# Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? II. Gas exchange and chlorophyll responses

**Joanne Rebbeck, Amy Scherzer, and Kurt Gottschalk**

**Abstract:** Understanding differences in physiological and growth strategies in low-light environments among upland oak species may help managers address the challenges of oaks' poor regeneration. Gas exchange and chlorophyll content were measured for northern red oak (*Quercus rubra* L.), chestnut oak (*Quercus prinus* L.), and white oak (*Quercus alba* L.) germinants grown at 25%, 18%, and 6% of full sun in one of two native forest soil mixes for two summers. Northern red and chestnut oak photosynthesis at saturating light ($A_{max, mass}$) increased by 23%–36% as light levels increased from 6% to 25% of full sun, while white oak $A_{max, mass}$ declined by 20% and plateaued at 18% of full sun. White oak light compensation point is representative of deep shade (7.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$), while northern red and chestnut oak averaged 17.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Total chlorophyll content increased as light levels decreased for all species. Of the three species, the slow-growing white oak seedlings appeared to be more efficient in utilizing light than northern red or chestnut oak seedlings. This suggests no additional benefits to increasing light above that typically found in a light shelterwood cut; however, it is crucial to control faster-growing competing vegetation.

**Résumé :** La compréhension des différentes stratégies physiologiques et de croissance dans les milieux ombragés, chez les espèces de chêne des milieux secs, peut aider les aménagistes à relever les défis que représente la faible régénération des chênes. Les échanges gazeux et la teneur en chlorophylle ont été mesurés chez des germinants de chêne rouge (*Quercus rubra* L.), de chêne châtaignier (*Quercuc prinus* L.) et de chêne blanc (*Quercus alba* L.) cultivés sous 25 %, 18 % et 6 % du plein soleil dans l'un des deux mélanges de sol forestier naturel. La photosynthèse à saturation lumineuse ($A_{max, masse}$) des chênes rouge et châtaignier a augmenté de 23 % à 36 % à mesure que l'intensité lumineuse augmentait de 6 % à 25 % du plein soleil, tandis que $A_{max, masse}$ du chêne blanc a diminué de 20 % et atteint un plateau sous 18 % du plein soleil. Le point de compensation lumineuse du chêne blanc est représentatif d'une situation très ombragée (7,2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) tandis qu'il atteignait en moyenne 17,8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ chez les chênes rouge et châtaignier. La teneur totale en chlorophylle augmentait à mesure que l'intensité lumineuse diminuait chez toutes les espèces. Des trois espèces, les semis du chêne blanc, une espèce à croissance lente, semblaient utiliser la lumière plus efficacement que les semis des chênes rouge et châtaignier. Cela implique qu'il n'y a pas de bénéfices additionnels à augmenter l'intensité lumineuse au-delà de ce qu'on retrouve dans une coupe progressive légère. Cependant, il est crucial de maîtriser la végétation compétitrice qui croît plus rapidement.

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## Introduction

The lack of the accumulation of large oak advance reproduction in heavily shaded forest understories is a widely recognized limiting factor in sustaining future oak stock on all but the most xeric sites (Loftis 1990). Faster-growing species such as tulip poplar (*Liriodendron tulipifera* L.), and red maple (*Acer rubrum* L.) have been accumulating within the understory of oak-dominated stands since the active suppression of fire over the last 80 plus years. These fire-intolerant species often successfully outcompete young oaks, especially on high-quality mesic sites (Brose 2011). Optimizing light levels to improve oak seedling competitiveness on these more challenging sites without promoting the growth of other species is critical in sustaining a viable component of oaks in eastern United States forests. Determining what that critical light level is and then implementing single or multiple treatments such as prescribed fire, herbicide application, or overstory thinning to achieve that light level at the appropriate time to benefit oak advance regeneration is paramount. To be successful, it is crucial to understand how individual oak species respond to low light and subsequent light manipulations.

**J. Rebbeck and A. Scherzer.** Northern Research Station, Forest Service, US Department of Agriculture, 359 Main Road, Delaware, OH 43015, USA.

**K. Gottschalk.** Northern Research Station, Forest Service, US Department of Agriculture, 180 Canfield Street, Morgantown, WV 26505, USA.

**Corresponding author:** Joanne Rebbeck (e-mail: jrebbeck@fs.fed.us).

Dominant upland oaks within the eastern United States include white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus prinus* L.), and scarlet oak (*Quercus coccinea* Muenchh.) (McWilliams et al. 2002). Most of these are classified as intermediate in shade tolerance, while competitors are classified as either shade intolerant (e.g., tulip poplar and trembling aspen (*Populus tremuloides* Michx.)) or shade tolerant (e.g., sugar maple (*Acer saccharum* Marsh.), red maple, and American beech (*Fagus grandifolia* Ehrh.)). These classifications tend to be more observational and anecdotal than empirically based measures of survival (Reich et al. 2003). The shorter-lived scarlet and black oak tend to be more shade intolerant than the slower-growing and long-lived white oak (Rogers 1990). Northern red oak is considered to be moderately shade tolerant (Loach 1967; Kaelke et al. 2001). Chestnut oak is intermediate in shade tolerance and is common on rocky ridges with dry, infertile soils (McQuilkin 1990). Northern red oak prefers mesic ravines and valleys, while white oak can be common across ridges and valleys (Rogers 1990). White and chestnut oak are considered to be more adapted to xeric ecosystems than northern red oak, which is considered more of a mesic species (Long and Jones 1996; Iverson et al. 1999). Of all upland oaks, white oak is the slowest growing and the longest lived, while northern red oak is moderate to fast growing.

Of the upland oaks, northern red oak is by the far the best characterized. It is an important species within many mixed-oak forests of the Midwest and eastern United States (McWilliams et al. 2002). Northern red oak justifiably deserves intense study given its wide distribution, but other oak species such as white oak are also keystone species over a wide geographic range spanning the eastern region of North America (Rogers 1990; Sander 1990). Numerous studies have been conducted in which light, water, and nutrient levels were manipulated to compare the ecophysiological response of northern red oak seedlings with a suite of common co-occurring competitors (Kolb et al. 1990; Latham 1992; Kaelke et al. 2001). Scattered reports exist that may include other oak species, but it is rare to find studies that concurrently compare the response of multiple upland oak species (Barton and Gleeson 1996). In many regions of the eastern United States, it is common to have two or more oak species dominating the overstory. Characteristics of upland oaks such as juvenile growth rate, life span, shade tolerance, and drought tolerance differ, and species are often stratified topographically across a landscape by slope, aspect, and soil conditions. All of these attributes have the potential to influence seedling establishment and survival. Most upland oak species possess adaptations to grow and dominate on xeric sites but also have the potential to grow best on rich, well-drained sites. All are fire-adapted species (Brose et al. 2001; Dey and Fan 2009) and thus have "disturbance" attributes including root-centered growth, reservoir of protected buds, and thick bark, characteristics that most shade-tolerant species lack. Despite ecophysiological adaptations to limiting soil moisture and nutrients, upland oaks do not compete well in closed-canopy, low-light environments.

