

# Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? Growth and biomass

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**Abstract:** Northern red oak (*Quercus rubra* L.) seedling growth has been extensively studied. White oak (*Quercus alba* L.) and chestnut oak (*Quercus prinus* L.), however, are far less investigated despite their importance among upland oak species in eastern North American forests. We characterized white and chestnut oak seedling response to light and available soil nutrients while using northern red oak as a benchmark. Germinants were grown within one of three shade treatments (25%, 18%, and 6% of full sun) in one of two native forest soil mixes over two growing seasons. Leaf area, shoot mass, and root mass of all three species showed positive growth responses to increasing light. Growth and biomass were higher for all species grown in the more nutrient-rich forest soil, but chestnut oak displayed the greatest positive responses to the higher nutrient levels. White oak seedlings were the slowest growers and demonstrated the most root-centered growth, with root to shoot ratios almost twice that of either chestnut or northern red oak seedlings. The oak species evaluated here responded differently to changes in resource availability. Our study demonstrates the differential response of upland oaks to low light and nutrients. These differences need consideration when developing oak management prescriptions for specific oaks.

**Résumé :** La croissance des semis de chêne rouge (*Quercus rubra* L.) a fait l'objet de plusieurs études. Toutefois, le chêne blanc (*Quercus alba* L.) et le chêne châtaignier (*Quercus prinus* L.) ont été beaucoup moins étudiés malgré leur importance parmi les espèces de chêne de milieu sec dans les forêts de l'est de l'Amérique du Nord. Nous avons caractérisé la réaction des semis de chêne blanc et de chêne châtaignier à la lumière et à la disponibilité des nutriments du sol en utilisant le chêne rouge comme référence. Les germinants se sont développés pendant deux saisons de croissance dans un des trois traitements d'ombre (25 %, 18 % et 6 % de la pleine lumière) et dans un des deux mélanges de sol forestier prélevés in situ. La croissance en surface foliaire, en biomasse des pousses et en biomasse racinaire des trois espèces a augmenté avec la disponibilité de la lumière. La croissance et la biomasse des trois espèces étaient plus élevées dans le sol forestier le plus riche, mais dans de telles conditions, la réaction du chêne châtaignier a été la plus forte. La croissance des semis de chêne blanc était la plus lente et la plus axée vers le développement racinaire avec un rapport entre la biomasse racinaire et celle des pousses presque deux fois plus élevé que ceux des semis de chêne châtaignier et de chêne rouge. Les espèces de chêne de la présente étude ont réagi différemment aux changements de disponibilité des ressources. Notre étude démontre que les chênes de milieu sec réagissent différemment à la faible disponibilité de lumière et de nutriments. Ces différences méritent d'être considérées pour mettre au point des prescriptions sylvicoles propres aux différentes espèces de chêne.

[Traduit par la Rédaction]

## Introduction

A continuing problem in the Appalachian region of eastern North America is the sustainability and regeneration of oak species within forests as overstory oaks are eliminated through natural mortality or harvesting. Typically, stand composition shifts to more shade-tolerant species such as red maple (*Acer rubrum* L.) and American beech (*Fagus grandifolia* Ehrh.) because of an inadequate number of competitive oak seedlings (Abrams and Downs 1990; Brose et al. 1998). Many factors have been implicated in the failure of oak regeneration, but the most common and widespread across eastern North America are the elimination of recurring fires

and the subsequent development of dense, low-light understories resulting from the growth of shade-tolerant and fire-sensitive species (Crow 1988; Abrams 1996; Buckley et al. 1998).

*Quercus* species produce large seeds that are typically few in number with short-lived viability. Large oak germinants have a high chance of establishing and growing quickly in the first year as stored cotyledon starch reserves are depleted. Following initial establishment, oaks typically display slow aboveground growth relative to the numerous fast-growing small-seeded competitors such as red maple, tulip poplar (*Liriodendron tulipifera* L.), and birch (*Betula* species) (Quero et al. 2007). Oaks, intermediate in shade tolerance,

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are more inflexible morphologically and physiologically than shade-intolerant competitors, which allocate more carbon to shoot growth (Kolb et al. 1990). Oaks' root-centered growth serves as an adaptive strategy to limiting resources and high-disturbance environments like low moisture and frequent fires. Generally, as the quality of a site increases, competition with faster growing species increases, making oak regeneration particularly challenging on fertile mesic sites (Johnson et al. 2009). A basic understanding of how different oak species acquire and utilize potentially limiting resources such as light and soil nutrients is needed to better manage and maintain a viable oak component within eastern mixed-oak forests. Over the past several decades, factors affecting northern red oak (*Quercus rubra* L.) regeneration, and in particular seedling growth and physiology, have been extensively studied (Phares 1971; Farmer 1975; Isebrands and Dickson 1994). However, white oak (*Quercus alba* L.) and chestnut oak (*Quercus prinus* L.) are far less studied than northern red oak despite their ecological and economic importance among upland oak species and the difficulties of sustaining them in eastern forests due to failures in regeneration.

Upland oak species demonstrate variable responses to light and soil fertility as is evidenced by differences in geographic distribution and adaptability to diverse site conditions. White and northern red oak are common across many sites and climates, spanning the Great Lakes, Central Plains, Midwest, Mid-Atlantic, Southeast, and Northeast regions of North America (Rogers 1990; Sander 1990). Chestnut oak is limited in distribution to the Northeast, Midwest, and Southeast Appalachian regions and is most commonly found on rocky ridges with dry, infertile soils (McQuilkin 1990). Most upland oak species possess adaptations to grow and dominate on xeric sites but have the potential to grow best on rich, well-drained sites. 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 the three, white oak is the slowest growing and the longest lived, while northern red oak is moderate to fast growing. 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, all of which 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. We observed differences in foliar gas exchange rates and chlorophyll content among chestnut, northern red, and white oak seedlings grown in varying light environments (Rebbeck et al. 2001; Rebbeck and Gottschalk 2010). The oak species studied here are classified as intermediate in shade tolerance, with white oak ranking as the most shade tolerant followed by chestnut and northern red oak (McQuilkin 1990; Rogers 1990; Sander 1990). The accumulation of large oak advance reproduction in heavily shaded forest understories is a widely recognized limiting factor in sustaining future oak stocking on all but the most xeric sites (Loftis 1990). Our primary goal was to test the hypothesis that an upland oak species' response to shading and soil fertility is related to growth and physiological attributes, which drive its competitiveness on different types of sites. A second objective was to determine

the influence of seed source on each species' response to varying light and soil nutrients.

