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A Comparison of the Survival and Development of the Seedlings of Four Upland Oak Species Grown in Four Different Understory Light Environments

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Oak (*Quercus* spp.) research and management often focus on northern red oak (*Quercus rubra*) and assume that associated upland oaks have similar growth patterns. To test this premise, we measured the survival and development of four species of acorn-origin oak seedlings growing in four different levels of understory sunlight for 8 years. Northern red oak had better survival than black (*Quercus velutina*), chestnut (*Quercus montana*), and white oak (*Quercus alba*) in 5% sunlight, but none of the species exhibited much growth. In 15 and 40% sunlight, survival was equal among species, but for growth the seedlings formed two groups with chestnut/northern red oak growing more than black/white oak. In 75% sunlight, survival was equal among species, but northern red oak grew faster than the other three species. Assuming that other oaks have growth habits similar to those of northern red oak could lead to a reduction in or the inadvertent loss of an oak species.

Keywords: Quercus, root collar diameter, root/stem ratio, shelterwood system, understory lighting

Of all the forest types that make up the temperate deciduous forest biome of eastern North America, the mixed-oak (*Quercus* spp.) forest is perhaps the most important because of its diversity, vastness, and many ecological and economic values (Smith 2006). At least 50 oak species grow east of the 100th meridian, and some type of mixed-oak forest is found in every state and adjacent Canadian province (Burns and Honkala 1990, Stein et al. 2003). These mixed-oak forests provide clean water, supply critical food and habitat for wildlife, produce valuable wood products, support quality recreation, and contribute aesthetic values (Smith 2006). In upland environments, mixed-oak forests generally consist of one or more oak species such as black (*Quercus velutina* Lam.), chestnut (*Quercus montana* Willd.), northern red (*Quercus rubra* L.), scarlet (*Quercus coccinea* Muenchh.), or white (*Quercus alba* L.) dominating the canopy with a mix of other hardwood species in the midstory and understory strata. Although these oaks often co-occur within the same forest types, the silvics of these five oak species vary considerably. For example, white oak is the slowest growing, longest lived, and most shade tolerant of this group (Rogers 1990), whereas northern red oak is the fastest growing and scarlet oak is the least shade tolerant and shortest lived (Johnson 1990, Sander 1990b). Northern red oak is also the least drought resistant and scarlet oak is the most fire sensitive, whereas chestnut oak is the most drought hardy and fire tolerant of the upland oaks (McQuilkin 1990). In terms of these aforementioned characteristics, black oak is similar to scarlet oak in longevity, similar to chestnut oak in drought and fire tolerance and intermediate in growth rate (Sander 1990a).

Despite the diversity and intrinsic value of the upland oak species, researchers have concentrated on northern red oak. Smith (1993) reported that northern red oak was

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the most studied upland oak species with considerably less research having been done on black, chestnut, scarlet, and white oak. Similarly, managers often treat the upland oaks as if they are all the same species; a generic "oak" with attributes resembling those of northern red oak. For example, the SILVAH decision-support system (Marquis et al. 1992, Brose et al. 2008) inventories all oaks as if they are the same species and develops a regeneration prescription for a generic mixed-oak forest.

This focus on northern red oak by researchers and managers is understandable, given the species' ecological and economic values, but the increasing emphasis on forest restoration and ecosystem management by public land agencies suggests that research into and management of the other oak species need development. For example, the long-lived white oak is the keystone species in the restoration of open oak woodlands, especially those managed toward recreating old-growth conditions. Similarly, the emergence of prescribed fire to restore and maintain xeric oak-heath forests implies an emphasis on chestnut oak. Managing for either of these communities based on the attributes of northern red oak would probably lead to undesirable results.

Unfortunately, comparative studies among the upland oaks are few, especially studies conducted during the regeneration phase. Bourdeau (1954) conducted one of the earliest comparative studies and showed that northern red oak germinant seedlings outgrew those of blackjack (*Quercus marilandica* Meunchh.), post (*Quercus stellata* Wangenh.), scarlet, and white oak, especially at low light. Based on several measures of growth, he ranked these five oak species in three categories: northern red, scarlet, white, blackjack, and post. Gottschalk (1985, 1987) determined that black and northern red oak seedlings grew equally well once understory sunlight exceeded 20%. Sung et al. (1998) examined the growth responses of northern red and white oak to three sunlight levels (30% sun, 70% sun, and full sun) and found that both species grew the least in 30% sun and grew equally well at the higher two levels. More recently, Rebbeck et al. (2011) compared the responses of chestnut, northern red, and white oak seedlings to different sunlight and soil nutrient conditions. They found that the three species responded differently to changes in resource availability. Commonalities among these studies are that they were short-term (1–2 years maximum) and were conducted in highly controlled environments such as planting plots or greenhouses. Oak seedlings growing in dissimilar understory light conditions in the forest and for longer periods of time may develop differently.