Our goal was to test the hypothesis that an upland oak species' response to shading and soil fertility is related to physiological and growth attributes, which drive its competitiveness on different types of sites. In a companion paper, we discussed the growth characteristics of these three upland oak species (Rebbeck et al. 2011). We report that white oak seedlings display more stress-tolerance attributes than either northern red or chestnut oak seedlings as measured by its overall slow growth, high root to shoot ratio, and relatively small proportion of biomass allocation to leaves. These combined traits resulted in a very limited positive aboveground response to increasing light and soil nutrients. Our intent in this paper is to relate physiological responses to growth responses. The ultimate goal is to improve our understanding of how different oak species acquire and utilize potentially limiting resources so that we can develop better management prescriptions to maintain a sustainable proportion of oaks.

## Materials and methods

### Plant culture and treatments

Three species of oak acorns were planted within six treatments that included three levels of light (6%, 18%, and 25% of full sun) and two soil treatments (West Virginia and Ohio forest soil mixes). Chestnut, northern red, and white oak acorns were collected at eight sites in Monongalia and Tucker counties, West Virginia, following a heavy seed masting in fall 1998. Our choice of oak species was opportunistic in nature, based on an abundant supply of chestnut, northern red, and white oak acorns within a localized geographic area. All oak species were not present at every collection site, and the number of maternal trees per site varied with species. In early May 1999, acorns from each maternal tree were float tested for soundness and individually planted in 15 cm by 41 cm (7.25 L) PVC pots containing a 1:1:1 mix of peat moss, horticultural-grade perlite, and forest soil. Approximately 20 acorns were planted from each maternal tree. Forest soils included either a sandy loam to silt-loam (Steinsburg–Gilpin Series) collected in Vinton County, Ohio, or a mixed fine loam (Buchanan–Ernest Series) collected in Monongalia County, West Virginia. The West Virginia (WV) soil mix had higher pH, higher water-extractable concentrations of nitrate, and higher calcium, potassium, and magnesium than the Ohio (OH) soil mix. Only phosphorus and soil ammonium (sodium acetate extracted) concentrations were higher in the OH forest soil (Rebbeck et al. 2011). Germination averaged 92% ($N = 540$) for northern red oak, 72% ($N = 462$) for chestnut oak, and 45% ($N = 234$) for white oak, resulting in 90 northern red oak, 77 chestnut oak, and 39 white oak germinants for six light level and soil mix combinations at the start of the treatments. The effects of maternal tree or site on seedling physiology were not studied (Rebbeck et al. 2011).

New germinants were randomly placed in one of three shade tents (each 3.1 m wide × 7.3 m long) covered with black polypropylene greenhouse shade cloth erected at the US Forest Service's Northern Research Station in Delaware, Ohio (40°21′N, 83°04′W). Temperatures in each shade tent were monitored continuously each growing season and found to be uniform, averaging 22.13 ± 0.64 °C in 1999 and 20.43 ± 0.25 °C in 2000. Seedlings were blocked by species in each shade tent and randomly rotated monthly in each species block. Northern red oak seedlings, the potentially fastest-

growing, hence tallest species, were positioned in the most northern two fifths of the shade tent to minimize shading of shorter plants. Chestnut oak pots were placed in the middle section, occupying two fifths of the tent area. The pots of white oak, the shortest species of the group, were positioned in the most southern section (one fifth of the tent area). Since species were stratified in each shade tent, the light environment for each species was characterized by measuring hourly ambient photosynthetic photon fluence rate over the 400–700 nm waveband. Measurements from both LI-COR (Lincoln, Nebraska) quantum sensors and Hamamatsu Photonics (Hamamatsu City, Japan) model G1118 GaASP photodiodes were recorded with a Campbell 21x datalogger. Light conditions were fairly uniform across each shade tent with seasonal means of weekly measures shown in Table 1. Treatments were maintained through late October 1999, and seedlings were subsequently housed in an unheated building until the following spring. The experiment resumed in early May 2000 and continued through late September 2000. Soil moisture was regularly monitored and seedlings were watered as needed. Details of plant culture and growing conditions are reported in Rebbeck et al. 2011.

### Physiological measurements

From among healthy seedlings, a subset was randomly measured with a LI-COR (Lincoln, Nebraska) 6200 portable photosynthesis system. Measurements were taken on fully expanded mature healthy leaves. An equal number of seedlings was sampled for every species. Numbers of individuals ranged from 12 to 24 depending on the type of gas exchange measurement.

### Season 1

All gas exchange measurements were delayed until early August to ensure young seedlings were not damaged and were using minimal reserves of residual cotyledonary energy. Instantaneous leaf photosynthetic measurements were conducted under constant saturating light conditions in early August to assess shading effects on midday photosynthesis ($A_{max}$) and stomatal conductance ($g_s$). For each of the three species, 16 seedlings within a given shade level (eight of each soil mix) were measured ($N = 48$ seedlings per species). All seedlings were measured under identical light environments outside the shade tents. If ambient light levels fell below 900 $\mu mol \cdot m^{-2} \cdot s^{-1}$, artificial light generated from a GE300W 120 V, cool-beam, full-spectrum, wide flood lamp was used to maintain an intensity of 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Diurnal gas exchange rates of eight seedlings per species per shade level ($N = 24$ seedlings per species) were measured every 3 h from 0600 to 1530 EST in ambient unshaded conditions on 1 September 1999 using two LI-COR 6200 instruments. Approximately 14 h before the first diurnal measurement period, all seedlings were removed from shade tents and grouped together in the ambient unshaded common area where the measurements occurred.

### Season 2

In late August 2000, light response curves were generated on a randomly selected subset of seedlings to determine if the photosynthetic response to light was impacted by the artificial shade treatments. Measurements were made in a cli-

**Table 1.** Seasonal growth environment light conditions of white (*Quercus alba*), chestnut (*Quercus prinus*), and northern red oak (*Quercus rubra*) measured in each shade tent during 2000 under cloudy and sunny skies.

| Ambient conditions | PAR ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | Tent 1: 6% of full sun | | | Tent 2: 18% of full sun | | | Tent 3: 25% of full sun | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Full sun | White oak | Chestnut oak | Northern red oak | White oak | Chestnut oak | Northern red oak | White oak | Chestnut oak | Northern red oak |
| Cloudy | 368.1±166.2 | 53.6±20.6 | 52.6±20.3 | 46.7±23.3 | 96.9±18.1 | 105.7±81.8 | 82.3±28.2 | 115.0±30.7 | 215.2±178.3 | 201.6±167.6 |
| Sunny | 1465.9±573.4 | 113.4±32.9 | 109.6±32.9 | 86.3±41.7 | 241.9±103.6 | 245.7±103.3 | 239.5±99.4 | 296.2±133.1 | 256.1±131.3 | 256.1±139.5 |

Note: Mean ± SD photosynthetically active radiation (PAR) values are presented for each oak species. Point measurements made weekly during the second growing season in each shade tent under cloudy ($N = 7$) and sunny ($N = 10$) conditions.

mate-controlled greenhouse maintained at approximately 28 °C from 1000 to 1500 EST. Light levels were altered using a series of neutral density filters to provide intensities ranging from 1200 to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation (PAR) (Rebbeck and Loats 1997; Loats and Rebbeck 1999). Light was generated from a GE300W 120 V, cool-beam, full-spectrum, wide flood lamp. Two measurements were also completed in darkness, which required 5 min for equilibration. Preliminary measurements determined that 3 min was an adequate equilibration time for all light measurements. From these light response curves, estimates of maximum carbon exchange rate (CER), quantum efficiency (QE), light compensation point (LCP), and dark respiration (RS) were derived based on two measurements at each target light level for each seedling. Measurement light levels were determined using the optimal sampling strategy method of Hanson et al. (1987), which was developed with northern red oak seedlings. This empirical model characterizes the nonlinear relationships between $CO_2$ exchange rate ($A_N$) and photosynthetic photo flux density ($I$). Because light response curves are time intensive, only those seedlings grown in the WV soil mix were measured within a given shade treatment ($N = 9$ per species). The WV soil mix was chosen because it represented more optimal nutrient conditions having a higher pH, higher cation-exchange capacity, and nitrate, calcium, and magnesium concentrations than the OH soil mix (Rebbeck et al. 2011).

