A comparison of the effects of different shelterwood harvest methods on the survival and growth of acorn-origin oak seedlings

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Abstract: Timely development of newly germinated oak (*Quercus* spp.) seedlings into competitive-sized regeneration is an essential part of the oak regeneration process. The amount of sunlight reaching the forest floor partly governs this development, and foresters often use the shelterwood system to expose oak seedlings to varying degrees of insolation. To further understand the seedling development–sunlight–shelterwood relationships, I conducted a multiyear study at five locations in Pennsylvania. Each location had four stands either uncut or recently treated with one of three shelterwood harvest methods (preparatory cut, first removal cut, or final removal cut) resulting in four different levels of sunlight reaching the forest floor. In each stand, four 32 m^2 plots were prepared, and each was planted with 400 acorns of black (*Quercus velutina* Lam.), chestnut (*Quercus montana* Willd.), northern red (*Quercus rubra* L.), or white oak (*Quercus alba* L.) and protected from wildlife. Germination success was universally high and for the next 8 years, I monitored seedling survival and measured seedling growth. The final and first removal cut treatments had higher seedling survival than the preparatory cut and uncut treatments. Oak seedling growth was positively related to sunlight availability; seedlings in the final removal cut grew the most, followed in descending order by those in the first removal cut, preparatory cut, and uncut treatments. These findings provide insight into the subtleties of regenerating oak forests with the shelterwood system.

Résumé : Le développement au moment opportun des semis de chêne (*Quercus* spp.) nouvellement germés vers une régénération de taille compétitive est une étape essentielle du processus de régénération du chêne. La quantité de lumière qui atteint la couverture morte régit en partie le développement des semis et les forestiers utilisent souvent le système de coupe progressive d'ensemencement pour exposer les semis de chêne à différents régimes lumineux. Pour mieux comprendre les relations entre le développement des semis, la lumière et la coupe progressive, j'ai réalisé une étude s'étalant sur plusieurs années dans cinq secteurs de la Pennsylvanie. Chaque secteur comportait quatre peuplements parmi lesquels un de ces peuplements avait été laissé intact alors que les autres avaient récemment subi une des trois coupes du système de coupe progressive (coupe préparatoire, première coupe d'ensemencement et coupe finale), ce qui a produit quatre régimes de lumière au niveau de la couverture morte. Dans chaque peuplement, quatre placettes de 32 m^2 ont été établies et protégées contre la prédation après y avoir planté 400 glands de chênes noir (*Quercus velutina* Lam.), de montagne (*Quercus montana* Willd.), rouge (*Quercus rubra* L.), ou blanc (*Quercus alba* L.). Le taux de germination était élevé dans tous les traitements et, au cours des huit années suivantes, j'ai suivi la survie des semis et mesuré leur croissance. Le taux de survie des semis établis après la coupe finale et la première coupe d'ensemencement était plus élevé que celui des semis établis après la coupe préparatoire et sous les peuplements non coupés. La croissance des semis de chêne était positivement reliée à la disponibilité de la lumière; elle était maximale dans la coupe finale suivie en ordre décroissant par, la première coupe d'ensemencement, la coupe préparatoire et les peuplements non coupés. Ces résultats fournissent un aperçu des subtilités de la régénération des chênaies à l'aide du système de coupe progressive d'ensemencement.

[Traduit par la Rédaction]

Introduction

Throughout eastern North America, mixed-oak (*Quercus* spp.) forests on upland sites are highly valued for their many ecological and economic attributes. Generally, these upland forests consist of one or more oak species (black (*Quercus velutina* Lam.), chestnut (*Quercus montana* Willd.), northern red (*Quercus rubra* L.), scarlet (*Quercus coccinea* Muenchh.), and white (*Quercus alba* L.)) dominating the canopy with a mix of other hardwood species in the midstory and understory strata. These mixed-oak forests have been an integral part of the eastern hardwood biome for millennia (Patterson 2006), but their long-term sustainability is now in doubt (Healy et al. 1997; Nowacki and Abrams 2008), especially on intermediate and mesic sites, due to a wide variety of factors (Lorimer 1993; McWilliams et al. 2007).

One of the factors complicating upland oak forest sustainability is oaks' protracted regeneration process, which typi-

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cally lasts 10 to 25 years (Crow 1988; Loftis 1990*a*; Lorimer 1993). This regeneration process consists of acorn production, seedling establishment, seedling development, and capture of enough growing space in a new stand to ensure eventual oak dominance (Johnson et al. 2009). Regenerating upland oak forests takes this much time because of two intrinsic silvical characteristics — sporadic acorn production and slow juvenile growth — and several extrinsic factors such as weather, insects and (or) disease, wildlife, shading, and competing vegetation that can slow or stall any of the phases. Of these characteristics and factors, the effects of shading on oak seedlings' survival and growth during the seedling development phase is especially deleterious because shading occurs throughout the range of oak forests in eastern North America (Lorimer 1993).