To help alleviate the lack of comparative studies among the upland oaks during the regeneration phase, we conducted an 8-year experiment documenting the survival and growth of black, chestnut, northern red, and white oak seedlings. Because the three-stage shelterwood system is frequently used to regenerate upland oak forests in eastern North America (Johnson et al. 2009), we carried out this study at four levels of understory lighting typically created by this multistage regeneration system. Because SILVAH currently prescribes oak regeneration treatments based on the growth attributes of northern red oak (Brose et al. 2008), we hypothesized that northern red oak was unrepresentative of the other upland oak species because of differential survival and growth responses to changes in understory lighting during the regeneration process. Specific predictions were that for each of the four lighting levels, northern red oak seedlings would exhibit higher survival, more stem and root growth, and larger root/shoot ratios than would black, chestnut, and white oak seedlings. In addition, there would be no differences among the latter three species in survival, stem and root growth, and root/shoot ratios. Understanding how seedlings of the different upland oak species compare in their growth under a broad array of understory light conditions for several years during the critical regeneration phase will be useful to foresters trying to manage oak ecosystems to meet diverse objectives.

Methods

Study Sites

This study was conducted at five sites in central and western Pennsylvania: Allegheny National Forest (ANF), Bald Eagle State Forest (BESF), Clear Creek State Forest (CCSF), Elk State Forest (ESF), and State Game Land 152 (SGL). The BESF, CCSF, and ESF sites are owned and managed by the Pennsylvania Bureau of Forestry, whereas SGL is a Pennsylvania Game Commission property. The ANF site is part of the US Department of Agriculture Forest Service National Forest System.

Because the sites were spread over one-quarter of the state, they differed in a number of characteristics (Table 1). The SGL site was glaciated (Yaworski et al. 1979), whereas the others were never glaciated (Zarichansky 1964, Braker 1981, Cerutti 1985, Kopas 1993). The SGL site was the wettest site, the ESF site was the coolest, and the BESF site was the hottest and driest. The BESF site was on a north-facing, mid-slope bench, whereas the others were on broad, flat hilltops where aspect was inconsequential. The ANF and ESF sites were channery loams, the BESF and CCSF sites were stony loams, and the SGL site was a silt loam. Site index$_{50}$ for northern red oak varied from 20 m at the ESF and BESF sites to 23 m at the ANF and CCSF sites to 27 m at the SGL site. Site quality differences were evident in the forest composition. The SGL site was dominated by northern red oak growing in association

Management and Policy Implications

This study points out key differences in the survival and growth of black, chestnut, northern red, and white oak seedlings at the light levels created by a three-cut shelterwood sequence. Important management recommendations based on those differences include the following:

1. In advance of an acorn crop, decrease dense shade to diffuse or partial shade (15–40% sunlight) by removing the midstory and understory canopies.
2. If premasting shade control is not possible, begin regeneration treatments no later than 1–2 years after black, chestnut, and white oaks mast or no later than 3–5 years after northern red oak produces acorns.
3. Conduct species-specific inventories for oak seedlings rather than grouping them together as oak reproduction.
4. To emphasize chestnut or northern red oak, use the two-cut or three-cut shelterwood sequence because seedlings of these two oak species can grow reasonably well in 15–40% sunlight.
5. To emphasize black or white oak, use a two-cut shelterwood because seedlings of these species need approximately 40% sunlight or more to initiate and sustain vigorous height growth.

Table 1. Climatic, physiographic, and forest composition characteristics of the five study sites.

Characteristic	ANF	BESF	CCSF	ESF	SGL
Location (latitude, longitude)	41°38′04″ N, 79°14′01″ W	41°09′49″ N, 77°12′30″ W	41°18′26″ N, 79°00′29″ W	41°26′57″ N, 78°06′34″ W	41°50′51″ N, 80°13′42″ W
Glaciated	No	No	No	No	Yes
Average temperature (° C)	8.0	9.8	8.1	7.5	8.3
Temperature range (° C)	−8.2 to 27.9	−6.8 to 28.1	−9.4 to 25.1	−11.6 to 24.4	−9.0 to 27.2
Rainfall (mm)	1,080	965	1,030	1,070	1,080
Snowfall (mm)	1,875	610	1,010	2,140	2,370
Growing season (days)	135	148	116	109	140
Elevation (m, above sea level)	565	500	535	575	300
Slope (%)	<5	5–10	<5	<5	<5
Slope position	Upper flat	Middle bench	Upper flat	Upper flat	Upper flat
Aspect (°)	90	340	180	130	225
Soil series	Hazleton channery loam	DeKalb stony loam	DeKalb stony loam	Hazleton channery loam	Venango silt loam
Soil family	Typic Dystrochrept	Typic Hapludult	Typic Hapludult	Typic Dystrochrept	Aeric Fragiaqualf
Site index (m, nro_{50})	23	20	23	20	27
Five most dominant canopy species (% of basal area)	Northern red oak Black cherry White oak Red maple Cucumbertree	White oak Chestnut oak Northern red oak Red maple Black gum	Northern red oak Red maple Black cherry White oak Chestnut oak	White oak Chestnut oak Northern red oak Red maple Black gum	Northern red oak Sugar maple Yellow-poplar White ash American beech

with sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), and yellow-poplar (*Liriodendron tulipifera* L.). Northern red oak also dominated at the ANF and CCSF sites, but associated species were red maple (*Acer rubrum* L.), sweet birch (*Betula lenta* L.), black cherry (*Prunus serotina* Ehrh.), white oak, and chestnut oak. These same species were present at the ESF and BESF sites, but white and chestnut oaks predominated and both sites had a considerable amount of black gum (*Nyssa sylvatica* Marsh.).