### Foliar SPAD and chlorophyll content

A portable nondestructive chlorophyll SPAD-502 (Minolta, New Jersey) meter was utilized to assess foliar chlorophyll content. It has been well established for use with agricultural species and has more recently been tested with forest species (van den Berg and Perkins 2004; Uddling et al. 2007). During both growing seasons, SPAD leaf greenness (relative chlorophyll content) was measured on the same seedlings measured for gas exchange as well as on an additional random subset of seedlings ($N = 48$ seedlings per species). Because the measurement area in the SPAD meter is 2 mm × 3 mm, seven or eight readings were taken and averaged for each measured leaf. To minimize negative impacts on seedling growth during the first year, chlorophyll determinations were not measured in the first growing season because they require destructive sampling of foliage. Two leaf disks (12 mm diameter) were removed from each fully expanded mature leaf being careful to avoid primary and secondary veins when taking leaf punches. SPAD readings were taken on each leaf punch and total chlorophyll ($C_{tot}$) was then extracted with dimethyl sulfoxide at 65 °C (Hiscox and Israelstam 1979; Greenwood et al. 1989). Previously reported extinction coefficients were used (Rebbeck et al. 1993). In late August 2000, an additional subset of 10 randomly selected seedlings of each species was sampled in each shade treatment. Total chlorophyll content was calculated on a fresh weight ($C_{tot, mass}$) and leaf area ($C_{tot, area}$) basis. The relationship between the SPAD measurements and total extracted chlorophyll (nanograms per square centimetre) was developed for each oak species (Campbell et al. 1990; Monje and Bugbee 1992) in Season 2.

### Statistical design and data analysis

The study was a nested design with shade treatment as the main factor and soil type nested within shade treatment. Analyses were conducted using SAS version 9.3 (SAS Institute Inc. 2008). Least squares means for changes in physiological characteristics of each oak species were compared among the shade treatments using general linear model (GLM) and repeated-measures analysis. Data from instantaneous $A_{max}$ and $g_s$ rates at saturating light were analyzed for each species separately by GLM. To assess shading effects on diurnal gas exchange, $A_{max, area}$ and $g_{s, area}$ integrals (area under diurnal curves) of the three oak species were estimated using SAS PROC MIXED and then tested for statistical significance using contrasts. Because specific leaf mass, mass per unit area (grams per square metre), was calculated from the destructive sampling for chlorophyll determinations in 2000, $A$ and $g_s$ were expressed per unit leaf area ($A_{max, area}$ and $g_{s, area}$) and per unit leaf mass ($A_{max, mass}$ and $g_{s, mass}$). Data from light response curves of individual seedlings were fit to the Hanson model by a modified Gauss–Newton nonlinear iterative method until model convergence was achieved (SAS Institute Inc. 2008) using the following model:

$$A_N = B_1 \left[ 1 - \left( (1 - \beta_3/\beta_1)^{(1 - I/\beta_2)} \right) \right]$$

where $B_1$ is $A_{max}$ at saturating light, $B_2$ is compensation irradiance, and $B_3$ = respiration rate at zero $I$. Estimates of the model parameters for CER, RS, LCP, and QE were analyzed by GLM. In Season 2, final seedling leaf biomass and total leaf area data (Rebbeck et al. 2011) were used with light response curve data to determine the effects of shading treatments on seedling $A_{max, area}$ and $A_{max, mass}$ at saturated light conditions (PAR at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$). These were analyzed by GLM separately for each species. Effects were considered significant if $p \leq 0.05$.

## Results

### Gas exchange

#### Season 1

Within a given species, no shading effects were detected on the gas exchange of northern red, white, and chestnut oak during the first growing season. However, differences among the three species were observed. In early August, white oak seedlings had the highest midday $A_{max, area}$ at 8.20 ± 0.89 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and highest $g_{s, area}$ at 0.161 ± 0.027 $mol \cdot m^{-2} \cdot s^{-1}$ followed by chestnut oak, which averaged 7.25 ± 0.34 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for $A_{max, area}$ and 0.135 ± 0.008 $mol \cdot m^{-2} \cdot s^{-1}$ for $g_{s, area}$. Northern red oak had the lowest rates of both $A_{max, area}$ at 4.47 ± 0.32 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and $g_{s, area}$ at 0.066 ± 0.006 $mol \cdot m^{-2} \cdot s^{-1}$.

In late August, diurnal gas exchange rates, which were measured every 3 h between 0600 and 1500 EST, did not differ among seedlings growing in light levels ranging from 6% to 25% of full sun ($p$ values ranged from 0.11 to 0.52). Based on integral estimates, white oak fixed, on average, 122.8 ± 15.8 mol $CO_2 \cdot m^{-2} \cdot day^{-1}$, while chestnut and northern red oak fixed 132.1 ± 7.9 and 146.6 ± 15.2 mol $CO_2 \cdot m^{-2} \cdot day^{-1}$, respectively (Fig. 1). Peak $A_{max}$ rates were observed at 0900 EST for all species when PAR averaged 950 ± 66 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

**Fig. 1.** First-season diurnal photosynthesis of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings. Seedlings were relocated to a common and uniform growing environment 14 h before the start of measurements for equilibration. Because $A_{max}$ was not significantly affected by shading or soil mix, values shown were averaged across treatments for each individual species ($N = 24$ per species).
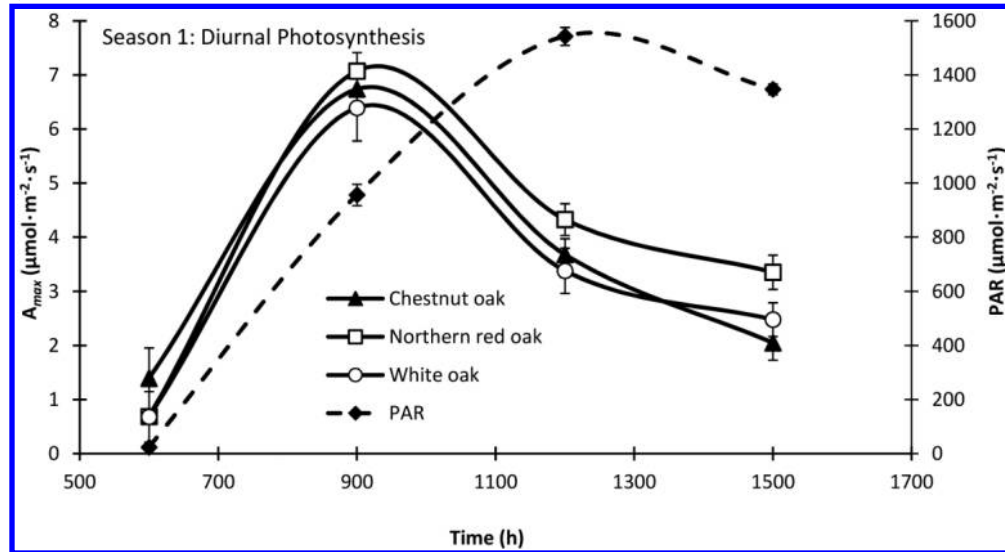