For decades, scientists have studied the sunlight requirements of oak seedlings (Bourdeau 1954; Phares 1971; Kolb et al. 1990). Young upland oaks are intermediate in their tolerance of shade (Burns and Honkala 1990). Shade-tolerance ranking of these five species is white > chestnut > northern red > black > scarlet (Johnson et al. 2009). Most species can survive for several years in as little as 5% of full sunlight (Hanson et al. 1987), but they need at least 20% of full sunlight before they can consistently maintain stem growth (Dickson 1991; Gottschalk 1994). Maximum photosynthesis of northern red oak seedlings occurs at about 30% of full sunlight, with little increase at higher light levels (Bourdeau 1954; Phares 1971; Kolb et al. 1990). To meet these light requirements, land managers often use the shelterwood system.

The partial sunlight effects of shelterwoods on oak seedling growth also have a rich research history. Gottschalk (1985, 1987) determined that black and northern red oak seedlings grew equally well once understory sunlight was increased to 20%–80%, a typical range for many shelterwoods, but black cherry (*Prunus serotina* Ehrh.) and red maple (*Acer rubrum* L.) seedlings outperformed the oaks. Kolb and Steiner (1990) compared the growth responses of northern red oak and yellow-poplar (*Liriodendron tulipifera* L.) seedlings at full sun and 37% sun. They found that reduced sunlight had less impact on the oak seedlings, suggesting that shelterwoods could be used to reduce competition from yellow-poplar on sites where both species occur. Canham et al. (1996) studied the growth responses of northern red oak, red maple, sugar maple (*Acer saccharum* Marsh.), and white pine (*Pinus strobus* L.) seedlings to a range of sunlight conditions and soil limitations. The northern red oak seedlings were more affected by reduced sunlight than by nutrient limitations and had comparable growth among all sunlight levels greater than 10%. Sung et al. (1998) examined the growth responses of northern red and white oak to three sunlight levels (full sun, 30% sun, and 70% sun) and found that both species grew the least in 30% sun and grew equally well at the other two levels. Commonalities among these studies are that they were short-term studies (1 to 2 years maximum) and were conducted in highly controlled environments such as planting plots or greenhouses. Oak seedlings growing in different understory light conditions in the forest and for longer periods of time may develop in markedly different manners. Unfortunately, such studies are rare. Three notable exceptions are Loftis (1990*b*), Lorimer et al. (1994), and Miller et al. (2004). All three studies followed survival and growth of naturally occurring cohorts of northern red oak seedlings to small increases in understory sunlight for at least 5 years. Collectively, they found high mortality of oak seedlings in untreated controls (<5% sun) with little growth by survivors. Increasing understory sunlight to 10% or more significantly increased oak seedling survival and growth. However, none of the studies included other species of oak, examined large increases in sunlight such as could be expected with shelterwood removal harvests, or directly measured root development.

The overall objective of this study was to increase understanding of how the understory sunlight conditions created by three common shelterwood harvest methods impact the survival and growth of black, chestnut, northern red, and white oak seedlings. Specific hypotheses were as follows.

1. The different shelterwood harvests will create distinct understory sunlight regimes, and these will remain relatively stable for at least 5 years.
2. For each oak species, fewer seedlings will survive in the uncut treatment than in the three shelterwood cuts, but seedling numbers will not differ among the three shelterwood cuts.
3. For each oak species, seedling root development and stem growth will differ among treatments based on whether they provide less than or more than 30% sunlight.
4. For each oak species, the timing of the shift in biomass allocation from roots to stems will differ among treatments as follows: 1st, final removal cut; 2nd, first removal cut; 3rd, preparatory cut; and 4th, uncut.
5. At the end of the study, the oak seedlings of each species will be in a stronger competitive position in the first removal cut than in any of the other treatments.

Understanding how oak seedlings develop roots as well as stems under a broad array of shelterwood harvest types and how they relate to other hardwood seedlings after several years will be useful to managers trying to regenerate oak forests with this silvicultural system.

Methods

Study sites

This study was conducted at five sites (Allegheny National Forest (ANF), Bald Eagle State Forest (BESF), Clear Creek State Forest (CCSF), Elk State Forest (ESF), and Game Land 152 (GL152)) in central and western Pennsylvania. The BESF, CCSF, and ESF sites are owned and managed by the Pennsylvania Bureau of Forestry, whereas GL152 is on Pennsylvania Game Commission property. The ANF site is part of the US 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). GL152 was glaciated (Yaworski et al. 1979), while the others were never glaciated (Zarichansky 1964; Braker 1981; Cerutti 1985; Kopas 1993). GL152 was the wettest site, while ESF was the coolest and BESF was the hottest and driest. BESF was on north-facing, midslope benches, while the others were on broad, flat hilltops where aspect was inconsequential. ANF and ESF were channery loams, while BESF and CCSF were stony loams, and GL152 was a silt loam. Site index for northern red oak at age 50 varied from 20 m at ESF and BESF to 23 m at ANF and CCSF to 27 m at

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

Characteristic	Allegheny National Forest	Bald Eagle State Forest	Clear Creek State Forest	Elk State Forest	Pennsylvania Game Land 152
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)	1080	965	1030	1070	1080
Snowfall (mm)	1875	610	1010	2140	2370
Growing season (days)	135	148	116	109	140
Elevation (m, above sea level)	565	500	535	575	300
Slope (%)	<5	5 to 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	White oak	Northern red oak	White oak	Northern red oak
	Black cherry	Chestnut oak	Red maple	Chestnut oak	Sugar maple
	White oak	Northern red oak	Black cherry	Northern red oak	Yellow-poplar
	Red maple	Red maple	White oak	Red maple	White ash
	Cucumbertree	Black gum	Chestnut oak	Black gum	American beech

*Height (in metres) of the dominant northern red oaks at age 50.