Study Design and Installation

In summer 2001, we chose four oak stands at each site that were visually judged to have markedly different understory light environments. The stands were either uncut or had recently undergone one of the harvests of a three-stage shelterwood sequence (preparatory cut, first removal cut, or final removal cut). The uncut stands had virtually no direct sunlight reaching the forest floor. They were fully stocked stands with intact main canopies, well-developed subcanopies, and little or no sign of any recent cutting. The preparatory cut stands had diffuse understory lighting. Structurally, they had intact main canopies but sparse subcanopies due to removal of most of the intermediate and suppressed trees. The uncut and preparatory cut stands either lacked understory herbaceous vegetation, or it had been controlled by a recent broadcast spraying of a glyphosate/sulfometuron methyl herbicide mix. The first removal cut stands had patchy understory lighting due to large gaps in the main canopy and a nearly nonexistent subcanopy. The final removal cut stands had nearly full sunlight except for occasional shading cast by a few residual trees retained for aesthetic, diversity, or wildlife considerations. The first removal cut and final removal cut stands also had widespread, rapidly developing tree regeneration. Generally, each stand was at least 4 ha, and all stands except those at SGL were surrounded by 2.3-m high woven wire fence to exclude whitetail deer (*Odocoileus virginianus*).

In each stand, we selected four 8-m × 4-m plots visually judged to have similar forest floor and overstory conditions. To verify the similarity of the forest floor of the plots within each stand, we collected a composite soil sample to determine the nutrient content of the soil. A soil core measuring 6 cm × 20 cm was taken from the center and both ends of each plot. These three cores were mixed together, and the composite sample was sent to the University of Maine for soil nutrient analysis. To verify the overstory conditions above the plots within each stand, we determined the basal area (BA) and relative density (RD), a measure of stocking (Marquis et al. 1992). From the center of each plot, we used a 2.3-m (10-factor) prism to determine which trees were "in," and these were identified to species and measured for dbh to the nearest 2.5 cm. RD was calculated from the basal area data using known tree-area equations for northwestern Pennsylvania (Marquis et al. 1992).

In fall 2001, we collected acorns of black, chestnut, northern red, and white oak from a single mother tree of each species in northwestern Pennsylvania. Mother trees were isolated mature dominant trees of good form and quality. We floated the acorns to identify and remove unsound seeds and then sorted the remaining sound acorns to remove small/deformed ones to provide a fairly uniform planting stock.

In each stand, the plots were raked clear of leaf litter and woody debris and tilled to a depth of 7.5 cm with a rototiller to loosen the soil and remove small surface rocks and roots. We randomly assigned a different oak species to each plot and then planted approximately 400 sound acorns (10–15/m^2) of that species at a depth of 2.5 cm. We planted the chestnut and white oak acorns in fall 2001, but the black and northern red oak acorns were cold stratified in a walk-in refrigerator at 1.5°C for 6 months and planted in spring 2002. Immediately after planting, each plot was completely covered with wire screen (0.63-cm mesh) to prevent acorn pilferage by small mammals. The screen was held flush to the ground with sod staples and remained in place for 1 year.

By summer 2002, each plot contained between 350 and 400 oak seedlings. Because understory lighting was central to this study and to further verify the similarity of the plots within each stand, we began using two bar ceptometers to determine the proportion of photosynthetically active radiation (PAR) reaching the oak seedlings in each plot (Parent and Messier 1996, Gendron et al. 1998). Measurements were taken annually from 2002 to 2009 inclusive on days of uniform cloudiness in late June or early July between 10 AM and 2 PM. We placed one ceptometer in fully open conditions to record the maximum ambient light level at 5-second intervals. With the second ceptometer, we took 15 systematic readings over each planting bed with the ceptometer pointing south at the height of the oak seedlings. We averaged both sets of readings and used the two means to calculate the percentage of full sunlight reaching each plot.

Data Collection

Beginning in fall 2002 and annually thereafter for 8 years, the living oak seedlings in each plot were tallied to compare the number of surviving seedlings among the four oak species through time. After counting, 15 seedlings were randomly selected and harvested to measure root and stem development. Harvesting was done shortly after soaking rains to facilitate root extraction and minimize disturbance to nearby seedlings.

Each harvested seedling was measured for root collar diameter to the nearest 0.1 mm and stem height to the nearest 0.1 cm. Root collar is the junction of the stem and the root and is marked by a ring of callous tissue. After drying at 30°C to a constant weight, stem and taproot dry masses were determined to the nearest 0.1 g using an electronic scale. Woody shoot mass included the main stem and all branches, but not the foliage. Root mass included the taproot as well as all lateral and feeder roots attached to the taproot. The root/shoot ratio of each seedling was calculated by dividing its root mass by its woody shoot mass.