**Table 2.** Season 2 mean ± SE photosynthetic light response parameter estimates of light compensation point (LCP), maximum carbon exchange rate (CER), dark respiration (RS), and quantum efficiency (QE) of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings grown under varying shade treatments measured in late August.

| Species | LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | CER ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) | RS ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) | QE ($\mu mol \cdot \mu mol^{-1}$) |
|---|---|---|---|---|
| Chestnut oak | 19.92±2.31 | 5.73±0.50* | −1.13±0.15 | 0.062±0.002 |
| | $p = 0.318$ | ***p = 0.032*** | $p = 0.126$ | $p = 0.120$ |
| Northern red oak | 15.72±1.83 | 6.44±0.25 | −0.74±0.08 | 0.054±0.007 |
| | $p = 0.887$ | $p = 0.074$ | $p = 0.082$ | $p = 0.113$ |
| White oak | 7.16±1.39 | 7.03±0.40* | −0.32±0.07 | 0.047±0.001 |
| | $p = 0.110$ | ***p < 0.001*** | $p = 0.123$ | $p = 0.468$ |

**Note:** Probability values for ANOVA test of shade treatment effects are presented below each species mean. Eighteen seedlings per species were randomly measured with two photosynthetic readings made at each light level. Values are presented on a leaf area basis and were calculated from light response curves. Tests of significance run on leaf mass were identical.

*Chestnut and white oak maximum carbon exchange rates were significantly affected by shade treatment; refer to Fig. 2.

Effects of soil type on gas exchange were limited to white oak seedlings measured in early August. For white oak seedlings grown in WV soil mix, $A_{max, area}$ was 54% higher than those grown in the OH soil mix ($p = 0.051$). No soil by shading interaction was detected.

### Season 2

CER of both chestnut and white oak seedlings was affected by the shading treatments after two seasons (Table 2; Fig. 2). Chestnut oak seedlings grown in 25% of full sun had the highest CER ($7.52 \pm 0.74\ \mu mol \cdot m^{-2} \cdot s^{-1}$) compared with those grown in either 6% or 18% of full sun (both averaging $4.8\ \mu mol \cdot m^{-2} \cdot s^{-1}$). The opposite response was observed for white oak, with seedlings grown in 6% of full sun having the highest CER ($8.99 \pm 0.39\ \mu mol \cdot m^{-2} \cdot s^{-1}$) compared with those grown in 18% of full sun ($5.89 \pm 0.39\ \mu mol \cdot m^{-2} \cdot s^{-1}$) or 25% of full sun ($6.21 \pm 0.39\ \mu mol \cdot m^{-2} \cdot s^{-1}$). No shading effects on RS, LCP, and QE were detected for any of the three oak species.

Only light-saturated photosynthesis measured in white oak in late August (light curve measurement at $400\ \mu mol \cdot m^{-2} \cdot s^{-1}$

PAR) was significantly impacted by shading treatment (Table 3; Fig. 3). White oak seedling $A_{max, area}$ declined as light increased from 6% to 18% of full sun, with no differences detected between 18% and 25% of full sun. Northern red oak and chestnut $A_{max}$ did not change as light levels increased.

The $g_{s, area}$ of white oak seedlings also decreased as light levels increased from 6% to 18% of full sun (Table 3; Fig. 3). Shading treatments had no effect on $g_{s, area}$ of either chestnut or northern red oak seedlings, which averaged $0.096 \pm 0.017$ and $0.102 \pm 0.008\ mol \cdot m^{-2} \cdot s^{-1}$, respectively, compared with $0.120 \pm 0.021\ mol \cdot m^{-2} \cdot s^{-1}$ for white oak $g_{s, area}$.

Of the three species, white oak seedlings had the highest CER and $g_s$ and the lowest RS and LCP (Table 2). White oak LCP was $7.16 \pm 1.39\ \mu mol \cdot m^{-2} \cdot s^{-1}$ compared with $15.72 \pm 1.83$ and $19.92 \pm 2.31\ \mu mol \cdot m^{-2} \cdot s^{-1}$ for northern red and chestnut oak seedlings, respectively.

When $A_{max, area}$ at saturating light was scaled up to an individual seedling rate, white oak $A_{max, area}$ did not vary with increasing light, while chestnut and northern red oak $A_{max, area}$

**Fig. 2.** Second-season photosynthetic light response curves of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings grown in shading treatments representing 6%, 18%, and 25% of full sun. Mean estimates of light compensation point, maximum carbon exchange rate, quantum efficiency, and dark respiration derived from these curves are found in Table 2. Nine seedlings per species were measured.
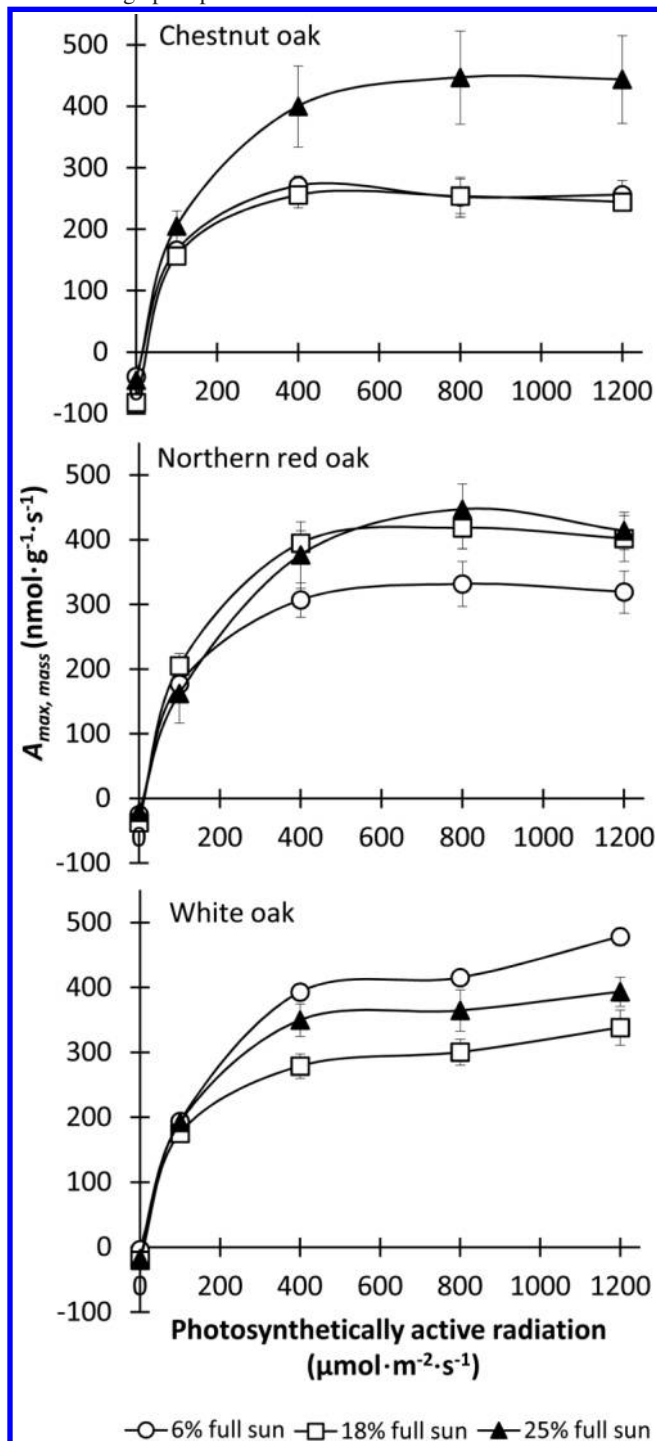