GL152. Site quality differences were evident in the forest composition. GL152 was dominated by northern red oak growing in association with sugar maple, white ash (*Fraxinus americana* L.), and yellow-poplar. Common tree species at ANF and CCSF were northern red oak, chestnut oak, white oak, black birch (*Betula lenta* L.), black cherry, and red maple. ESF and BESF had the same species, but white and chestnut oaks predominated and both had a considerable amount of black gum (*Nyssa sylvatica* Marsh.).

Study design and installation

In summer 2001 at each site, I chose four oak stands. Three had been treated recently with one of the harvests of a three-cut shelterwood system (preparatory cut, first removal cut, or final removal cut), and the fourth was uncut and served as the control. Shelterwood terminology follows Smith (1986). The uncut stands were fully stocked stands with intact main canopies, well-developed subcanopies, little or no sign of any recent cutting, and a dark, dense understory shade. The preparatory cut stands had intact main canopies, but sparse subcanopies due to recent removal of most of the intermediate and suppressed trees, and a diffuse understory shade. Also, in the uncut and preparatory cut stands, understory herbaceous vegetation either was lacking or had been controlled by a recent broadcast spraying of a sulfometuron methyl herbicide. The first removal cut stands had large gaps in the main canopy, a limited subcanopy, and a partial patchy understory shade due to a recent large-scale harvest. The final removal cut stands had received a complete overstory harvest 1 to 2 years earlier. They were devoid of any canopy cover, except for occasional 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 GL152 were surrounded by 2.3 m high woven wire fence to exclude white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)).

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

Also in fall 2001 in each stand, four 8 m × 4 m plots were selected for acorn planting based on the plot being suitable for mechanical tilling, i.e., free of large surface rocks. Each plot was 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. Each plot was randomly assigned to one of four oak species for acorn planting. In each plot, approximately 400 sound acorns (10 to 15 acorns·m^{-2}) of the assigned species were planted at a depth of 2.5 cm. Chestnut and white oak acorns were planted in fall 2001, and 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. Deer penetrated fences that same summer at the ANF final removal cut, BESF uncut, ESF first removal cut, and ESF final removal cut stands, resulting in those plantings being destroyed by browsing. Deer also destroyed the plantings in the unfenced final removal cut stand at GL152. All these stands were replanted in fall 2002 and protected with additional fencing. Replanted plots also had at least 350 seedlings but lagged behind the other plantings by 1 year.

Data collection

Commencing in summer 2002 and annually thereafter for 8 years, the stand structure and understory lighting of each plot was quantified by calculating the relative density (RD) and measuring the photosynthetically active radiation (PAR). To calculate RD (a measure of stand stocking), basal area was determined from the center of each plot using a 10-factor prism. All trees viewed as "in" with the prism were identified to species and measured for diameter at the height of 1.37 m. RD was then calculated for each plot from the basal area data using established crown-area equations (Brose et al. 2008). PAR was measured with a bar ceptometer in late June or early July between 1100 hours and 1400 hours on uniformly overcast days (Parent and Messier 1996; Gendron et al. 1998). Fifteen readings were taken systematically over each entire planting bed directly above the tallest oak seedlings. Also, the ceptometer was pointed south to avoid accidentally shading the photoreceptors. At the same time, a second light meter was used in fully open conditions to record the maximum ambient light level at 5 s intervals. Both sets of readings were averaged, and the two means were used to calculate the proportion of full sunlight reaching each plot.

Beginning in fall 2002 and annually thereafter for 8 years, the living oak seedlings were tallied (COUNT) in each plot to compare the number of surviving seedlings among the four treatments 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 basal diameter (BD) and root collar diameter (RCD) to the nearest 0.1 mm and stem height (STH) and taproot length (TRL) to the nearest 0.1 cm. BD is where the stem arises above the leaf litter, while RCD 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 mass, stem dry mass (STM) and taproot dry mass (TRM) were determined to the nearest 0.1 g using an electronic scale. STM included the main stem and all branches, but not the foliage, whereas TRM included the taproot, as well as all lateral and feeder roots attached to the taproot. The root-to-stem ratio (RSR) of each seedling was calculated by dividing its TRM by its STM.

Soil compaction data were collected for use as a covariate in the analysis because that factor may influence root development. Beginning in 2002 and annually thereafter, soil compaction (depth in centimetres to a pressure of 14 065 $g \cdot cm^{-2}$) was measured in each plot to a maximum depth of 75 cm with a penetrometer. Five readings were made in each plot, at the four corners and the center, and these were averaged to obtain one reading for the plot.