Statistical Analysis

The seedling data were analyzed using a repeated-measures split-plot design via PROC MIXED (SAS Institute, Inc. 2000). The sunlight level was the whole-plot unit, and oak seedling species was the subplot unit. Time since planting was the repeated effect in the model. The four oak seedling species, four sunlight levels, and time since planting were the fixed effects in the model and site and site × sunlight level effects were the random effects in the model. The dependent variables were the annual seedling tallies and the measures of stem heights, root collar diameters (RCD), and root/shoot ratios (RSR). Comparisons among and within the main effects and interactions were obtained with Tukey's procedure (Day and Quinn 1989). Residuals were examined to ensure that the assumptions of normality and homogeneity of variances were met. For all comparisons, α was 0.05.

Table 2. The proportion of full sunlight reaching the oak seedlings at the beginning (Yr1), middle (Yr5), and end (Yr8) of the study by shelterwood stand type (uncut, preparatory cut, first removal cut, and final removal cut) and site (ANF, BESF, CCSF, ESF, and SGL).

		Uncut			Preparatory cut			First removal cut			Final removal cut		
Site	Oak species	Yr1	Yr5	Yr8	Yr1	Yr5	Yr8	Yr1	Yr5	Yr8	Yr1	Yr5	Yr8
		(%)											
ANF	Black	2	3	3	10	18	14	46	33	33	93	74	58
	Chestnut	2	4	3	10	12	14	58	34	35	95	78	51
	Northern red	2	3	3	11	13	15	51	38	34	90	71	56
	White	2	4	3	11	16	14	54	34	36	91	76	55
BESF	Black	4	5	6	12	11	15	52	38	29	95	73	62
	Chestnut	5	4	5	13	12	13	46	37	28	92	71	61
	Northern red	5	4	4	13	11	14	49	38	25	96	74	61
	White	5	5	4	11	10	12	54	39	28	94	70	63
CCSF	Black	4	6	5	14	14	14	45	40	28	94	78	46
	Chestnut	3	5	5	16	14	14	43	46	32	86	69	44
	Northern red	3	6	7	14	13	14	44	42	29	85	69	45
	White	3	5	6	15	16	14	43	48	32	87	67	46
ESF	Black	5	4	6	16	15	13	50	40	42	96	78	68
	Chestnut	5	4	6	13	14	11	49	40	40	96	71	68
	Northern red	5	5	6	12	14	13	50	39	39	96	76	67
	White	4	5	6	13	13	15	51	37	37	96	76	67
SGL	Black	3	7	5	11	17	13	48	39	27	85	60	58
	Chestnut	3	6	6	13	16	15	45	40	30	84	61	60
	Northern red	4	6	6	12	14	12	51	39	27	86	68	56
	White	4	6	7	12	14	14	44	41	29	89	65	55

Note the consistency of the sunlight levels within each site/shelterwood type/year grouping, among years for the uncut and preparatory cut stands, and the change in sunlight levels among years for the first removal cut and final removal cut.

Results

Initial measures of overstory showed that the starting conditions varied among the four shelterwood types. The uncut stands averaged 152 ft^2 of BA and 99% RD, whereas the preparatory cut stands averaged 106 ft^2 of BA and 75% RD. The average BA and RD of the first removal cut stands were 73 ft^2 and 55%, respectively, whereas the final cut stands had an average of 19 ft^2 BA and 13% RD. Within each of these four shelterwood types, PAR was rather uniform, especially among the planting plots at each site (Table 2). In the uncut stands, 2–5% full sunlight reached the oak seedlings. This range of sunlight increased to 10–16% in the preparatory cut stands and to 45–58% for the first removal cut stands. The final cut stands had nearly full sunlight (84–96%). Soil conditions varied among the sites with the SGL site generally having more nitrate nitrogen, ammonium nitrogen, and effective cation exchange capacity than the other four sites (Table 3). However, within the sites, soil conditions were quite uniform, especially among the four planting plots within each shelterwood type.

At each site, the understory light regime remained stable during the study in the uncut and preparatory cut stands but changed in the first removal cut and final removal cut stands (Table 2). Initially, PAR in the uncut stands ranged from 2 to 5%, and at the end of the study it ranged from 3 to 7%. The preparatory cut stands showed the same stability in PAR levels: from 10 to 16% initially to 11 to 15% in the final year of the study. Conversely, the first removal cut stands averaged nearly 50% PAR at the beginning of the study, but this level declined to 30% PAR by 2009. Similarly, the final removal cuts averaged 91% PAR in 2002, 71% PAR in 2005, and 57% PAR in 2009. Overall, PAR measurements averaged 5% sunlight for the uncut stands, 15% sunlight for preparatory cut stands, 40% sunlight for first removal cut stands, and 75% sunlight for final cut stands. For the remainder of this article, we will use these overall average sunlight levels to represent the understory lighting conditions created by the harvests.

Initially, all plantings had between 368 and 391 seedlings with no statistical differ-

Table 3. Soil conditions of the four shelterwood stands (uncut, preparatory cut, first removal cut, and final removal cut) at the five study sites (ANF, BESF, CCSF, ESF, and SGL) at the beginning of the oak seedling development study.