## Foliar SPAD and chlorophyll content

### Season 1

No shading effects on leaf greenness, as measured with the SPAD meter, were detected for either white or chestnut oak seedling foliage during the first season. Leaf greenness of northern red oak seedlings grown in 6% of full sun was 8% higher than for those seedlings grown in either 18% or 25% of full sun ($p = 0.019$). Mean SPAD values were 43.84 ± 0.50 for chestnut oak, 42.00 ± 0.95 for white oak, and 34.97 ± 0.95 for northern red oak seedlings in August.

### Season 2

During the second season, both SPAD and $C_{tot, mass}$ in foliage significantly decreased as light levels increased in all three species (Table 4).

The following polynomial equations were derived for each species to predict $C_{tot, mass}$ based on SPAD readings:

$$\text{Chestnut oak: } Y = 4.252 - 0.017X + 0.002X^2;$$
$$R^2 = 0.54, N = 48$$

$$\text{Red oak: } Y = 1.66 - 0.029X + 0.004X^2;$$
$$R^2 = 0.89, N = 48$$

$$\text{White oak: } Y = 4.017 - 0.077X + 0.004X^2;$$
$$R^2 = 0.84, N = 48$$

where $Y$ is total leaf chlorophyll content (milligrams per gram) and $X$ is the SPAD reading.

White oak foliage had the highest $C_{tot, mass}$ (7.84 ± 0.30 mg·g$^{-1}$) followed by chestnut oak (7.14 ± 0.20 mg·g$^{-1}$) and northern red oak (5.09 ± 0.21 mg·g$^{-1}$). White oak foliar $C_{tot, mass}$ decreased by 28% as light levels increased from 6% to 25% of full sun. Northern red and chestnut oak foliar $C_{tot, mass}$ decreased by 25% and 21%, respectively, as light levels increased from 6% to 25% of full sun. Soil mix had a significant effect on foliar $C_{tot, mass}$ of northern red and chestnut oak but not on that of white oak (Table 4). Foliar $C_{tot, mass}$ was 16% and 25% higher in chestnut and northern red oak, respectively, grown in WV soil mix compared with those grown in the OH soil mix. Because similar results for all species were observed when chlorophyll content was expressed per unit leaf area, those data are not shown.

Shading effects on the specific leaf mass varied with oak species (Table 4). White and northern red oak seedlings grown in 25% of full sun had the highest specific leaf mass relative to the other light levels, suggesting either thicker leaves or increased foliar carbohydrates with increasing light. The opposite was observed for chestnut oak, with those grown in 6% of full sun having the highest specific leaf mass (Table 4).

## Discussion

Optimizing light levels in the forest understory to allow oak advance regeneration to survive and thrive without promoting faster-growing competitive stems is crucial for maintaining sustainable mixed-oak ecosystems in the eastern United States. Our goal was to characterize the physiological

increased with increasing light (Fig. 4). Slope coefficients were similar for chestnut oak ($b = 1701.4$) and northern red oak ($b = 1135.2$), both of which were much steeper than that for white oak ($b = 72.85$).

**Table 3.** Statistical summary of Season 2 effects of shading on the photosynthesis ($A_{max}$) and stomatal conductance ($g_s$) measured at saturating light conditions (PAR at 400 µmol·m$^2$·s$^{-1}$) of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings.

| Species | Shading effect | | 6% vs. 18% and 25% of full sun | | 18% vs. 25% of full sun | |
| --- | --- | --- | --- | --- | --- | --- |
| | df | *p* | df | *p* | df | *p* |
| **Chestnut oak** | | | | | | |
| $A_{max, area}$ | 2 | 0.545 | 1 | 0.485 | 1 | 0.408 |
| $A_{max, mass}$ | 2 | 0.576 | 1 | 0.832 | 1 | 0.322 |
| $g_{s, area}$ | 2 | 0.553 | 1 | 0.350 | 1 | 0.612 |
| $g_{s, mass}$ | 2 | 0.624 | 1 | 0.455 | 1 | 0.557 |
| **Northern red oak** | | | | | | |
| $A_{max, area}$ | 2 | 0.418 | 1 | 0.327 | 1 | 0.454 |
| $A_{max, mass}$ | 2 | 0.105 | 1 | 0.060 | 1 | 0.412 |
| $g_{s, area}$ | 2 | 0.431 | 1 | 0.799 | 1 | 0.217 |
| $g_{s, mass}$ | 2 | 0.333 | 1 | 0.517 | 1 | 0.217 |
| **White oak** | | | | | | |
| $A_{max, area}$ | 2 | **0.036** | 1 | **0.014** | 1 | 0.615 |
| $A_{max, mass}$ | 2 | 0.140 | 1 | 0.086 | 1 | 0.293 |
| $g_{s, area}$ | 2 | 0.112 | 1 | **0.047** | 1 | 0.847 |
| $g_{s, mass}$ | 2 | 0.315 | 1 | 0.148 | 1 | 0.816 |