In the last year of the study, the stems of non-oak reproduction growing in and within 2 m of each plot's sides were identified to species and tallied into three height classes (<1 m, 1 to 2 m, and >2 m). Also, the height of the tallest stem of each non-oak species was measured to the nearest 0.5 m, and each plot was designated as being dominated by birch, cherry, maple, oak, or other based on the species of the tallest stem.

Statistical analysis

The light regime and seedling data were analyzed using repeated-measures analysis of variance (ANOVA) and covariance (CANOVA) split-plot designs via Proc Mixed (SAS Institute Inc. 2000). Shelterwood type was the whole-plot unit, and oak seedling species was the subplot unit. The four shelterwood types and four oak seedling species were fixed effects in the model, and site and site × shelterwood effects were random effects in the model. Growing season was the repeated effect in the model. The dependent variables were RD, PAR, COUNT, BD, STH, RCD, RTL, STM, TRM, and RSR. For RCD, RTL, and RSR, soil compaction was added to the model as a covariate. Comparisons among and within main effects and interactions were by 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, $\alpha = 0.05$.

Results

Stand structure and understory light

The treatments created four distinct stand structures and understory light regimes. Initially, the uncut treatment averaged 98% RD and 4% PAR. These were significantly different from the preparatory cut treatment (80% RD and 13% PAR), and both of these treatments were different from the first removal cut treatment (60% RD and PAR). The final removal cut was different from all these treatments as it had 12% RD and 91% PAR. RD never changed in any treatment enough to cause a significant difference among years, but PAR did change through time for three of the four treatments. In the final removal cut treatment, PAR declined substantially to 81% by 2005 and eventually to approximately 60% by 2009. The first removal cut treatment also showed significant decreases for PAR during the same time period: to approximately 43% and 32% for 2005 and 2009, respectively. PAR significantly increased in the uncut treatment to between 9.5% and 12% in 2003 and 2004 before returning to 4% to 5% levels for the duration of the study.

Seedling survival

Analysis of the COUNT variable revealed significant differences ($p < 0.001$) among treatments, species, and years and a treatment × year interaction (Table 2; Fig. 1). Initially, all plantings averaged between 368 and 391 seedlings, with no differences among sites, treatments, or species. From that starting point, the number of living oak seedlings of all four species declined through time. Part of this decline was due to the annual harvesting of 15 seedlings from each planting plot. However, despite this annual harvest, seedling numbers eventually differed among the four treatments. For black, chestnut, and white oak, the uncut treatment had fewer seedlings (178 to 225) than the other three treatments (246 to 296) starting in year 2, and this continued throughout the study. Also for these three species, seedling numbers began

Table 2. ANOVA and CANOVA results for each of the dependent seedling variables.

Variable	Value	Site	Treatment	Species	Treatment × Species	Year	Treatment × Year	Species × Year	Treatment × Species × Year
COUNT	*F*	1.29	13.48	8.14	1.14	50.63	3.66	1.14	0.25
	p	0.175	**<0.001**	**<0.001**	0.336	**<0.001**	**<0.001**	0.696	1.00
BD	*F*	0.20	8.25	11.61	1.73	34.74	3.94	0.55	0.33
	p	0.911	**0.003**	**<0.001**	0.0962	**<0.001**	**<0.001**	0.951	1.0
STH	*F*	3.65	4.28	4.11	1.08	28.15	4.86	0.93	0.62
	p	0.347	**0.027**	**0.011**	0.393	**<0.001**	**<0.001**	0.552	0.988
RCD	*F*	0.22	10.81	11.16	1.95	38.31	4.42	0.72	0.43
	p	0.927	**0.001**	**<0.001**	0.057	**<0.001**	**<0.001**	0.816	1.0
RTL	*F*	0.19	7.62	3.62	0.29	20.82	4.59	0.77	0.12
	p	0.917	**0.004**	**0.016**	0.975	**<0.001**	**<0.001**	1.00	0.938
STM	*F*	0.66	4.38	3.34	1.36	4.98	2.90	0.72	0.63
	p	0.631	**0.026**	**0.021**	0.167	**<0.001**	**<0.001**	0.811	0.987
TRM	*F*	0.71	7.18	12.09	0.34	22.84	3.95	0.98	0.49
	p	0.634	**0.002**	**<0.001**	0.401	**<0.001**	**<0.001**	0.487	0.996
RSR	*F*	0.41	4.86	5.42	1.24	50.62	2.86	0.99	0.95
	p	0.799	**0.019**	**0.004**	0.275	**<0.001**	**<0.001**	0.471	0.588

Note: COUNT, the number of living oak seedlings; BD, basal diameter; STH, stem height; RCD, root collar diameter; RTL, taproot length; STM, stem dry mass; TRM, taproot dry mass; RSR, root-to-stem ratio; *p* values in bold indicate significant differences.

to differ among the three shelterwood cuts in year 4 when counts in the preparatory cut were less than those in the final removal cut. By year 8, the number of black and white oak seedlings in the preparatory cut was no different than that in the uncut, but this was not the case for chestnut oak. For northern red oak, seedling numbers in the uncut did not differ from the other treatments until year 6. Also beginning in year 6, the number of northern red oak seedlings in the preparatory cut treatment was less than in the final removal cut treatment. At year 8, seedling counts averaged 17 in the uncut, 82 in the preparatory cut, 173 in the first removal cut, and 162 in the final removal cut. In all treatments, northern red oak was the most common species.