## Materials and methods

### Acorn collections

Acorns of northern red oak, chestnut oak, and white oak were collected during fall 1998 from eight sites in Monongalia and Tucker counties, West Virginia, following a heavy seed masting. To test the influence of seed source on seedling growth, acorns were collected and identified by maternal tree and site. All species were not present at all collection sites, and number of maternal trees per site varied with species. Northern red oak acorns were collected from seven maternal trees at three sites with one, two, or four trees at a given site. Chestnut oak acorns were collected from six maternal trees at two sites with two or four trees at a given site. Acorns from 13 white oak maternal trees were collected at four sites with one, three, four, or five trees at a given site. The acorns from each individual maternal tree were floated to identify and remove unsound seeds. Acorns were then maintained at 15 °C within sealed plastic bags containing damp sphagnum moss and activated charcoal (Schopmeyer 1974) until planting the following spring. Chestnut and white oak, members of the taxonomic group *Quercus* section *Quercus* (white oak group), have acorns that mature in one growing season. Root radicles rapidly emerge in the autumn, but the immature stem (epicotyl) does not develop until the following spring (Johnson et al. 2009). Northern red oak, a member of the group *Quercus* section *Lobatae* (red oak group), has acorns that require 2 years to mature with embryos that remain dormant until the next spring (Johnson et al. 2009).

### Plant culture and shade treatments

On 3–4 May 1999, all stored northern red oak acorns were refloated and sorted to remove dead, weevil-infested, or deformed individuals to maintain uniformity within each source. Chestnut and white oak acorns were further sorted to remove desiccated or dead (those with no viable root radicles) individuals. Two acorns per pot were planted in 15 cm diameter by 41 cm tall (7.25 L) PVC pots containing a 1:1:1 mix of forest soil, peat moss, and horticultural-grade perlite. Soils had been collected in fall 1998 from two oak-dominant forests to prepare the growing media. A sandy loam to silt-loam (Steinsburg–Gilpin Series) was collected in Vinton County, Ohio, and a mixed fine loam (Buchanan–Ernest Series) was collected in Monongalia County, West Virginia. Water extracts of the soil mixes were chemically analyzed for macro- and micronutrients, pH, and cation-exchange capacity by the University of Maine Analytical Laboratory and Maine Soil Testing Service (Table 1). The amount of plant-available nitrate was  $17.33 \pm 4.89$  mg·kg<sup>-1</sup> in the West Virginia (WV) soil mix and  $1.00 \pm 0$  mg·kg<sup>-1</sup> in the Ohio (OH) soil mix. Ammonium levels were not determined for the two soil mixes but were for the native forest soils using a modified Morgan ammonium acetate extraction and concentrations were found to be quite different. The OH forest soil had concentrations of  $31.00 \pm 1.73$  mg·kg<sup>-1</sup> ammonium compared with the WV forest soils at  $6.00 \pm 0$  mg·kg<sup>-1</sup>. These levels of ammonium and nitrate are within ranges

**Table 1.** Soil pH, cation-exchange capacity (CEC), and chemical nutrient concentrations of Ohio (OH) and West Virginia (WV) soil mixes (1:1:1 mix of forest soil, peat moss, and horticultural-grade vermiculite) from water extracts.

Parameter	OH forest soil ( <i>N</i> = 3)	OH soil mix ( <i>N</i> = 6)	WV forest soil ( <i>N</i> = 6)	WV soil mix ( <i>N</i> = 3)
pH		4.33±0.05		4.5±0.58
CEC (cmol kg <sup>-1</sup> )		5.60±0.10		5.83±0.15
Phosphorus (mg·kg <sup>-1</sup> )		0.70±0.00		0.40±0.16
Potassium (mg·kg <sup>-1</sup> )		5.33±0.47		7.00±3.74
Calcium (mg·kg <sup>-1</sup> )		7.67±0.47		20.67±7.17
Magnesium (mg·kg <sup>-1</sup> )		4.33±0.47		7.83±4.75
Aluminum (mg·kg <sup>-1</sup> )		4.97±2.09		5.72±3.05
Manganese (mg·kg <sup>-1</sup> )		0.57±0.11		2.20±2.34
Nitrate (mg·kg <sup>-1</sup> )	2.00±0.00	1.00±0.00	13.00±0.00	17.33±4.89
Soil ammonium (mg·kg <sup>-1</sup> )	31.00±1.73		6.00±0.00	

**Note:** Data are means ± 1 SD. Mean nitrate and ammonium concentrations were measured in sodium acetate extracts (modified Morgan extraction) in forest soils collected in Ohio and West Virginia. Ammonium was not measured in the soil mixes. The water extract values provided for the two soil mixes represent plant available nutrients. Random samples of each soil type were collected and analyzed.

previously reported for the same watershed within south-eastern Ohio and for similar areas within West Virginia (Boerner and Sutherland 1995). With the exception of soil ammonia and phosphorus, all other nutrients were higher in the WV soil mix. Six hundred pots of northern red oak, 600 of chestnut oak, and 500 of white oak acorns were planted, with half containing the OH soil mix and half containing the WV mix. Pots were maintained within a greenhouse until early May. During that period, date of emergence for each pot was recorded. 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 each light level and soil mix combination at the start of the treatments.

The potted germinants were placed under black polypropylene greenhouse shade cloth (Sundance Supply Co., Olga, Washington) in three shade tents (each 3.1 m × 7.3 m) erected at the US Forest Service Northern Research Station's Forestry Sciences Laboratory in Delaware, Ohio (40° 21'N, 83°04'W). Germinants of northern red oak, 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, and the pots of white oak, the shortest of the group, were positioned in the most southern section (one fifth of the tent area). Three target light levels were selected to simulate understory conditions found in mixed-oak forests: 8% of full sunlight to represent deep shade in unthinned stands and 20% and 27% to represent understory light after either a light or a moderate shelterwood cutting, respectively (Gottschalk 1994). Higher light levels, more reflective of a heavy shelterwood cutting, were not included because the intent was to characterize oak seedling growth under low-light conditions, when the interference of potential non-oak competitors might be low. Actual light levels measured within the shade tents were 6%, 18%, and 25% of full sunlight. Although the shade cloth created uniform light, it does not represent actual forest light conditions because of the lack of sun flecks and other light

quality characteristics such as the red to far red light ratio. A 1.3 m high welded-wire fence reinforced with trenched poultry netting was erected around the perimeter of the study area to minimize rodent damage and deter deer browsing. Each pot was thinned to one seedling in early June. Seedlings were regularly hand watered to saturation to maintain uniform soil moisture across all shading treatments. Gravimetric soil moisture was measured at least once weekly on a random subset of pots for each species within each shade treatment. Once soil moisture was determined, pots were watered to saturation. Given that the pots grown in 25% of full sunlight were exposed to more solar radiation, they sometimes required more frequent watering to maintain equivalent moisture levels compared with the two other shade treatments. The treatments were maintained through late October 1999 and seedlings were subsequently housed within an unheated building until the following spring for protection from severe weather and rodents. The experiment resumed in early May 2000 and continued through late September 2000.