**Fig. 3.** Leaf area-based photosynthesis and leaf area-based stomatal conductance measured at saturating light (400 µmol·m$^{-2}$·s$^{-1}$) of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings grown in 6%, 18%, and 25% of full sun for two growing seasons. Probability values for tests of significance of shading effects based on per unit mass and per unit area are shown in Table 3.
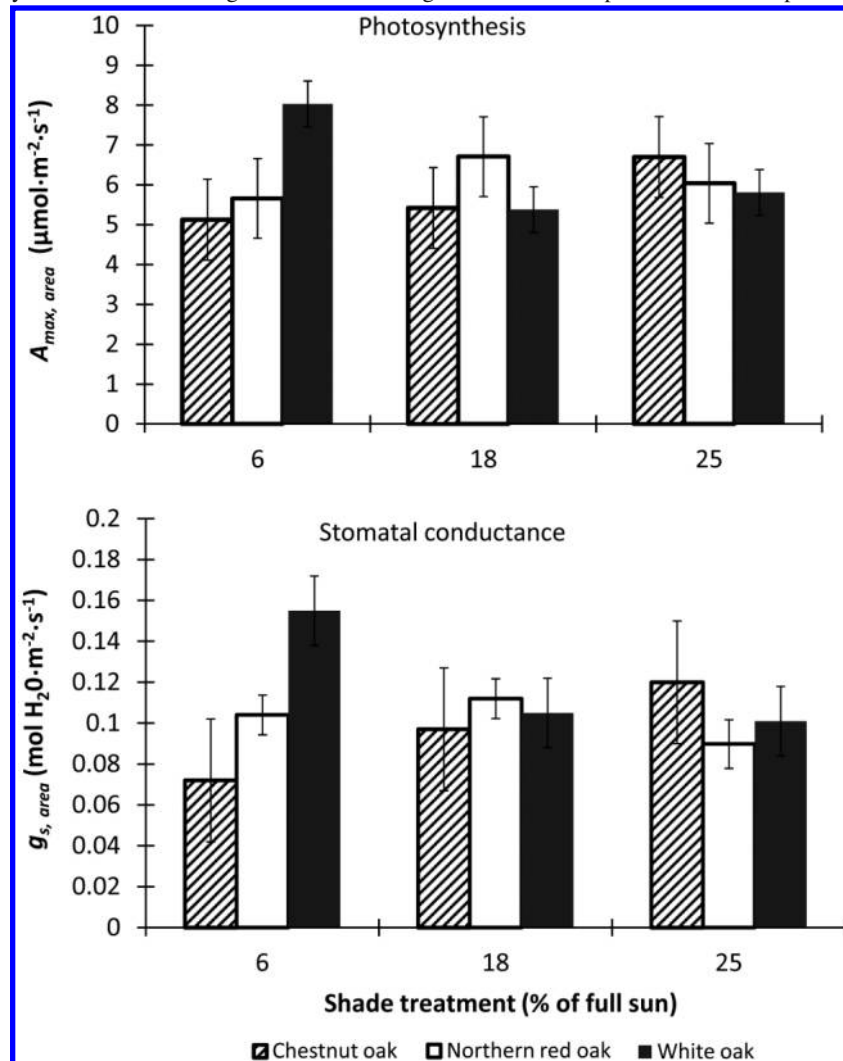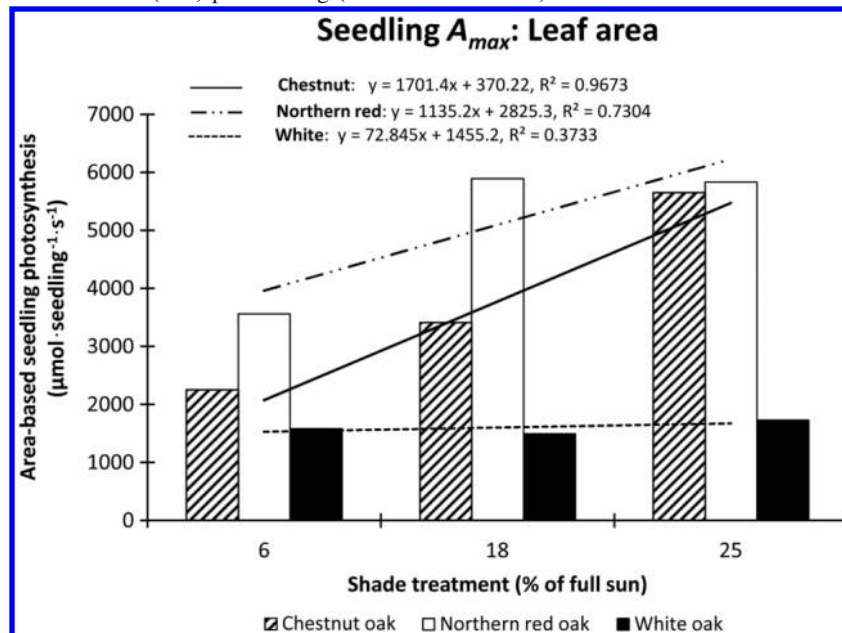
**Fig. 4.** Estimates of leaf area based photosynthesis expressed per individual seedling for chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings grown in 6%, 18%, and 25% of full sun for two growing seasons. Values were calculated using previously reported mean total leaf (cm$^2$) per seedling (Rebbeck et al. 2011).



responses of three important upland oak species during seedling establishment to light levels typically found in forest understories of untreated and shelterwood-thinned stands and to link these measures to a given oak species' growth. Physiological responses to light and soil nutrients were similar to growth and biomass allocation patterns previously reported over the 2-year study (Rebbeck et al. 2011). As we saw with the growth data, first-year physiological responses associated with shade treatments were very limited. This suggests that oak's large pool of cotyledonary reserves may have overshadowed the effects of any resource limitations such as light, nutrients, or water during the first year.

The white oak seedlings in the current study allocated about three times more carbon to root systems compared with either chestnut or northern red oak (Rebbeck et al. 2011). Kobe (1997) proposed that allocation to storage may be an effective strategy of shade tolerance because it requires less energy to translocate carbohydrates to roots under low light compared with the respiratory costs associated with producing and maintaining new shoot tissue. These energy reserves could then be used to mediate the impacts of stressors. Dillaway et al. (2007) reported that white oak seedling carbohydrates increase in roots with moderate increases in light. This conservation strategy is supported by these data, given that oaks are a disturbance-adapted group using root-centered growth as defense against fire, herbivory, drought, low fertility, low light, and frost damage. Northern red and chestnut oak seedlings also displayed a strong pattern of root-centered growth with root to shoot ratios averaging 1.6 (Rebbeck et al. 2011), which are considerably higher than root to shoot ratios of competitors such as tulip poplar at 0.37 (Kolb et al. 1990; Loats and Rebbeck 1999) and red maple at 0.39, American beech at 0.52, and trembling aspen at 0.74 (Loach 1970).

Of the three upland oaks studied, white oak appears to be the most shade tolerant. Johnson et al. (2009) stated that common upland oaks in the eastern United States are relatively shade intolerant as seedlings and suggested the following ranking based on Burns and Honkala (1990) starting with the most shade tolerant: white oak > chestnut oak > northern red oak > black oak > scarlet oak representing the least shade tolerant of the group. We agree with the relative rankings within this group of upland oak species. However, our findings suggest that oaks in the seedling stage are more shade tolerant than previously reported.

White oak seedlings had the lowest LCPs and RS rates and the highest $A_{max}$ rates and chlorophyll content of the three species studied. White oak seedlings were able to maintain a positive carbon balance in dense shade ($\sim$7 μmol·m$^{-2}$·s$^{-1}$ PAR), while chestnut and northern red oak seedlings were able to maintain carbon fixation at a PAR of ~18 μmol·m$^{-2}$·s$^{-1}$. Similar LCPs have been previously reported for all three species (Loach 1967; Bazzaz and Carlson 1982; Teskey and Shrestha 1985; Abrams 1996). The LCPs of northern red and chestnut oak were considerably lower than values reported for shade-intolerant competitors such as tulip poplar and black cherry (*Prunus serotina* Ehrh.) and shade-tolerant competitors such as sugar maple but were comparable with previous reports. In previous work, we measured a LCP of 40 μmol·m$^{-2}$·s$^{-1}$ for both black cherry and tulip poplar seedlings grown at 18% of full sun (Loats and Rebbeck 1999). LCPs of 12–41 μmol·m$^{-2}$·s$^{-1}$ have been previously reported for red and sugar maple seedlings (Abrams 1996). The differences in LCP between these oak seedlings and competitors such as tulip poplar and maple illustrate that oak seedlings can be relatively shade tolerant. We cannot predict how long these seedlings would survive at these light conditions based on our current 2-year study, but others re-