Stem growth

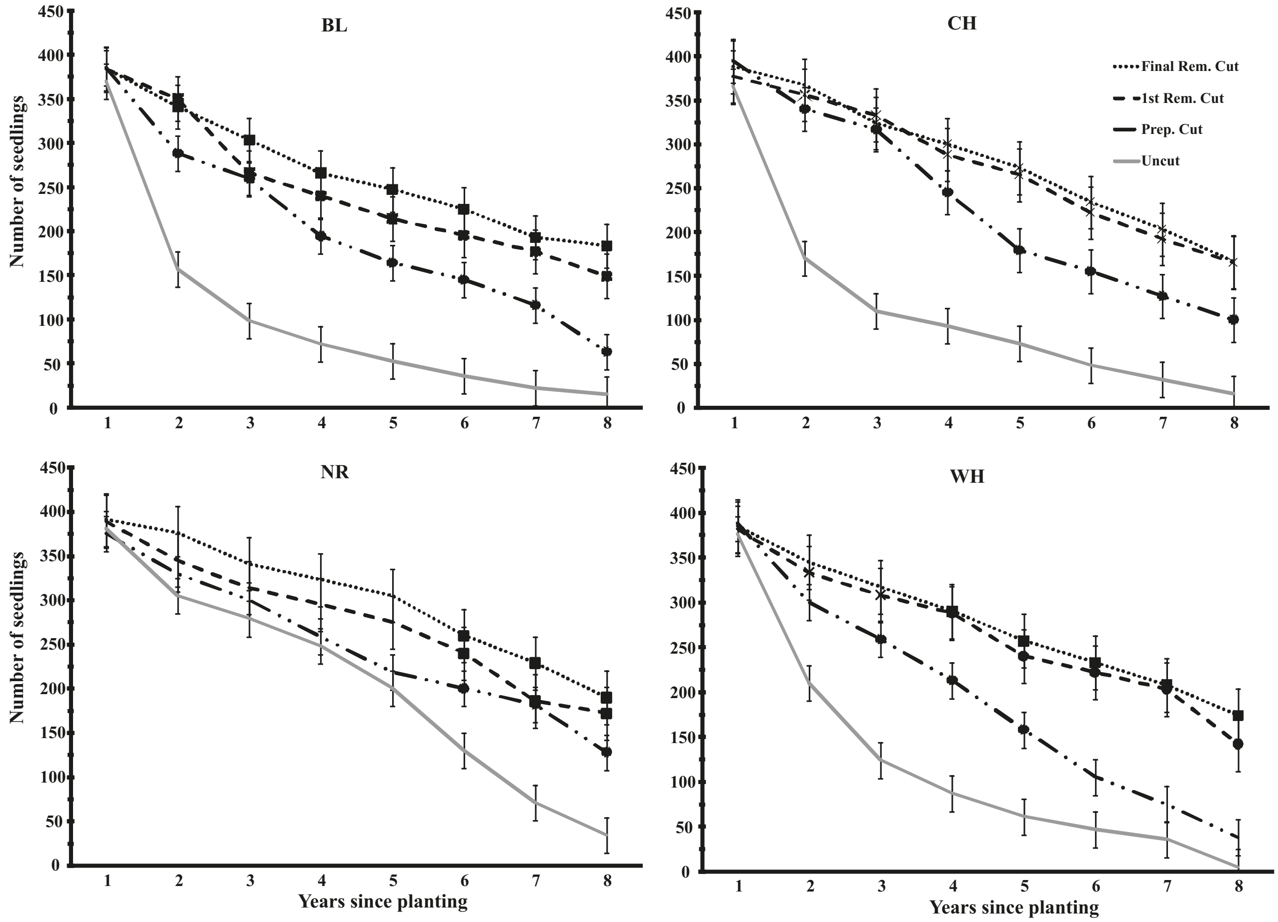
Analysis revealed significant differences among treatments, species, and years and a treatment × year interaction for the two stem variables BD and STH (Table 2; Figs. 2 and 3). Initially, the oak seedlings formed BDs between 2.0 and 3.5 mm with no discernible differences among the four treatments for any of the oak species. That began changing in year 2 when northern red oak seedlings in the final removal cut had larger BD than those in the preparatory cut and uncut treatments. For northern red oak, the treatment means continued differentiating in subsequent years as the final and first removal cut treatments became significantly larger than the preparatory cut and uncut treatments in year 3, the preparatory cut became larger than the uncut in year 4, and all four treatments were different from each other from year 5 through the end of the study. For black, chestnut, and white oak, the four treatments diverged into two or three groups. Commencing in year 3 and continuing through the end of the study, mean BD was larger in the final and first removal cut treatments than in the preparatory cut and uncut treatments. Additionally for black oak, the final and first removal cut treatments became different from each other from year 5 through year 8. At year 8, oak seedlings had average BDs of 4.2 mm in the uncut, 5.5 mm in the preparatory cut, 10.6 mm in the first removal cut, and 13.8 mm in the final removal cut. Black oak had the largest BD in the first three treatments, whereas northern red oak had the largest BD in the final removal cut treatment.