Ambient photosynthetic photon fluence rate over the 400–700 nm waveband (using both LI-COR (Lincoln, Nebraska) quantum sensors and Hamamatsu Photonics (Hamamatsu City, Japan) GaASP photodiodes, model G1118) and percent relative humidity (%RH) (Hydrometrix RH sensor) and air temperature (Fenwal Electronics UUT51J1 thermistor) were monitored continuously with a Campbell 21X datalogger (model XN217; Campbell Scientific, Logan, Utah) within each shade tent and in the open. Periodically under both cloudy (*N* = 9) and sunny conditions (*N* = 8), photosynthetically active radiation (PAR) was measured at six positions within each shade tent using a hand-held LI-COR quantum sensor to determine if light levels varied within each shade treatment. Mean daily (0800–2000 EST) PAR during both growing seasons differed among the shading treatments. On sunny days, PAR readings averaged 82 ± 2, 253 ± 98, 279 ± 137, and 1502 ± 597 μmol·m<sup>-2</sup>·s<sup>-1</sup> in 6%, 18%, 25%, and 100% (outside the tents) of full sun, respectively. On cloudy days, PAR readings averaged 59 ± 27, 118 ± 72, 189 ± 104, and 580 ± 49 μmol·m<sup>-2</sup>·s<sup>-1</sup> in 6%, 18%, 25%, and 100% (unshaded outside) of full sun, respectively. Sea-

sonal mean air temperatures inside shade tents were within 1.1 and 0.3 °C of each other in 1999 and 2000, respectively. Little difference in air temperature was detected between the shade tents and the adjacent unshaded (full sun) area during either season.

### Growth measurements

Stem height, basal diameter, leaf number, and flush number of each seedling were measured each growing season. Seedlings were destructively harvested in September 2000 after two full growing seasons. Final growth measurements were made just prior to the destructive harvest. Total leaf area (leaf blade plus petiole) per seedling was determined with a LI-3100 area meter (LI-COR). Tissue was then separated into roots, leaves, stem, and branches, oven-dried at 70 °C to constant mass, and weighed to determine stem, leaf, and root mass. Root to shoot ratio and leaf mass per unit area were calculated and specific leaf area (SLA) was determined by dividing leaf area by dry mass.

### Statistical design and analysis

The study was a nested design with shade treatment as the main factor and soil type and seed collection site nested within shade treatment for each individual oak species. Seedling height, diameter, leaf area, and mass data were analyzed with general linear mixed models (GLMM) via GLIMMIX to test for shading, soil, and seed source effects (SAS Institute Inc. 2008). All variables in the models were considered as fixed effects. Mean values for each seed source (individual maternal tree), soil, and shade combination were used as the sampling unit to avoid pseudoreplication. Using the SAS UNIVARIATE procedure, each variable for each species was tested for normality using the Shapiro–Wilk statistic. Those variables with a gamma distribution were log-transformed within a GLIMMIX model (see Table 3 for details). All variables of chestnut oak were normally distributed. Because of the nested design, direct tests of soil and seed source could not be made; instead, specific contrasts were developed to include OH versus WV soil, 6% of full sun versus 18% and 25% of full, and 18% versus 25% of full sun. Given the complexity of the statistical design, no direct comparisons among the species were made. Effects were considered significant if  $p \leq 0.05$ . Due to the small number of white oak germinant seedlings per individual maternal tree (seed source), trees at a given site were grouped ( $N = 4$  sites) and site was tested.

## Results

### Seedling response to shading

#### Season 1

Significant differences in shoot height and basal stem diameter attributable to shading were detected after one growing season (Table 2). White oak seedlings were approximately half the height of chestnut and northern red oak seedlings. The effects of shading on white oak were limited to smaller basal diameter of seedlings grown in 6% of full sun compared with either 18% or 25% of full sun. Chestnut and northern red oak seedling growth responded positively to increasing light. Both shoot height and basal diameter of northern red oak were 12.5% lower in 6% of full

sun compared with those grown at 25% of full sun. Chestnut oak seedlings grown in 6% of full sun had 23% shorter shoots and 9% smaller basal stem diameters than those grown in 25% of full sun.

#### Season 2

The breaking of dormancy in spring 2000 was unaffected by the previous growing season shade treatment but varied with species. Dormant white oak seedlings broke bud more sporadically than the other two species, covering a wider range of dates with 23% from 3 to 5 April and 47% from 12 to 17 April. The majority of chestnut oak seedlings resumed growth the earliest (80% broke dormancy from 3 to 5 April), while the majority of northern red oak seedlings resumed growth several days later (75% from 12 to 17 April).

All species showed positive growth responses to increasing light, although the magnitude of those responses varied with species (Fig. 1). White oak seedling basal diameter increased 15% and leaf area increased 30% for seedlings grown in either 18% or 25% of full sun compared with those grown in 6% of full sun (Fig. 1a). No significant mass or growth differences were detected between white oak grown in 18% and 25% of full sun treatments (Fig. 1a). White oak leaf, stem, and root mass increased 32%–49% for seedlings grown in either 18% or 25% of full sun compared with those grown in 6% of full sun (Table 3).

Chestnut oak shoot height, basal stem diameter, and leaf area increased 45%, 35%, and 95%, respectively, for seedlings grown in 25% of full sun compared with those grown in 6% of full sun (Fig. 1b). Chestnut oak leaf, stem, and root mass increased between 51% and 55% as light levels increased from 6% to 25% of full sun (Table 3). Significant differences were detected for most chestnut oak growth and mass parameters as light increased from 18% to 25% of full sun.

Northern red oak shoot height and basal stem diameter increased 25%, while leaf area increased 55% for seedlings grown in 25% of full sun compared with those grown in 6% of full sun (Fig. 1c). Northern red oak leaf, stem, and root mass increased between 43% and 55% for seedlings grown in 25% of full sun compared with those grown in 6% of full sun (Table 3).

After two growing seasons, chestnut and northern red oak biomass was approximately twice as large as white oak seedling biomass (Table 4). The mean seedling mass (sum of leaf, stem, and root) of northern red oak was  $18.8 \pm 0.4$  g, of chestnut oak was  $14.8 \pm 0.4$  g, and of white oak was  $8.8 \pm 0.4$  g. Overall, chestnut and northern red oak seedlings showed greater increases in shoot height, basal stem diameter, and leaf area with increasing light levels compared with white oak.

SLA was similar across species with SLA decreasing as light increased. Chestnut oak SLA decreased from  $217 \pm 5$  to  $204 \pm 5$   $\text{cm}^2\cdot\text{g}^{-1}$  as light increased from 6% to 25% of full sun ( $p < 0.001$ ). Northern red oak SLA decreased from  $207 \pm 2$  to  $189 \pm 2$   $\text{cm}^2\cdot\text{g}^{-1}$  from 6% to 25% of full sun ( $p < 0.001$ ). White oak SLA decreased from  $210 \pm 3$  to  $188 \pm 3$   $\text{cm}^2\cdot\text{g}^{-1}$  from 6% to 25% of full sun ( $p = 0.001$ ).