		Uncut			Preparatory cut			First removal cut			Final removal cut		
Site	Oak species	NO_3N	NH_4N	ECEC	NO_3N	NH_4N	ECEC	NO_3N	NH_4N	ECEC	NO_3N	NH_4N	ECEC
		. . . .(mg/kg). . . .			. . . .(mg/kg). . . .			. . . .(mg/kg). . . .			. . . .(mg/kg). . . .		
ANF	Black	17.6	7.6	4.5	3.7	8.4	5.4	3.5	2.0	2.7	8.4	13.3	2.4
	Chestnut	18.2	4.9	4.9	3.0	13.3	4.8	5.5	2.0	4.3	7.9	14.6	3.5
	Northern red	21.3	6.1	7.0	2.6	6.1	4.8	1.7	3.5	2.8	11.6	14.8	4.1
	White	26.4	6.0	6.8	5.3	7.8	5.0	4.1	1.2	5.0	9.8	13.8	6.1
BESF	Black	1.0	8.1	4.6	5.6	7.9	3.9	17.9	5.5	3.8	1.8	6.0	6.7
	Chestnut	2.7	15.9	5.0	5.5	6.6	3.6	26.6	6.7	7.0	0.7	11.1	7.1
	Northern red	1.5	12.2	5.2	8.9	5.9	3.4	30.2	7.4	4.9	0.7	8.1	8.1
	White	0.8	10.9	4.0	1.3	6.5	3.4	30.7	7.4	3.9	1.3	10.3	6.8
CCSF	Black	0.5	18.1	6.3	0.5	19.9	4.8	0.6	4.4	4.0	0.9	17.5	5.3
	Chestnut	0.5	23.9	6.3	0.5	12.7	3.8	0.9	6.2	3.6	2.9	16.3	6.3
	Northern red	0.5	30.6	8.1	0.7	15.1	4.2	0.8	9.2	8.1	2.6	15.6	5.2
	White	0.6	13.4	5.0	0.5	13.7	3.9	0.8	8.6	4.2	1.1	18.6	3.5
ESF	Black	6.6	21.2	4.3	5.1	12.9	4.6	22.4	27.5	7.5	11.9	4.7	5.6
	Chestnut	7.2	9.6	3.9	5.9	18.3	4.2	20.1	9.1	4.6	9.3	2.2	5.3
	Northern red	5.5	23.2	4.6	6.5	13.7	3.8	16.0	12.7	5.4	3.4	1.3	5.7
	White	8.0	12.3	5.4	2.7	18.7	4.2	25.4	9.7	4.9	3.6	1.1	4.4
SGL	Black	46.1	27.0	9.9	25.6	19.3	9.6	27.7	48.0	9.7	43.5	19.7	8.0
	Chestnut	39.4	47.4	8.9	25.3	26.7	7.2	30.7	35.1	8.2	50.8	42.0	6.4
	Northern red	45.2	22.1	7.6	34.3	43.1	9.8	19.3	24.9	8.2	48.5	29.2	7.1
	White	40.4	28.6	8.5	20.0	21.6	9.1	27.3	27.1	7.7	49.1	48.3	7.5

NO_3N, nitrate nitrogen; NH_4N, ammonium nitrogen; ECEC, effective cation exchange capacity.

ences among species regardless of the sunlight level (Figure 1). From that starting point, the number of living oak seedlings declined in all sunlight levels with the most mortality occurring at 5% sunlight and the least occurring at 75% sunlight. The only statistically significant difference in seedling survival among the four oak species was in 5% sunlight. In that level, the number of northern red oak seedlings was greater than that of the other three oak species between years 2 and 7 ($P < 0.025$). At 15, 40, and 75% sunlight, there were no statistical differences in the number of seedlings among the four oak species for any year. By the final year of the study, oak seedling counts ranged from 0 to 200 stems per plot with the fewest being found in 5% sunlight and the most occurring in the 40 and 75% sunlight levels.