STH varied among treatments for the four oak species (Fig. 3). During the first year, all oak seedlings grew to between 10 and 18 cm tall with no discernible difference among the four treatments for any of the four species. By year 3 or year 4 and thereafter, STH was different among the four treatments for each of the species. For black and northern red oak, year 3 STH was larger in the final removal cut than in the preparatory cut and uncut treatments. Commencing in year 4 for northern red oak and year 5 for black oak, STH was larger in the final removal cut than in all other treatments. For black oak, STH never differed between the preparatory cut and uncut treatments, but they did differ for northern red oak in year 8. STH showed nearly identical patterns through time for chestnut and white oak. No differences among treatments were detected until year 4 when STH for both species separated into two groups, final–first removal cuts and preparatory cut – uncut. For white oak, these groupings continued until the end of the study, but the first and final removal cuts diverged in year 8 for chestnut oak. At the end of the study, the oak seedlings STHs averaged 27 cm in the uncut, 33 cm in the preparatory cut, 98 cm in the first removal cut, and 114 cm in the final removal cut. Northern red oak was the tallest species in all treatments, except in the first removal cut in which chestnut oak had the tallest seedlings.

Root development

After adjusting for differences in soil compactness among the planting plots, analysis showed significant differences among species, treatments, and years and a treatment × year

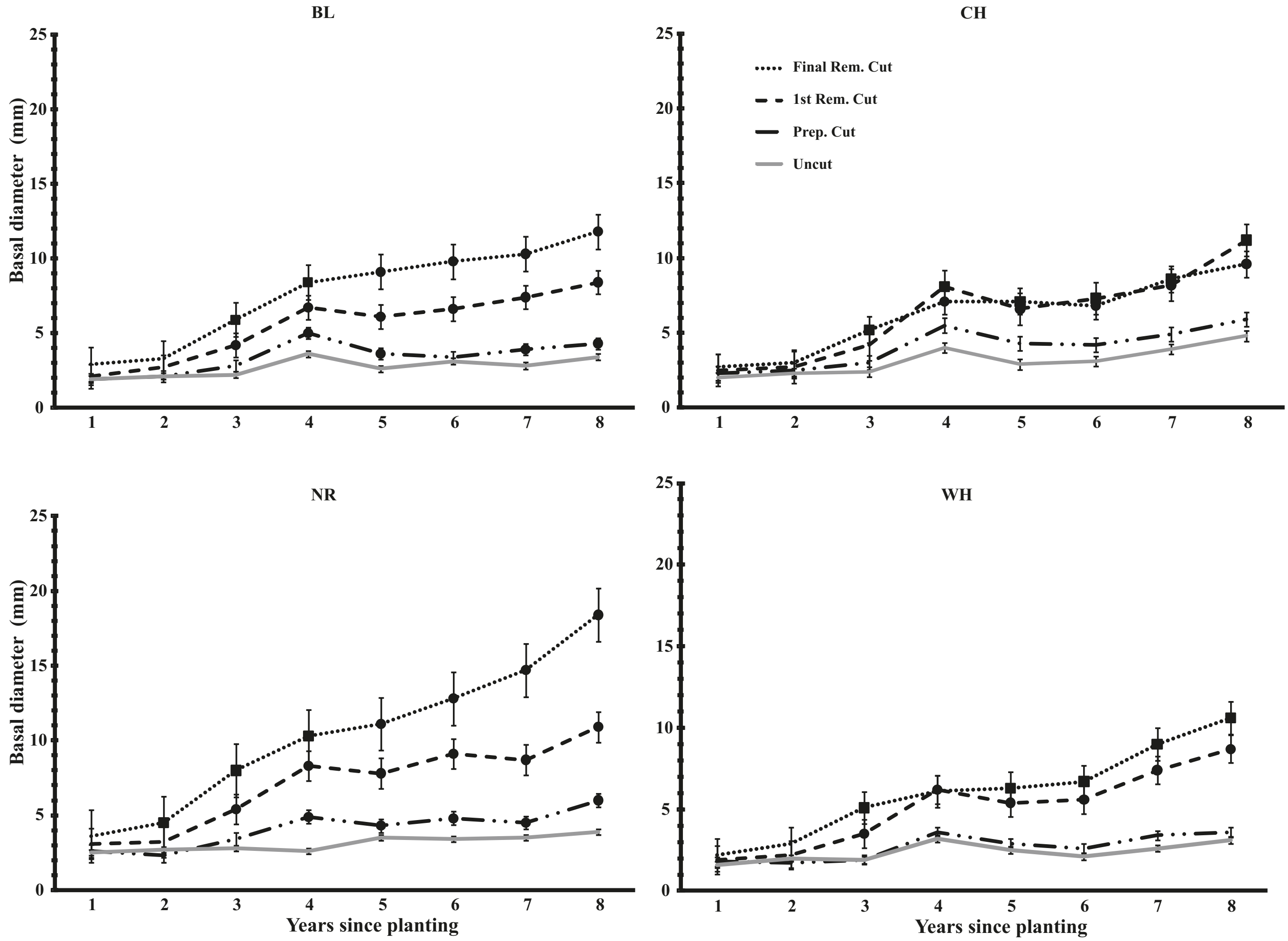
Fig. 1. The number of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings surviving in four different shelterwood treatments for 8 years in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.