**Table 4.** Statistical summary of Season 2 effects of shading and soil mix on the specific leaf mass and foliar chlorophyll content of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings.

| Species | Shade treatment | | | Shading effect | | 6% vs. 18% and 25% of full sun | | 18% vs. 25% of full sun | | Soil effect* | | WV vs. OH soil mix | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 6% | 18% | 25% | df | *p* | df | *p* | df | *p* | df | *p* | df | *p* |
| **Chestnut oak** | | | | | | | | | | | | | |
| Specific leaf mass (g·m$^{-2}$) | 59.49±1.40 | 54.11±1.45 | 55.24±1.40 | 2 | 0.026 | 1 | 0.008 | 1 | 0.577 | 3 | 0.113 | 3 | 0.317 |
| Total chlorophyll content (mg·g$^{-1}$) | 8.30±0.25 | 6.51±0.26 | 6.58±0.25 | 2 | <0.001 | 1 | <0.001 | 1 | 0.835 | 3 | 0.004 | 1 | 0.001 |
| SPAD | 45.56±1.68 | 38.59±1.74 | 39.44±1.68 | 2 | 0.012 | 1 | 0.003 | 1 | 0.728 | 3 | 0.160 | 1 | 0.049 |
| **Northern red oak** | | | | | | | | | | | | | |
| Specific leaf mass (g m$^{-2}$) | 52.12±1.18 | 60.09±1.26 | 60.45±1.21 | 2 | <0.001 | 1 | <0.001 | 1 | 0.837 | 3 | 0.754 | 1 | 0.420 |
| Total chlorophyll content (mg·g$^{-1}$) | 6.02±0.28 | 4.75±0.30 | 4.51±0.29 | 2 | 0.001 | 1 | <0.001 | 1 | 0.570 | 3 | 0.010 | 1 | 0.002 |
| SPAD | 37.42±1.54 | 34.10±1.64 | 32.45±1.58 | 2 | 0.083 | 1 | 0.036 | 1 | 0.471 | 3 | 0.065 | 1 | 0.017 |
| **White oak** | | | | | | | | | | | | | |
| Specific leaf mass (g·m$^{-2}$) | 51.47±1.38 | 54.90±1.31 | 59.37±1.22 | 2 | 0.001 | 1 | 0.002 | 1 | 0.018 | 3 | 0.880 | 1 | 0.775 |
| Total chlorophyll content (mg·g$^{-1}$) | 9.26±0.47 | 7.83±0.45 | 6.65±0.42 | 2 | 0.001 | 1 | 0.001 | 1 | 0.062 | 3 | 0.765 | 1 | 0.364 |
| SPAD | 49.43±1.88 | 43.48±1.79 | 39.45±1.66 | 2 | 0.002 | 1 | 0.001 | 1 | 0.108 | 3 | 0.457 | 1 | 0.122 |

**Note:** Leaves from 48 seedlings of each species were sampled.

*Both chestnut and northern red oak foliage had significantly higher total chlorophyll content (8%–20%) and higher SPAD readings when grown in WV soil mix than when grown in OH soil mix.

ported low survival of northern red oak seedlings after 5–10 years in high understory shade and suggested that factors other than light contributed to the mortality (Loftis 1990; Crow 1992). Combining low LCPs and low respiration rates for white oak suggests a trade-off of fast growth for resource conservation, which would result in seedling survival in low light. Loach (1967) focused on respiration as a key physiological driver for shade tolerance for seedlings of five tree species. He suggested that it may be the most important determinant of success or failure because seedlings typically spend more time in light levels well below their LCP. In our study, white oak had the lowest respiration rates, whether expressed per unit leaf mass or leaf area, of the three oak species studied, but no significant effect of shading treatment on respiration was detected.

Although chestnut and white oak both belong to the *Quercus* section *Leucobalanus* taxonomic group, they differed in physiological responses to varying light environments. This contradicts reports by McQuilkin (1990) that they are similar in shade tolerance. Chestnut and white oak are also considered more adapted to xeric environments than northern red oak (Abrams 2003). However, we found greater similarities between chestnut and northern red oak, which had very similar $A_{max}$ and RS rates and LCPs. The $A_{max}$ rates of both chestnut and northern red oak seedlings increased as light levels increased, whereas those of white oak did not. We argue that even within a related group of species such as *Quercus*, there is a wide range of variation in physiological and growth attributes that drives its competitiveness on different types of sites. Ashton and Berlyn (1994) compared the physiological and anatomical responses of *Quercus* section *Erythrobalanus* species (black, northern red, and scarlet oak) to varying light levels and found relationships between light responses and habitat specialization. They reported that northern red oak, the most drought-intolerant species in the group, exhibited the least amount of leaf anatomical plasticity and the lowest $A_{max, area}$, while black oak, the most drought-tolerant and light-demanding species, exhibited the most leaf anatomical plasticity and the highest $A_{max, area}$ in different light conditions. Unfortunately, neither white nor chestnut oak was studied by Ashton and Berlyn (1994).

After 2 years, chestnut and northern red oak seedlings grown in 25% of full sun had 23% and 6% higher $A_{max, area}$, respectively, than those grown in 6% of full sun, and seedling mass increased (50%–54%) as light increased from 6% to 25% of full sun (Rebbeck et al. 2011). White oak seedlings showed the opposite response: $A_{max, area}$ rates were 38% lower for seedlings grown in 25% of full sun compared with those grown in 6% of full sun, and seedling mass increased 45% but plateaued at 18% of full sun. This suggests that for white oak, there would be no additional benefits to increasing light levels above 18% of full sun; it might stimulate faster-growing competitors (Gottschalk 1994; Brose 2011) These $A_{max, area}$ rates were measured at saturating light (400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR) and represent ambient light levels that can be found in shelterwood-thinned oak stands (J. Rebbeck, unpublished). These gas exchange measurements, as well as the photosynthetic parameter estimates derived from light response curves, were comparable with earlier studies using a similar life stage under similar growing conditions, regardless of whether they were expressed on a leaf mass or leaf area basis (Abrams 1996; Walters and Reich 1999). Parameter estimates derived from light response curves were not impacted by the shading treatments for northern red oak. Shading effects were detected on white and chestnut oak CERs; however, their responses were opposing. The highest CERs were observed for chestnut oak grown in 25% of full sun, while the highest CERs for white oak were observed for those grown in 6% of full sun.

When white oak $A_{max}$ rate was expressed per individual seedling leaf area, it did not change as light increased and averaged 1601 $\mu mol \cdot m^{-2} \cdot s^{-1}$. This response strongly supports that white oak seedlings are shade tolerant (Walters and Reich 1999; Reich et al. 2003). Mean individual seedling $A_{max, area}$ was 2.4 times more for chestnut oak (3773 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and 3.2 times more for northern red oak (5096 $\mu mol \cdot m^{-2} \cdot s^{-1}$) than for white oak. Individual chestnut and northern red oak seedling $A_{max}$ did increase as light levels increased, which may be more reflective of intermediate shade-tolerant to shade-intolerant species. This same pattern was also observed during the first growing season with diurnal measurements when northern red oak, followed closely by chestnut oak, fixed 1.19 times more $CO_2$ per day than white oak seedlings. When $CO_2$ fixation rates were scaled to an individual seedling level or were integrated over a day, the higher rates of $A_{max}$, combined with the observed low respiration rates, reflected a twofold difference in seedling mass (shoots plus roots) of northern red and chestnut oak compared with white oak (Rebbeck et al. 2011).

