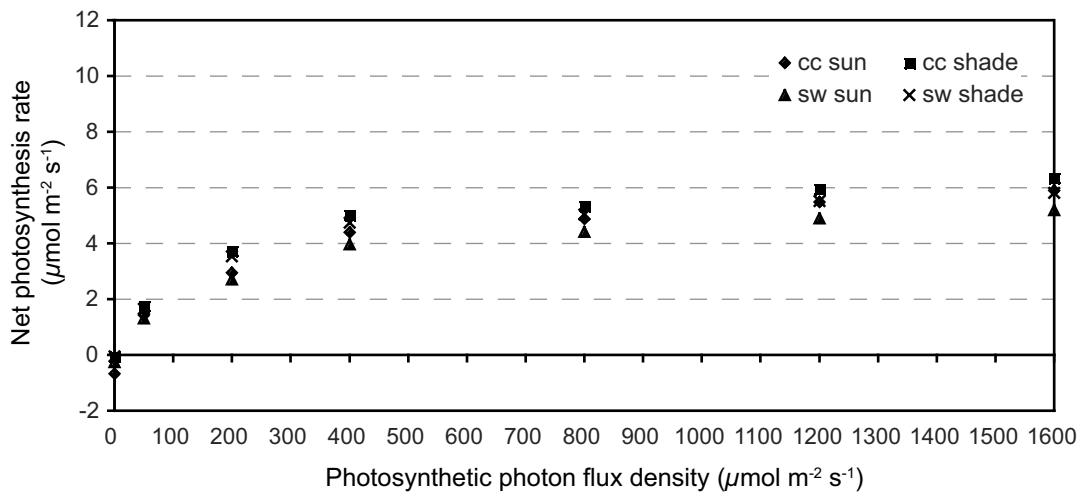


Figure 1—June 2003 photosynthetic light response of northern red oak seedlings raised under two light regimes (sun = full sunlight; shade = 45 percent full sunlight) and outplanted under two silvicultural prescriptions (cc = clearcut; sw = shelterwood).

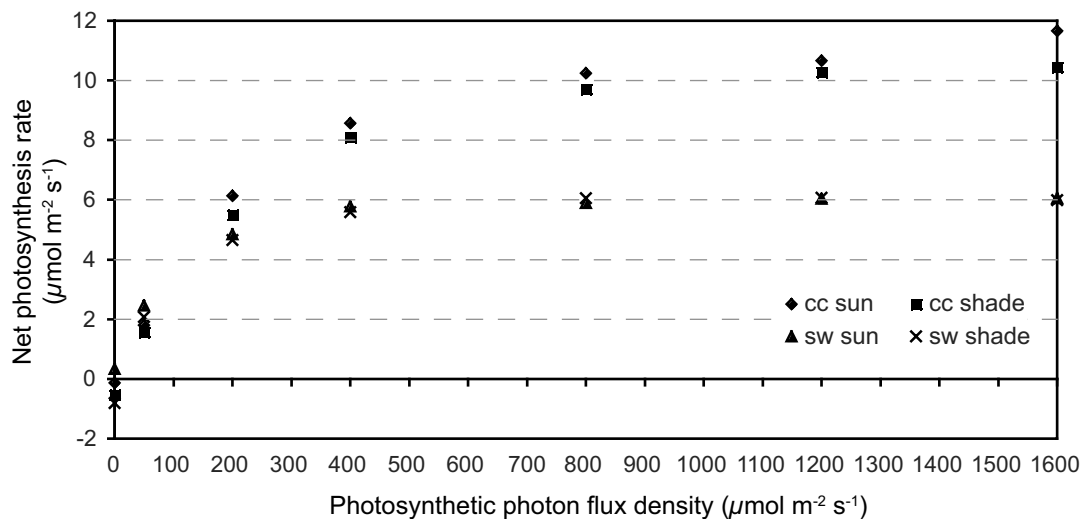


Figure 2—September 2003 photosynthetic light response of northern red oak seedlings raised under two light regimes (sun = full sunlight; shade = 45 percent full sunlight) and outplanted under two silvicultural prescriptions (cc = clearcut; sw = shelterwood).

the average light saturation level recorded for those seedlings ($131 \mu\text{mol m}^{-2}\text{s}^{-1}$).

Response mechanisms behind the observations in this study can only be postulated, as seedlings were not destructively sampled for intensive study. Root biomass may be more sensitive to light environment than leaf or stem biomass (Gottschalk 1987). Higher leaf area in low light may allow seedlings to harvest light more effectively; however, higher leaf areas may be more reflective of growth mechanisms than of acclimation to low-light environments (Groninger and others 1996). Quantum yield has been shown to increase in shade-grown plants, allowing more efficient energy transfer from light-harvesting chlorophyll to photosystem II (Demmig and Bjorkman 1987). Gardiner and others (2001) found no difference in quantum yield or leaf area for Nuttall oak (*Quercus nuttallii* Palm.) seedlings grown in full and 43 percent of full sun. In

our study, shade seedlings grown in shelterwoods had greater quantum yield than shade seedlings in clearcuts and sun seedlings in shelterwoods, suggesting a response towards increased efficiency.

CONCLUSIONS

Species that adapt rapidly to their environment may have a competitive advantage in habitats with changing light intensities. Efforts to increase outplanting success for oak seedlings should continue to emphasize competition control and the importance of high-quality seedlings. Results from this study suggest that outplanted northern red oak seedlings are plastic in their photosynthetic response and are able to acclimate to changing light conditions. No immediate gain was incurred by subjecting these seedlings to low light prior to outplanting.

Table 4—Survival, growth, and photosynthetic characteristics of northern red oak seedlings measured on sun and shade seedlings outplanted on shelterwood and clearcut plots, September 2003, Jackson County, AL

Variable	Clearcut		Shelterwood	
	Sun seedlings	Shade seedlings	Sun seedlings	Shade seedlings
Survival (%)	97a	92a	97a	100a
Diameter growth (mm)	3a	2ab	2b	1c
Height growth (cm)	2a	-1a	3a	-2a
P_{g-sat} ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	13.08a	13.69a	6.64c	7.47b
P_{n-sat} ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	11.01a	10.63ab	5.60c	6.38bc
R_d ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	0.41a	0.97a	0.68a	0.76a
Q^a	0.07ab	0.05b	0.06b	0.09a
LCP ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	5.31b	19.33a	10.33ab	8.79b
K ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	189.4ab	245.1a	91.33bc	68.3c

P_{g-sat} = gross photosynthesis at light saturation; P_{n-sat} = net photosynthesis at light saturation; R_d = dark respiration rate; Q = quantum yield; LCP = light compensation point; K = light needed to attain one-half of P_{g-sat} .

Means in a row followed by the same letter do not differ at the 0.05 probability level.

^a ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1} / \mu\text{mol photon m}^{-2}\text{s}^{-1}$).

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