interaction for the root development variables RCD and TRL (Table 2; Figs. 4 and 5). All species initially formed mean RCDs of 3.0 to 6.5 mm, with no differences detected among treatments until year 2 when northern red oak mean RCD in the final removal cut became significantly larger than in the preparatory cut and uncut treatments. In year 3, northern red oaks mean RCD in the first removal cut became larger than in the uncut control. Commencing in year 5 and lasting until the end of the study, northern red oak mean RCD became distinct in all four treatments. Black, chestnut, and white oak began showing different RCDs among treatments in year 4. For black oak, the treatments formed three groups: final removal cut, first removal cut, and preparatory cut – uncut combined. For chestnut and white oaks, the treatments formed two groups: final–first removal cuts and preparatory cut – uncut. By the end of the study, mean RCDs were 5.5 mm in the uncut, 7.5 mm in the preparatory cut, 13.4 mm in the first removal cut, and 16.7 mm in the final removal cut, and these all differed from each other. Chestnut oak had the largest RCD in the uncut, whereas northern red oak had the largest RCDs in the other three treatments.

Initially, all oak seedlings formed a taproot between 10 and 30 cm in length, and differences in mean TRL were detected among treatments, depending on the oak species (Fig. 5). For northern red oak, differences among treatments began in year 1 with the final removal cut mean TRL being larger than that of the preparatory cut and uncut control. That treatment difference continued for northern red oak until year 4 when the mean TRL of the first removal cut became larger than that of the uncut treatment. In year 5, mean TRLs for northern red oak formed three distinct groups: final removal cut, first removal cut, and preparatory cut – uncut combined. TRL development for white oak was quite similar to that of northern red oak except that the treatment differences lagged by a year (years 2 and 5 instead of years 1 and 4 for manifestation of treatment differences). Black and chestnut oak began showing treatment differences in mean TRL starting in year 4. At that time, for black oak, mean TRL was largest in the final removal cut, smallest in the preparatory cut and uncut control, and intermediate in the first removal cut. Chestnut oak had a similar pattern except that final and first removal cuts did not become significantly different from each other until year 7. At the end of the study, mean TRLs in the treatments were 28 cm in the uncut, 35 cm in the preparatory cut, 69 cm in the first removal cut, and 92 cm in the final removal cut. Black oak had the largest roots in the first and final removal cuts, whereas northern red oak had the largest roots in the uncut and preparatory cut.

Fig. 2. Mean stem basal diameters (mm) of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings grown for 8 years in four different shelterwood treatments in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.