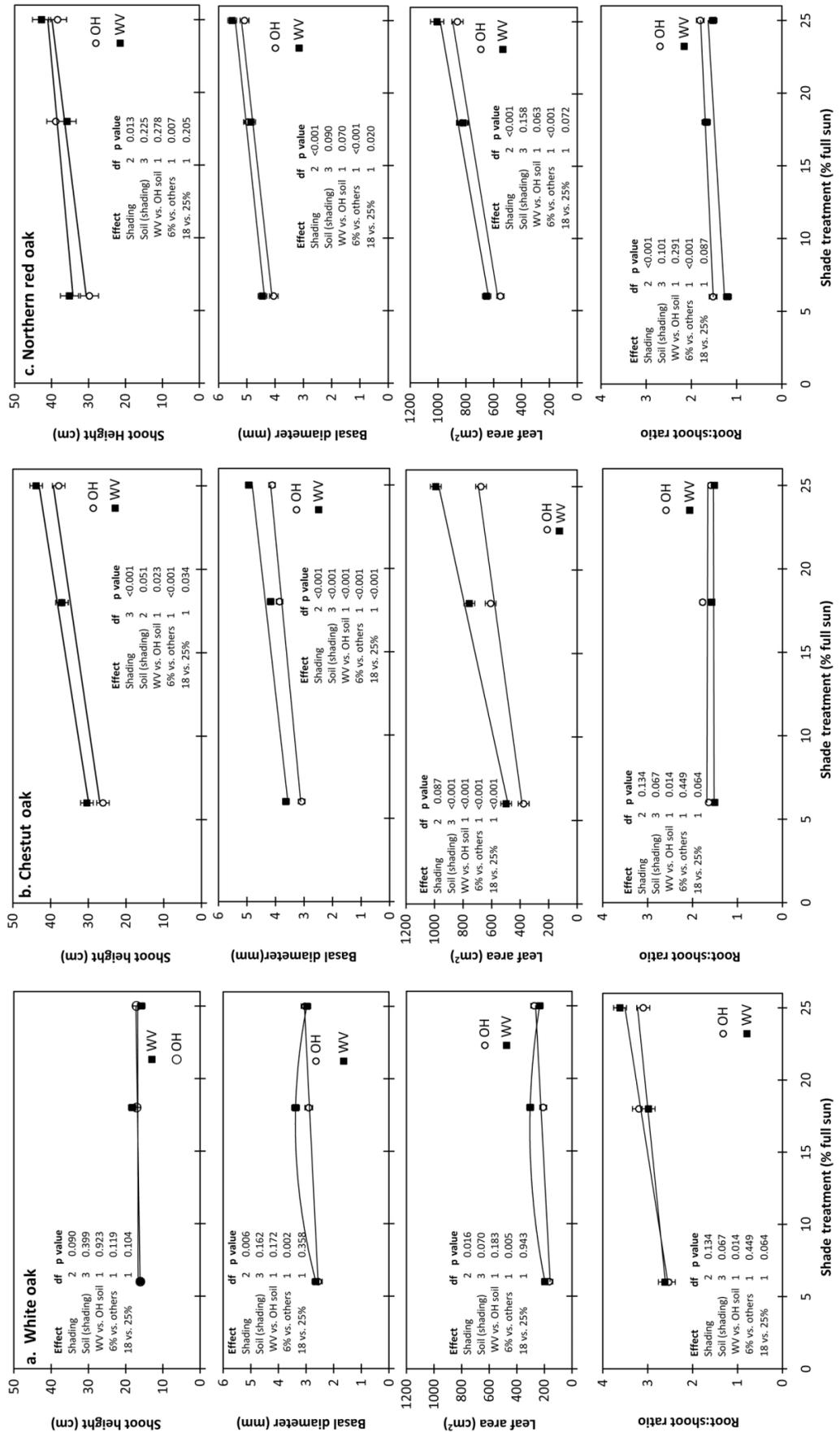
The root mass of all three species increased significantly (49%–55%) as light levels increased, but only white oak allocation patterns changed. Although absolute growth was much lower for white oak compared with northern red or chestnut

**Table 2.** Season 1: least square means  $\pm$  SEM and statistical summary of shading, soil (WV, West Virginia; OH, Ohio), and seed source (cohort or site) effects on the growth of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings.

	Least square means shading treatment (% of full sun)							Soil effect (df, p)	WV vs. OH soil (df, p)	Seed source effect (df, p)
	6%	18%	25%	Shading effect (df, p)	6% vs. 18% and 25% of full sunlight (df, p)	18% vs. 25% of full sunlight (df, p)				
<b>Chestnut oak</b>										
Seedling height (cm)	13.49 $\pm$ 0.35a	16.33 $\pm$ 0.35b	17.61 $\pm$ 0.35b	2, <0.001	1, <0.001	1, 0.022	3, 0.096	1, 0.017	15, <0.001	
Basal diameter (mm)	2.31 $\pm$ 0.04a	2.51 $\pm$ 0.04b	2.56 $\pm$ 0.04b	2, <0.001	1, <0.001	1, 0.351	3, 0.557	1, 0.277	15, 0.011	
<b>Northern red oak</b>										
Seedling height (cm)	15.88 $\pm$ 0.41a	17.13 $\pm$ 0.41ab	18.0 $\pm$ 0.41b	2, 0.006	1, 0.004	1, 0.145	3, <0.001	1, <0.001	18, 0.063	
Basal diameter (mm)	3.12 $\pm$ 0.03a	3.46 $\pm$ 0.03b	3.56 $\pm$ 0.03b	2, <0.001	1, <0.001	1, 0.063	3, 0.002	1, 0.025	18, <0.001	
<b>White oak</b>										
Seedling height (cm)	8.88 $\pm$ 0.36a	9.48 $\pm$ 0.36a	8.59 $\pm$ 0.36a	2, 0.247	1, 0.745	1, 0.107	3, 0.375	1, 0.244	12, 0.135	
Basal diameter (mm)	1.84 $\pm$ 0.06a	2.10 $\pm$ 0.06b	2.04 $\pm$ 0.06b	2, 0.038	1, 0.014	1, 0.504	3, 0.681	1, 0.788	12, 0.076	

**Note:** Soil and seed source effects were tested as nested within shading. Due to the small number of white oak germinant seedlings per individual mother tree (seed source), mother trees at a given site were grouped ( $N = 4$  sites). Chestnut oak was represented by six seed source trees at two sites and northern red oak by seven seed source trees across three sites. Means of a given species followed by the same letter are not significantly different from the Tukey–Kramer mean separation test at  $\alpha = 0.05$ .