All three species displayed significant increases in $C_{tot}$ as light levels decreased, as previously reported by Loach (1967). Typically, shade leaves contain more chlorophyll than sun leaves to enhance light-harvesting capacity in low-light conditions (Boardman 1977). Probability values for tests of significance of shading and soil mix effects on $C_{tot}$ (destructively sampled) and SPAD readings were in close agreement with one exception; no soil mix effects on chestnut oak SPAD were detected. The use of the SPAD leaf greenness meter to quickly estimate chlorophyll content nondestructively in oaks shows promise as a field tool. It has been used successfully with other tree species (Chang and Robison 2003; van den Berg and Perkins 2004; Uddling et al. 2007).

Another commonly reported phenotypic response of shade leaves is a lower specific leaf mass compared with sun leaves of oaks and non-oak species (Abrams and Kubiske 1990; Gottschalk 1994; Reich et al. 2003). Lower specific leaf mass was observed for foliage of northern red and white oak seedlings grown in low light, confirming that these shade leaves were thinner than leaves grown in higher light. Typically, thinner leaves capture more light per unit area with less investment in leaf tissue compared with sun leaves. Chestnut oak seedlings grown in 6% of full sun, on the other hand, displayed an opposite and atypical response. These shade-grown chestnut oak leaves had significantly greater specific leaf mass than the higher-light treatments. No other reports of this novel response to low-light conditions were found and may warrant further investigation.

Effects of soil mix on gas exchange measurements during the first season were limited to white oak photosynthesis in early August (two times higher rates for WV soil grown seedlings). Because no soil mix effects were detected during the two subsequent sampling periods in the first season, gas

exchange rates were measured only on WV soil grown seedlings in Season 2. We did, however, test for soil effects on $C_{tot}$ and specific leaf mass. Soil mix had no effect on specific leaf mass of any of the three oak species. Northern red and chestnut oak seedlings grown in the WV soil mix did have higher $C_{tot}$, most likely due to the increased levels of water-extractable nitrate, calcium, potassium, and magnesium (Rebbeck et al. 2011). No effects of soil mix on $C_{tot}$ were detected in white oak. Of the three species studied, chestnut oak growth was the most responsive to the increased nutrient availability of the WV soil mix as light levels increased (Rebbeck et al. 2011). Stimulatory responses were also observed for chestnut oak $A_{max}$ and $C_{tot}$. Although chestnut oak is typically found on xeric, infertile rocky ridges, it does grow best on rich, well-drained soils along streams. Our hypothesis that additional nutrients could enhance seedling physiology and growth was only supported for chestnut oak.

Consistent across species and independent of the light environment that seedlings grew in for 2 years, the light saturation point of photosynthesis occurred between 18% and 25% of full sun, although white oak grown at lower light levels displayed some plasticity. Previous studies investigating the response of black and northern oak seedlings to varying light levels reported that these same light levels result in a plateau of biomass and growth (Phares 1971; Gottschalk 1985; Kaelke et al. 2001). This suggests that the photosynthetic capacity is saturated with no additional benefits afforded to oaks. If light levels are higher, only faster-growing shade-intolerant competitors such as red maple and black cherry, which display more plastic growth responses, would benefit (Gottschalk 1994).

The findings reported corroborate previous ecophysiological studies on oak seedlings (Loach 1967; Walters et al. 1993; Abrams 1996). The interpretation of these results does require some caution because the light treatments were not replicated. However, the environmental conditions, including light levels and air temperatures, were monitored and found to be uniform in a given shade tent. We are confident that the observed physiological responses of the three oak species do reflect differences in light intensities among the shade tents.

## Summary

The three upland oak species that we studied expressed attributes associated with shade-tolerant species. This is contrary to previous reports that white and chestnut oak are both intermediate and more tolerant of shade than northern red, black, or scarlet oak (McQuilkin 1990). Kaelke et al. (2001) reported that northern red oak seedlings exhibit more shade-tolerant than shade-intolerant attributes. In the current study, white oak seedlings displayed a different suite of physiological and growth attributes compared with the faster-growing chestnut and northern red oak seedlings, which may enhance its ability to persist in low-light environments until a light-creating disturbance occurs. Given the observed high $A_{max}$ rates and foliar $C_{tot}$ and the low LCPs and RS rates, white oak appears to have the potential to maintain positive carbon gain under denser shade compared with either chestnut or northern red oak seedlings. White oak's physiological attributes as well as its slow growth and extended longevity

(up to 600 years) support a survival strategy that is unique to that of other upland oak species.

It has been suggested that because oaks have the potential to persist in low-light environments, there must be other factors contributing to oak regeneration failures. Observed declines in oak regeneration are often attributed to the absence of fire for the past 80 plus years and increased deer herbivory (Abrams 1996; Kaelke et al. 2001; McEwan et al. 2011). These are plausible explanations for the multidecades-long trend of failing oak seedling regeneration but can vary substantially with site and geographic location.

Reintroduction of recurring fire or its surrogate, such as stem-injection herbicide applications, to reduce or eliminate faster-growing, fire-intolerant, competing woody vegetation in advance of a harvest has the potential to improve oak regeneration in mixed-oak forests (Miller et al. 2004; Hutchinson et al. 2005). Hutchinson et al. (2005) reported that closed-canopy, low-light conditions (<6% of open sky) persisted after a series of multiple low-intensity fires and failed to improve oak regeneration. However, oak seedling vigor did increase within these burned areas after a synchronous mortality of overstory white oak created moderately sized canopy gaps (200–400 m$^2$) with light levels averaging 19% full sun in the burned areas compared with 7% of full sun in comparable gaps in adjacent unburned areas (Hutchinson et al. 2012). Studies conducted in eastern North America reported that long-term frequent prescribed fires are needed to improve oak competitiveness and persistence (Dey and Fan 2009).

To target white oak seedling regeneration, we propose that light levels need not be increased above 18% of full sun; to target chestnut and northern red oaks, light levels need not be increased above 25% of full sun. These light levels could be achieved by cutting 35%–40% of the stand basal area in a shelterwood harvest. Dillaway et al. (2007) reported that white oak seedling root diameter and soluble nonstructural carbohydrate levels increased with increasing light environments associated with midstory thinning and clearcuts. This supports our findings that white oak seedlings respond positively to fairly small increases in light. In addition, faster-growing competing vegetation must be reduced or eliminated (Brose 2011) with a series of multiple low-intensity prescribed burns before the overstory or midstory is thinned or removed (Hutchinson et al. 2012). Because the use of fire to reduce competing vegetation is difficult on mesic sites, the use of herbicides may be most effective. If the advance regeneration pool is composed primarily of sprout-origin stems, a higher target light level may be appropriate because the stock should have a well-developed root system. However, regardless of the method used to reduce competition, it will be a lengthy process to reverse 80 plus years of highly successful fire-suppression programs across the extensive geographic range of these upland oak species.

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