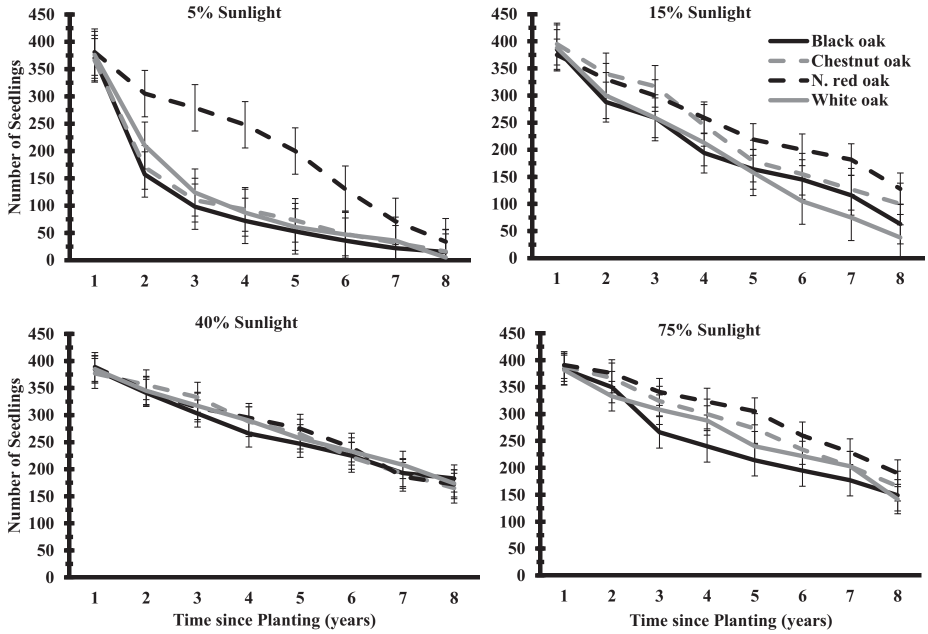

Figure 1. The mean survival of black, chestnut, northern red, and white oak seedlings in 5, 15, 40, and 75% sunlight from germination through the 8th growing season. Vertical bars indicate 1 SE.

Initial heights of all the oak seedlings ranged from 9 to 14 cm in all four light levels (Figure 2). From this stating point, the seedlings grew at differential rates and eventually formed two groups with chestnut/northern red oak always growing taller than black/white oak at 5, 15, and 40% sunlight. This grouping became statistically apparent at year 4 in 40% sunlight ($P = 0.014$) and at year 6 in 5% and 15% sunlight ($P = 0.013$). In 75% sunlight, chestnut oak heights did not differ from those of black and white oak throughout the course of the study. Conversely, in 75% sunlight height of northern red oak seedlings was greater than the heights of the other three oak species beginning in year 3 ($P = 0.01$). By the end of the study, the tallest oak seedlings were those of northern red oak in 75% sunlight, and the shortest were white oak seedlings in 5% sunlight.

Development of the seedling's root collars closely followed the patterns of their height growth (Figure 3). Initial root collars were 3–7 mm, and no statistically significant differences were found among species or among light levels. In 15 and 40% sunlight, the four oak species formed the same two groups, chestnut/northern red and black/white, that they had for stem height. In both light levels, the two groups diverged in year 6 with chestnut and northern red oak having larger root collars than black and white oak ($P < 0.001$). At 5 and 75% sunlight, northern red oak had larger root collars than did

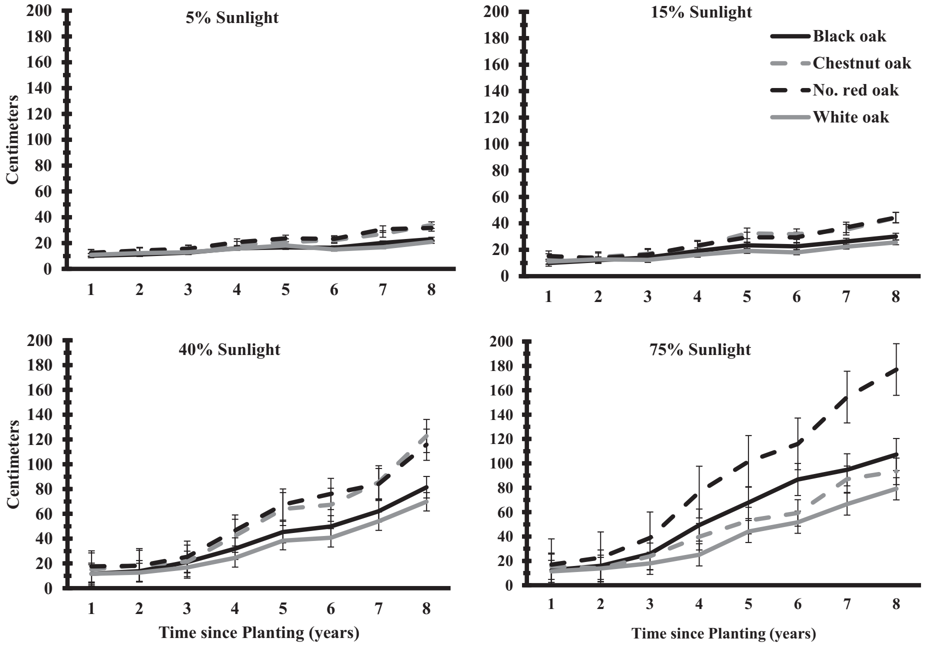

Figure 2. The mean height growth of black, chestnut, northern red, and white oak seedlings in 5, 15, 40, and 75% sunlight from germination through the 8th growing season. Vertical bars indicate 1 SE.