**Fig. 1.** Mean seedling height, basal diameter, and leaf area per seedling of (a) white oak (*Quercus alba*), (b) chestnut oak (*Quercus prinus*), and (c) northern red oak (*Quercus rubra*) seedlings grown under shade treatments at 6%, 18%, and 25% of full sun and in growing media mix containing either Ohio or West Virginia native forest soils for two growing seasons. A summary of PROC GLIMMIX analyses (*p* value and *df*) for each growth variable tested for each individual species is shown on each panel: shading effects and soil effects nested within shading were tested. Contrasts tested the following: (i) differences between the two soil types, WV versus OH soil, (ii) low light (6% of full sun) versus all other levels (18% and 25% of full sun), and (iii) intermediate light (18% of full sun) versus high light (25% of full sun). Chestnut oak was represented by six seed sources and northern red oak by seven seed sources. Due to the small number of white oak germinant seedlings per individual maternal tree (seed source), mother trees at a given site (*N* = 4) were grouped and tested for the seed source effects.



**Table 3.** Season 2: least square means  $\pm$  SEM and statistical summary of shading, soil (WV, West Virginia; OH, Ohio), and seed source (cohort or site) effects on leaf, stem, and root mass of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedlings.

		Least square means shading treatment (% full sun)									
		6%	18%	25%	Shading effect (df, p)	6% vs. 18% and 25% of full sunlight (df, p)	18% vs. 25% of full sunlight (df, p)	Soil effect (df, p)	WV vs. OH soil (df, p)	Seed source effect (df, p)	
<b>Chestnut oak</b>											
Leaf mass (g dry mass)	OH	1.71 $\pm$ 0.20d	3.03 $\pm$ 0.20bc	3.40 $\pm$ 0.20b	2, <0.001	1, <0.001	1, 0.001	3, <0.001	1, <0.001	15, 0.068	
	WV	2.29 $\pm$ 0.20cd	3.66 $\pm$ 0.20b	4.89 $\pm$ 0.20a							
Stem mass (g dry mass)	OH	1.19 $\pm$ 0.19c	2.25 $\pm$ 0.19b	2.34 $\pm$ 0.19b	2, <0.001	1, <0.001	1, 0.003	3, <0.001	1, <0.001	15, 0.019	
	WV	1.87 $\pm$ 0.19c	2.67 $\pm$ 0.19b	3.93 $\pm$ 0.19a							
Root mass (g dry mass)	OH	4.56 $\pm$ 0.49c	9.47 $\pm$ 0.49b	9.54 $\pm$ 0.49b	2, <0.001	1, <0.001	1, <0.001	3, <0.001	1, <0.001	15, 0.002	
	WV	6.05 $\pm$ 0.49c	9.98 $\pm$ 0.49b	14.12 $\pm$ 0.49a							
<b>Northern red oak</b>											
Leaf mass (g dry mass)*	OH	2.65 $\pm$ 0.13c	4.36 $\pm$ 0.21b	4.60 $\pm$ 0.22ab	2, <0.001	1, <0.001	1, 0.002	3, 0.018	1, 0.042	18, 0.011	
	WV	3.12 $\pm$ 0.15c	4.05 $\pm$ 0.19b	5.45 $\pm$ 0.26a							
Stem mass (g dry mass)*	OH	1.79 $\pm$ 0.10d	3.28 $\pm$ 0.19ab	3.33 $\pm$ 0.19ab	2, <0.001	1, <0.001	1, 0.012	3, 0.003	1, 0.007	18, 0.005	
	WV	2.40 $\pm$ 0.14c	3.04 $\pm$ 0.18ab	4.12 $\pm$ 0.24a							
Root mass (g dry mass)*	OH	6.51 $\pm$ 0.25c	12.57 $\pm$ 0.49ab	14.41 $\pm$ 0.56a	2, <0.001	1, <0.001	1, 0.012	3, 0.003	1, 0.007	18, 0.005	
	WV	6.34 $\pm$ 0.25c	11.71 $\pm$ 0.46b	13.90 $\pm$ 0.54b							
<b>White oak</b>											
Leaf mass (g dry mass)	OH	0.82 $\pm$ 0.13b	1.15 $\pm$ 0.13ab	1.57 $\pm$ 0.13a	2, <0.001	1, <0.001	1, 0.696	3, 0.045	1, 0.249	12, 0.030	
	WV	0.90 $\pm$ 0.13b	1.67 $\pm$ 0.13a	1.34 $\pm$ 0.13ab							
Stem mass (g dry mass)	OH	0.59 $\pm$ 0.10b	0.80 $\pm$ 0.10ab	0.94 $\pm$ 0.10ab	2, 0.005	1, 0.002	1, 0.543	3, 0.114	1, 0.136	12, 0.177	
	WV	0.64 $\pm$ 0.10b	1.16 $\pm$ 0.10a	0.90 $\pm$ 0.10ab							
Root mass (g dry mass)*	OH	3.55 $\pm$ 0.17c	6.14 $\pm$ 0.28b	7.17 $\pm$ 0.34ab	2, <0.001	1, <0.001	1, 0.615	3, 0.009	1, 0.008	12, <0.001	
	WV	3.82 $\pm$ 0.34c	8.09 $\pm$ 0.38a	7.26 $\pm$ 0.34ab							

**Note:** Soil and seed source effects were tested as nested within shading. Due to the small number of white oak germinant seedlings per individual mother tree (seed source), mother trees at a given site were grouped ( $N = 4$  sites). Chestnut oak was represented by six seed source trees at two sites and northern red oak by seven seed source trees across three sites. Means of a given species followed by the same letter are not significantly different from the Tukey–Kramer mean separation test at  $\alpha = 0.05$ .

\*A Shapiro–Wilk test for normality was significant at  $p < 0.05$ , so a generalized linear mixed model (GLMM) via GLIMMIX was run with gamma distribution with a log link function.

**Table 4.** Characterization of chestnut (*Quercus prinus*), northern red (*Quercus rubra*), and white oak (*Quercus alba*) seedling size and mass after two growing seasons.

	Chestnut oak	Northern red oak	White oak
Seedling height (cm)	35.65±0.71	37.86±0.58	17.57±0.43
Basal diameter (mm)	3.97±0.05	4.87±0.04	2.95±0.05
Flush number	1.82±0.02	1.55±0.02	1.23±0.03
Leaf number per seedling	29.50±0.78	12.39±0.27	15.63±0.51
Area per individual leaf (cm <sup>2</sup> )*	23.32±0.45	71.79±1.18	16.51±0.53
Leaf area per seedling (cm <sup>2</sup> )	652.01±17.25	828.03±16.53	260.16±11.83
Specific leaf area (cm <sup>2</sup> ·g dry mass <sup>-1</sup> )	212.81±4.67	199.28±1.01	197.21±2.68
Root to shoot ratio	1.60±0.02	1.56±0.02	2.99±0.05
Seedling mass	14.83±0.43	18.77±0.38	8.76±0.38
Leaf mass	3.18±0.09	4.22±0.09	1.35±0.06
Stem mass	2.39±0.08	3.14±0.07	0.88±0.04
Root mass	9.01±0.27	11.20±0.24	6.51±0.28
Number of seedlings	449	545	230

**Note:** Means (±SEM) were calculated across light and soil treatments for each individual species.

\*Includes leaf blade plus petiole.

oak, its allocation patterns were dramatically different (Table 4). When averaged across shade treatments, mean root to shoot ratio for white oak seedlings ( $3.0 \pm 0.05$ ) was almost twice that for both chestnut and northern red oak ( $1.6 \pm 0.02$ ) (Fig. 1). White oak root to shoot ratios increased 30% as light levels increased from 6% to 25% of full sun, whereas chestnut and northern red oak ratios were unchanged (Fig. 1).

### Seedling response to soils

#### Season 1

No significant soil media effects were detected on the growth of either chestnut or white oak seedlings (Table 2). For northern red oak seedlings grown in the OH soil mix, shoot height ( $18.3 \pm 0.4$  cm) and basal diameter ( $3.45 \pm 0.04$  mm) were 11.8% and 3.1% larger than northern red oak grown in the WV soil.

#### Season 2

In general, growth and biomass were higher for all species when grown in WV soil compared with the OH soil mix, although significant differences were not detected for all biomass parameters for all species (Table 3; Fig. 1). The WV soil mix had higher pH and higher water-extractable concentrations of nitrate, calcium, potassium, and magnesium than the OH mix (Table 1), although the antagonistic cations aluminum and manganese were higher. Only phosphorus concentration was higher in the OH soil mix, and although not directly tested in the soil mix, ammonium concentrations in the forest soil used in the OH mix were five times higher than in the forest soil used in the WV mix. Growth and biomass of chestnut oak grown in the WV soil mix increased by the largest percentage of the three species, with root mass accounting for most of the increase (Table 3). Mass of chestnut oak seedlings (sum of leaves, stem, and roots) grown in the WV soil mix had 25% more mass than those grown in the OH mix. Northern red and white oak seedlings grown in the WV soil mix had 5% and 12% more mass, respectively, than those grown in the OH mix. No significant interactions were

detected between shading and soil type for any of the species (Fig. 1; Table 3).

### Seed source

#### Season 1

Seed source significantly affected seedling height and basal diameter of chestnut and northern red oak germinants, while white oak was unaffected by seed source site (Table 2).

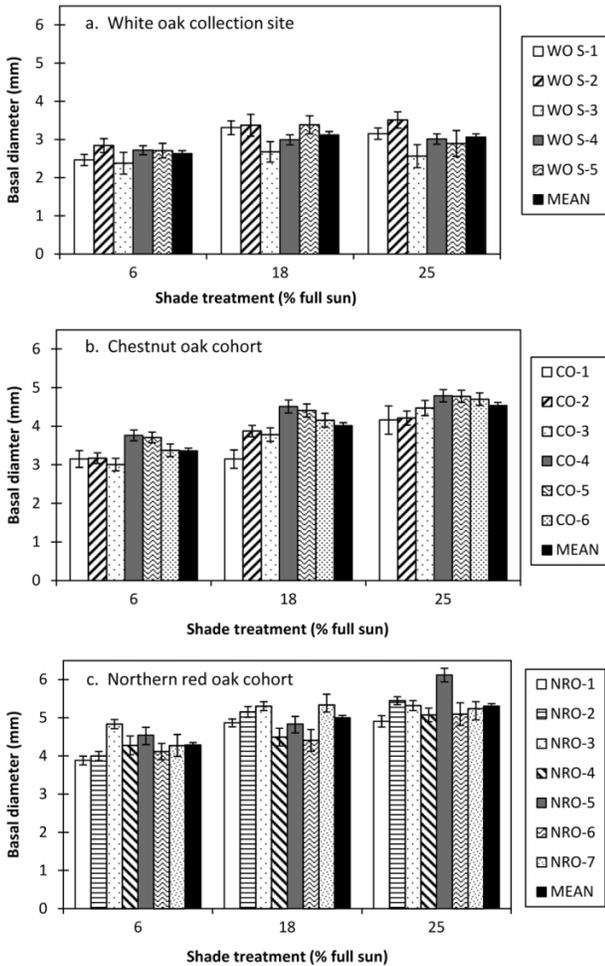
#### Season 2

Significant growth and biomass differences among seed sources were detected for chestnut and northern red oak as well as collection sites for white oak (Table 3; Figs. 2 and 3). Within a given species, the basal stem diameter of some seedling cohorts increased linearly with increasing light (e.g., CO-1, CO-3, and NRO-5), while others showed little to no positive response (e.g., NRO-4, WO S-3, and WO S-4) (Fig. 2). Seedling mass (shoot plus root) of individual seedling cohorts within a given species showed a wider range of responses to increasing light compared with basal diameter growth. This result was consistent for all species (Fig. 3). Certain cohorts appeared to respond more positively to increasing light levels (e.g., NRO-5), while others did not (e.g., NRO-3). Despite the variation in growth among the individual cohorts, overall, chestnut and northern red oak growth increased as light levels increased. No further increases in white oak growth occurred above 18% of full sun.

### Discussion

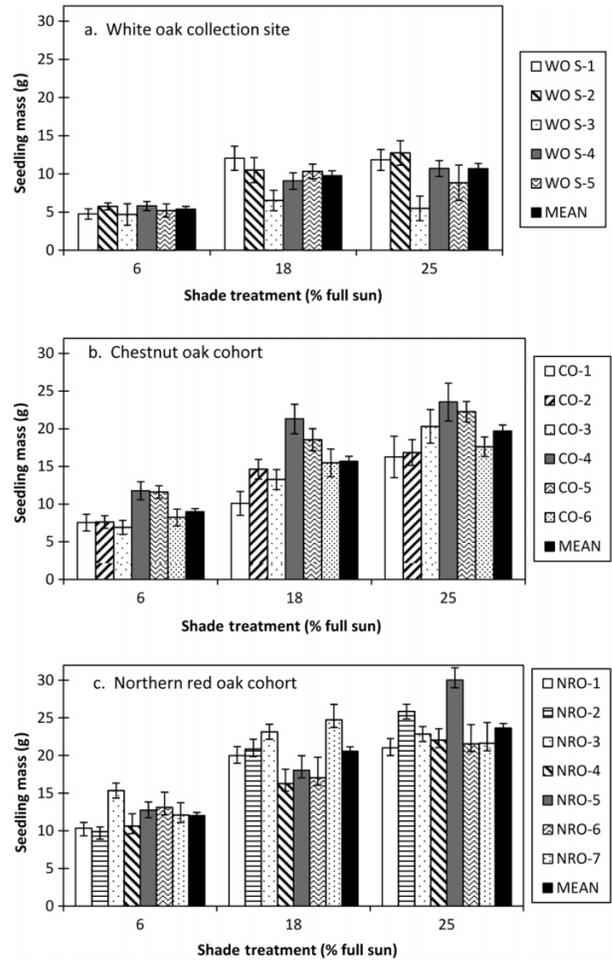
Although it is well known that different oak species, even those found within the eastern deciduous biome, differ in shade tolerance, drought resistance, productivity, and longevity (Burns and Honkala 1990), management recommendations to promote advance reproduction are often developed as though they are a single species. We seized the opportunity following an abundant acorn mast event to characterize the response to shading and soil fertility of three upland oak