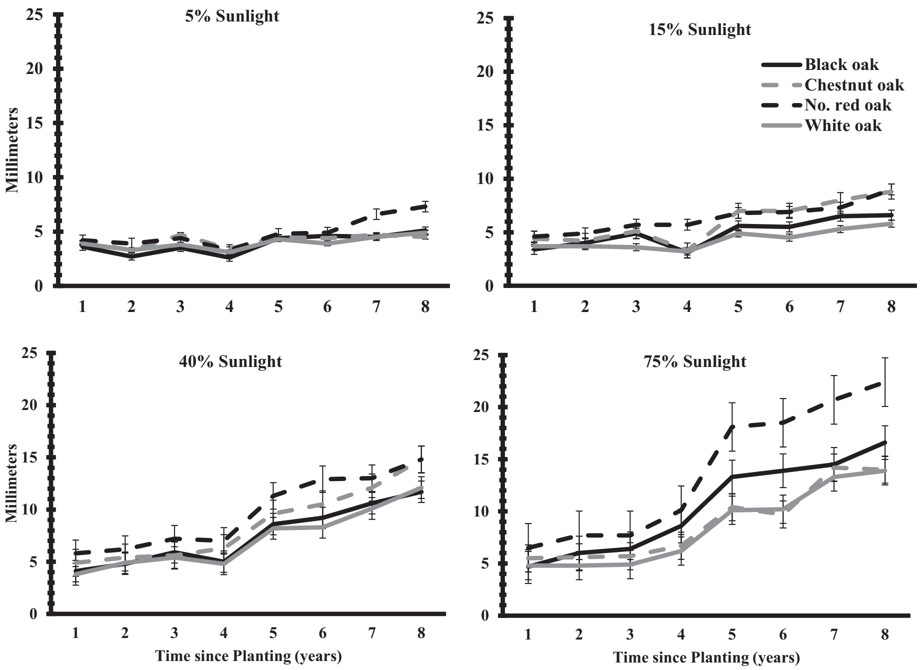

Figure 3. The mean root collar development of black, chestnut, northern red, and white oak seedlings in 5, 15, 40, and 75% sunlight from germination through the 8th growing season. Vertical bars indicate 1 SE.

black, chestnut, and white oak ($P < 0.001$). The difference became statistically detectable at year 5 in 75% sunlight ($P < 0.001$) and at year 7 in 5% sunlight ($P = 0.025$). By the end of the study, northern red oak seedlings had the largest root collars (22 mm in 75% sunlight) and white oak seedlings had the smallest root collars (4 mm in 5% sunlight).

Relative to the increasing heights and root collars through time, the RSRs of the four oak species generally decreased during the course of the study (Figure 4). Initial RSRs averaged 3.0 (75% of growth going into the roots) with no statistical differences among the four oak species in any of the four light levels. From there, the RSRs separated into the two groups with black and white oak having higher RSRs than chestnut and northern red oak ($P < 0.05$). In 5% sunlight, the RSRs declined slowly, eventually reaching 1.0 (equal root and stem growth) by year 5 for chestnut and northern red oak and year 7 for black and white oak. At 15% sunlight, the RSRs stayed between 2.0 and 3.0 until year 6 and then declined suddenly to less than 1.0. At 40 and 75% sunlight, black and white oak RSRs rose to 4.5 and 6.0, respectively, before declining to 1.0 in year 6. Chestnut and northern red oak RSRs showed no such increase; rather they stayed constant at 3.0 for 2 years or began to decline steadily to 1.0 in year 6.

Discussion

Generally, the results confirm the test hypothesis: northern red oak seedlings are substantially different from those of black and white oak in survival and growth in all four sunlight levels. These three species formed two groups: northern red oak and black/white oak. For 5 years in 5% sunlight, more northern red oak seedlings survived than did black and white oak seedlings. At this light level during the last 2–3 years of the study, northern red oak seedlings grew taller and developed larger roots than did the black and white oak seedlings. Northern red oak's RSR also differed from that of black and white oak, but not as expected. Instead of having a larger RSR, northern red oak had a smaller ratio than black and white oak, indicating that northern red oak allocated a larger proportion of its biomass to stem growth than did black and white oak.

Increasing sunlight levels to 15, 40, or 75% accentuated the differences in height growth and root development between northern red oak and black/white oak. Depending on the specific light environment and attribute, northern red oak seedlings began outgrowing white oak seedlings by year 2 and black oak seedlings by year 3–5. By the end of the study, northern red oak seedlings were 2–3 times taller than black and white oak seedlings. This same degree of difference occurred in root collar development. By the end of the study, RCDs of northern red oak ranged from 8 to 20 mm, whereas RCDs of black and white oak were only half as large. Increasing sunlight to the 15, 40, and 75% levels improved the survival of black and white oak seedlings to the point that it was equivalent to that of northern red oak seedling survival. The RSR patterns of northern red and black/white oak growing in 5% sunlight also occurred in the other three light