**Fig. 2.** Effect of seed source, nested within shading, on the mean basal stem diameter of (a) white oak (*Quercus alba*) ( $p = 0.302$ ), (b) chestnut oak (*Quercus prinus*) ( $p = 0.017$ ), and (c) northern red oak (*Quercus rubra*) ( $p = 0.226$ ) seedlings grown under shade treatments at 6%, 18%, and 25% of full sun and in growing media mix containing either Ohio or West Virginia native forest soils for two growing seasons. Individual cohorts are shown for chestnut (CO-1 through CO-6) and northern red oak (NRO-1 through NRO-7). Due to the low number of white oak germinants, individual cohorts at a given collection site were grouped together and analyzed; those values are presented in Fig. 2c as WO S-1 through WO S-5.



species: northern red oak, a well-studied species during its early life stage, and white and chestnut oak, both of which have not been as extensively investigated as seedlings. This work demonstrates differences in the early growth and biomass accumulation patterns among the three species. Although chestnut and white oak are closely related species and considered more adapted to xeric environments than northern red oak, their growth was dissimilar. Chestnut and northern red oak were more alike, with similar seedling growth and biomass allocation patterns, irrespective of light and soil nutrient levels. Generally, plant species that can succeed when resources are limiting, such as shaded conditions or drought-prone and infertile soils, typically grow slowly even when resources are readily available (Latham 1992). White oak was the slowest growing of the group, suggesting that it was more tolerant of shaded conditions. White oak

**Fig. 3.** Effect of seed source, nested within shading, on the seedling dry mass (shoot plus root) of (a) white oak (*Quercus alba*) ( $p < 0.001$ ), (b) chestnut oak (*Quercus prinus*) ( $p = 0.005$ ), and (c) northern red oak (*Quercus rubra*) ( $p = 0.092$ ) seedlings grown under shade treatments at 6%, 18%, and 25% of full sun and in growing media mix containing either Ohio or West Virginia native forest soils for two growing seasons. Individual cohorts are shown for chestnut (CO-1 through CO-6) and northern red oak (NRO-1 through NRO-7). Due to the low number of white oak germinants, individual cohorts at a given collection site were grouped together and analyzed; those values are presented in Fig. 3 as WO S-1 through WO S-5.



also appears to be more of a stress-tolerant species in that it displayed few to no responses to increasing light levels and soil nutrient resources. It allocated a lower proportion of energy to leaves compared with either chestnut or northern red oak seedlings. The proportion of total seedling mass allocated to leaves was 15% for white oak compared with 22% and 23% for chestnut and northern red oak, respectively, across shade treatments. White oak displayed the least amount of shoot plasticity (e.g., leaf area) to changes in light conditions. As light levels increased from 6% to 25% of full sun, total leaf area of white oak seedlings increased 30% compared with increases of 55% and 95% for northern red and chestnut oak seedlings, respectively. White oak seedlings instead exhibited the most dominant root-centered growth of the three species studied, with root to shoot ratios of  $3.0 \pm$

0.02 compared with  $1.6 \pm 0.02$  for chestnut and northern red oak seedlings. Work by Dillaway et al. (2007) supports our findings that white oak seedlings respond to increases in light by preferentially allocating carbon to root systems. By measuring total nonstructural carbohydrates, they found an increased allocation to roots over shoots as light increased, which supports the hypothesis that oaks have a conservative growth strategy. Our chestnut and northern red oak root to shoot ratios are similar to those previously reported for northern red oak seedlings (Gottschalk 1994; Crow 1992; Phares 1971).

Despite being in the same taxonomic group, *Quercus* section *Quercus*, white and chestnut oak grew very differently. Young chestnut oak seedlings grew much faster and allocated more biomass to shoots than did those of its closer relative white oak, which displayed growth patterns similar to those of northern red oak. Chestnut oak is considered more drought tolerant than northern red oak and is most commonly found on xeric upland, rocky sites with low fertility. Conversely, northern red oak is considered a more mesic species. However, both northern red and chestnut oak have been reported to produce their best growth on rich, well-drained sites (McQuilkin 1990; Sander 1990).

Differences in seedling (shoot plus root) mass were quite dramatic with chestnut and northern red oak seedlings averaging  $16.8 \pm 0.4$  g compared with white oak averaging  $8.8 \pm 0.4$  g. This nearly twofold difference in seedling mass validates the slow-growth survival strategy of white oak. A paucity of information on white and chestnut oak seedling responses to changes in resource availability such as light and soil nutrients begs for further characterization. Forest management treatments should consider these differences among oak species. When these oaks occur together in mixed stands, it will be difficult to develop a prescription that benefits each species' needs. Research on the stump sprout capacity among oak species demonstrates significant differences in height growth and survival among upland oak species (Weigel et al. 2006). Dey et al. (1996) reported that stump sprouts originating from white oak had the lowest probability of surviving to age 5 compared with other upland oak species. Regrettably, few multispecies comparison studies focusing on oak seedlings exist. Brose (2008) investigated the root development of acorn-origin seedlings of black (*Quercus velutina* Lam.), chestnut, northern red, and white oak grown under varying light regimes (4%–89% of full sunlight) within mixed-oak stands on intermediate and mesic sites on the Allegheny Plateau of Pennsylvania. After four growing seasons, root sizes among species reflected differences in relative growth rates; northern red oak, the fastest growing oak, had the largest roots and white oak, the slowest growing oak, had the smallest. Chestnut and black oak were intermediate in growth and root mass. Root to shoot ratios were not reported. Gottschalk (1994) examined the response of black and northern red oak seedlings to shade treatments ranging from 8% to 94% of full sunlight and found no light effect on root to shoot ratios after the first year. It was concluded that increasing light to more than 20% of full sunlight (levels comparable with those following a shelterwood thinning cutting) would improve seedling establishment and growth. If light levels exceeded 30% of full sun, however, significantly more biomass growth was not produced, suggesting that light saturation for growth and

photosynthesis occurs at around this light intensity. Kaelke et al. (2001) suggested that increasing light beyond 20% of full sun provides little additional benefit to northern red oak seedlings but instead preferentially stimulates less shade-tolerant, faster growing competitors such as tulip poplar, American birch, and trembling aspen (*Populus tremuloides* Michx).

The response of white oak carbon allocation to changing light levels in our current study is similar to that previously reported by Latham (1992) for mockernut hickory (*Carya tomentosa* Nuttall) seedlings grown under varying light and nutrient conditions. The mockernut hickory seedlings were like our white oak seedlings, investing heavily in roots, including a large taproot, regardless of the growing conditions. In that same study, northern red oak displayed shoot and leaf growth increases associated with increasing light similar to those that we have reported here for northern red oak. Latham (1992) proposed that mockernut hickory may trade the ability to compete for light in the short term for the ability to remain alive in the event of a severe environmental limitation. We propose that white oak seedlings possess a similar survival strategy. Intrinsic slow growth is a consequence of adaptations enabling some species to grow in challenging environments (Chapin 1980), and root-centered growth facilitates greater tolerance to drier sites where interspecies competition is typically low. Conversely, competitors of oak tend to allocate more carbon to shoot growth, making them more successful on mesic sites and resulting in the development of dense, low-light understories where oaks such as northern red most often fail.

In our study, northern red oak seedlings produced more leaf and shoot growth as light increased, suggesting a survival strategy different from that of white oak. Northern red oak is the least drought tolerant of the upland oaks and prefers mesic habitats, growing best in moist coves and ravines with northerly or easterly aspects (Sander 1990). Relative to its non-oak competitors, northern red oak displays more root-centered growth; however, compared with white oak, it allocates more carbon above ground to produce relatively fast-growing shoots. We propose that northern red oak's survival strategy as a young seedling is to allocate more carbon above ground given its preference for mesic habitats where faster growing shade-tolerant competitors are common.

We were able to document that seed source does impact oak seedling growth after 2 years. We observed growth differences associated with seed source for each species. Some cohort groups grew inherently more or less than others, and some responded more positively to increases in light levels than others. Of the three species studied, chestnut oak had the greatest number of significant growth response effects associated with seed source after two growing seasons (eight of 12) compared with six for white oak and five for northern red oak. The root mass of all species was significantly affected by seed source (chestnut and northern red oak) or seed collection site (white oak). Long and Jones (1996) compared the first- and second-year growth of 14 North American oak species (excluding white and chestnut) representing xeric, mesic, and hydric habitats in greenhouse and common garden experiments with abundant soil water and soil nutrients. Seedling growth and morphology were impacted by the mother tree's environmental habitat. Oak species native to xeric environments produced the smallest seedlings, while

those from hydric sites had the lowest root to shoot mass ratios. Our study was not designed to determine the influence of mother tree environmental and site conditions on seedling growth but identified that research is needed to determine the role of ecotypes on oak responses to limited resources such as light, soil moisture, and nutrients. Individual oak species are inherently genetically heterogeneous, a characteristic that has been proposed as a mechanism to survive in resource-limited environments (Abrams 1996).

Few effects of either light or soil nutrients on seedling growth were detected in year 1, perhaps in part because of the influence of acorn reserves on early seedling growth. Stored carbohydrates are rapidly utilized by the germinating seedling to produce a large, well-developed root system. Since reserves are depleted early in the first year, the influence of light and soil fertility on seedling growth becomes more apparent during the second year. In fact, after two growing seasons, seedlings of all species grown in the WV soil mix were larger than those grown in the OH soil mix. The most responsive species was chestnut oak. The observed growth differences were not surprising, since water-extractable concentrations of nitrate, calcium, potassium, and magnesium were higher in the WV soil mix compared with the OH mix. Chestnut oak is commonly found on dry, infertile soils and rocky ridges but grows best on rich, well-drained soils along streams. In our study, chestnut oak appeared to effectively utilize these additional resources, while northern red and white oak seedlings did not. We hypothesized that additional soil nutrients could enhance seedling growth as light levels increased, but only chestnut oak supported that hypothesis. No interactions between light and soil nutrients were observed. Previous work evaluating the responses of northern red oak to varying levels of light, soil nutrients, and moisture has also reported its tolerance to low resource levels (Kolb et al. 1990; Latham 1992; Kaelke et al. 2001). Even when grown under high light and increased available soil nitrogen, northern red oak did not respond positively (Tripler et al. 2002). Kolb et al. (1990) described northern red oak's limited growth response as a stress-tolerance strategy when compared with tulip poplar's growth response. All of this evidence suggests that oaks as a group are more inflexible morphologically and physiologically than their shade-intolerant competitors. Our study supports the differentiation within upland oaks of low-resource survival strategy. We propose that white oak has the greatest stress-tolerant survival strategy of the group.

### Summary and management implications

Our results show that initial seedling growth of three common upland oak species in eastern US mixed-oak forests can be considerably different. The oak species evaluated here responded differently to changes in light levels and soil conditions. White oak seedlings displayed higher shade tolerance and demonstrated a successful survival strategy in resource-limited environments with limited competition. The slow-growing white oak may be able to persist longer in low-light conditions by developing a root system that will accumulate stored carbohydrates and be poised to respond to a light-creating disturbance. In stands with either a shelterwood cut or a final removal harvest, the slow-growing white oak would not persist but would instead be overtopped and outcompeted by

faster growing neighbors. In stands with no immediate harvest planned (e.g., 10–20 years), multiple low-intensity burns over several years or herbicide application to the understory and midstory could be used to increase the competitive status of white oak regeneration by reducing the density of the sapling layer. The vigor and competitiveness of white oak regeneration would improve as it developed a larger root system in these relatively low-light environments. Low-intensity fires that do not create canopy openings have been shown to reduce the density of faster growing competitors, including both fire-intolerant (e.g., maples) and shade-intolerant species (e.g., tulip poplar). Hutchinson et al. (2005) reported that closed-canopy (<6% of open sky) conditions persisted after multiple low-intensity fires within mixed-oak forests of Ohio. They found that the density of tulip poplar initially increased from the seed bank but did not persist due to the sustained low-light environment. Once adequate stocking (Brose et al. 2008) of competitive white oak stems is achieved with the multiple fires, an overstory treatment such as a shelterwood harvest or a series of patch clearcuts could follow. For the faster growing northern red and chestnut oak, a reverse sequence of a shelterwood cut (e.g., light to moderate) followed in 3–5 years with one or more prescribed burns may be more appropriate (Brose et al. 2008). After a shelterwood cut, these species would have a greater probability of persisting and competing with fast-growing species in the open conditions (e.g., >20% of full sun) than would white oak. Of course, these regeneration strategies are dependent on adequate numbers of oak seedlings being present prior to the initiation of treatments. Although upland oak species share many common “disturbance” traits, our results show that there are significant differences in response to available resources that need to be considered and incorporated into the development of successful oak management practices. If regeneration of a white oak stand is the desired goal, than the implementation of a slower, more gradual approach to opening up the canopy may be necessary.

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