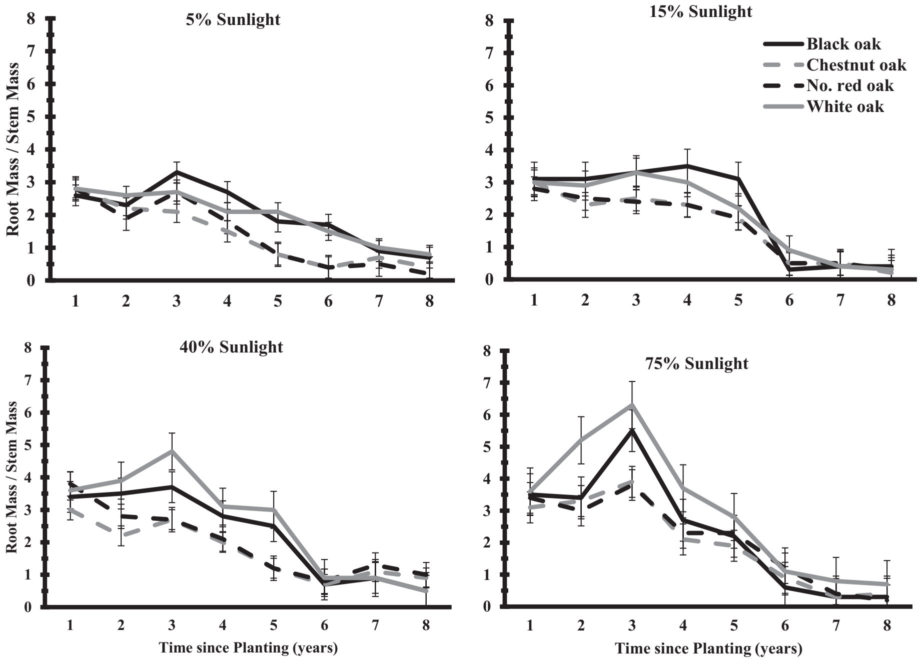

Figure 4. The mean RSR of black, chestnut, northern red, and white oak seedlings in 5, 15, 40, and 75% sunlight from germination through the 8th growing season. Vertical bars indicate 1 SE.

levels. Black and white oak RSRs were generally double those of northern red oak, indicating that they allocated more resources to root development than did northern red oak.

Depending on the light level, chestnut oak displayed survival, growth, and biomass allocation attributes of both oak groups. Most of the time chestnut oak responded similarly to northern red oak, but at times it responded like black and white oak. At 5% sunlight, chestnut oak height growth and biomass allocation were equivalent to those of northern red oak, whereas its survival and root collar growth tracked that of black and white oak. Increasing sunlight to 15 and 40% made chestnut oak seedlings grow and allocate biomass similar to northern red oak. However, 75% sunlight resulted in chestnut oak seedlings growing and allocating biomass in manners consistent with those of black and white oak. At the 15, 40, and 75% sunlight levels, survival of chestnut oak seedlings was comparable to that of the other three oak species.

These findings both support and are at variance with accepted knowledge regarding white oak. Among the upland oaks, white oak is considered to be one of the slowest growing species and to be more shade tolerant than its associated oak species (Rogers 1990, Johnson et al. 2009). This study clearly supported the first point: white oak seedlings were the shortest and had the smallest root collars in all four different light levels after 8 years. In contrast, the superior survival of northern red oak seedlings at 5% sunlight suggests it might be more shade tolerant than white oak. Similarly, the fact that northern red oak seedlings grew in 15% sunlight whereas white oak showed little improvement further suggests that northern red oak is more shade tolerant than white oak. However, the use of single mother trees as the acorn source for each species may be the reason for this discrepancy as shade tolerance can vary within a species (McGee 1968). The shade tolerance ranking of these specific mother trees may have been northern red > white.

The findings of this study support those of previous studies. Gottschalk (1985) found that, in eight different light levels after 2 years, northern red oak seedlings were approximately twice as large as black oak seedlings. This study produced comparable results; in four light levels after 8 years, northern red oak seedlings were 50–100% larger than the black oak seedlings. The result that chestnut oak's growth and biomass allocation closely mirrored that of northern red oak agrees with the finding of Rebbeck et al. (2011) who reported that the two species had nearly identical seedling height, basal diameter, and RSR measurements in three different light environments after 2 years. The modest growth response of northern red oak and the lack of a growth response by black and white oak to 15% sunlight are consistent with previous research (Loftis 1990, Lorimer et al. 1994, Kass and Boyette 1998, Miller et al. 2004) and indicate that small increases in understory lighting favor northern red oak seedlings but provide negligible benefits for black and white oak seedlings.

Beyond the comparisons among the four oak species, this study clearly illustrates that seedling inventories need to be species specific so prescriptions can be tailored to meet the growth requirements of the individual species. Second, this study demonstrates that the results of earlier comparative oak seedling studies accurately reflect and are transferable to actual forest conditions despite them having been conducted in tightly controlled environments such as planting plots or greenhouses and only lasting 1 or 2 years. Finally, the study reiterates the fact that regenerating oak stands of any of the oak species is a protracted process that will involve multiple treatments.

This study has limitations and shortcomings. The four mother trees used for the seed source may not have been representative of the four species, despite selection of dominant healthy mature individuals, so the ranking of northern red and chestnut oak as faster growing than black and white oak may be erroneous. Similarly, the single mother trees may have amplified between-tree variation in such things as shade tolerance. Scarlet oak could not be included in the study because sufficient seed could not be found. Caution needs to be exercised when these results are applied outside the parameters of this study. This research was conducted on acorn-origin oak seedlings planted in fenced stands on intermediate and mesic sites in Pennsylvania. Existing oak seedlings growing on other sites elsewhere may respond differently due to differences in physiological condition, site quality, interspecies competitive relationships, and deer browsing impact.

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