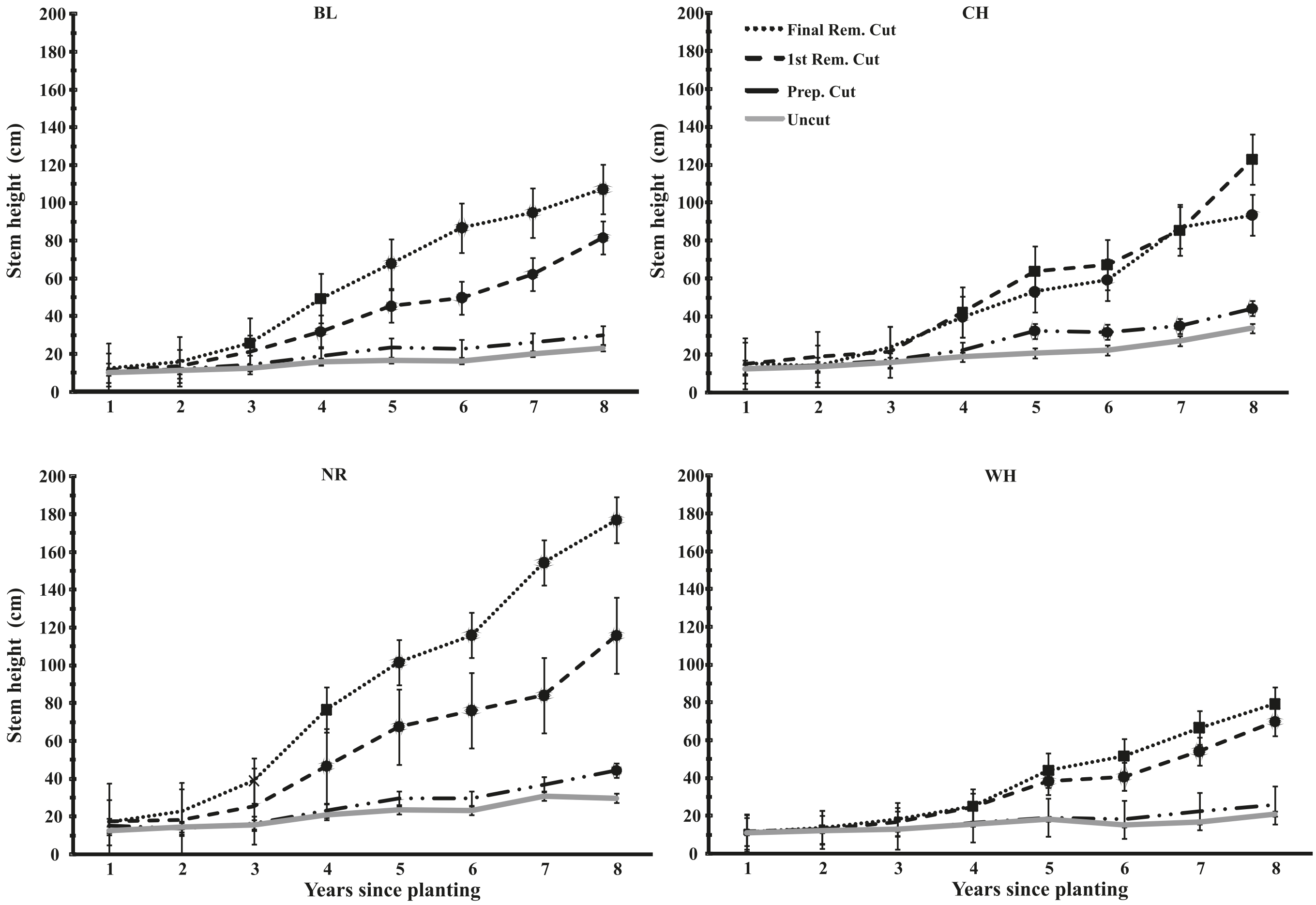


Biomass accumulation and allocation

Like the root and stem variables, the biomass variables (STM, RTM, and RSR) had significant differences among species, treatments, and years and a treatment × year interaction (Table 2). Initial STM accumulations were miniscule (<0.5 g) and remained that way for the first 3 years, regardless of species or treatment (Fig. 6). However, starting in year 4, northern red oak seedlings in the final removal cut began having larger STM than in the preparatory cut and uncut treatments. Black oak showed the same treatment differences as northern red oak beginning in year 5, and in year 7, both species had significant differences in mean STM between the first and final removal cuts and between both of these treatments and the preparatory cut – uncut grouping. Chestnut and white oak had nearly identical differences among treatments. Both showed no differences among treatments until year 7 when the treatments separated into three groups: final removal cut, first removal cut, and preparatory cut – uncut combined. At the end of the study, mean STMs among treatments were 4.5 g in the uncut, 5.7 g in the preparatory cut, 34.3 g in the first removal cut, and 88.0 g in the final removal cut. In the uncut, preparatory cut, and first removal cut treatments, northern red oak had the largest STM of the four species. However, in the final cut, black oak and northern red oak had nearly equal STMs. This was due to the black oak seedlings developing more branches than the northern red oak seedlings.

Relative to their respective STMs, the average TRMs of the four oak species were considerably larger and quickly differentiated by treatment (Fig. 7). Initial TRMs were 0.5 to 3.0 g, with no differences among treatments for any of the species. By year 3 or year 4, mean TRM was larger in the final removal cut than in the preparatory cut and uncut control for all species. Starting in year 4, mean TRM for black and northern red oak formed three treatment groupings (final removal cut > first removal cut > preparatory cut = uncut) that persisted until the end of the study. For chestnut and white oak, the treatments formed two distinctive groups: final–first removal cuts and preparatory cut – uncut commencing in either year 3 or year 4, depending on species. At the end of the study, mean RTMs were 5.3 g in the uncut, 7.9 g in the preparatory cut, 28.7 g on the first removal cut, and 35.2 g in the final removal cut. In all treatments, northern red oak had the largest RTMs.

Fig. 3. Mean stem heights (cm) of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings grown for 8 years in four different shelterwood treatments in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.



The final biomass variable (RSR) showed an overall downward trend through time for all species (Fig. 8). Initial average RSRs for all species ranged from 2.6 to 3.9 regardless of treatment, with no differences detected among treatments. From those starting points, RSRs generally increased through year 3 in all treatments from 3.9 to 6.3. At that time, for each species, RSR was significantly greater in the final removal cut than in all other treatments. This was the only significant treatment effect found for black, chestnut, and northern red oak. For white oak, RSR in the first removal cut was also greater than in the preparatory cut and uncut treatments in years 2 and 3. From years 3 to 6, RSRs for all species in all treatments decreased to approximately 1.0, where they stabilized for the rest of the study.

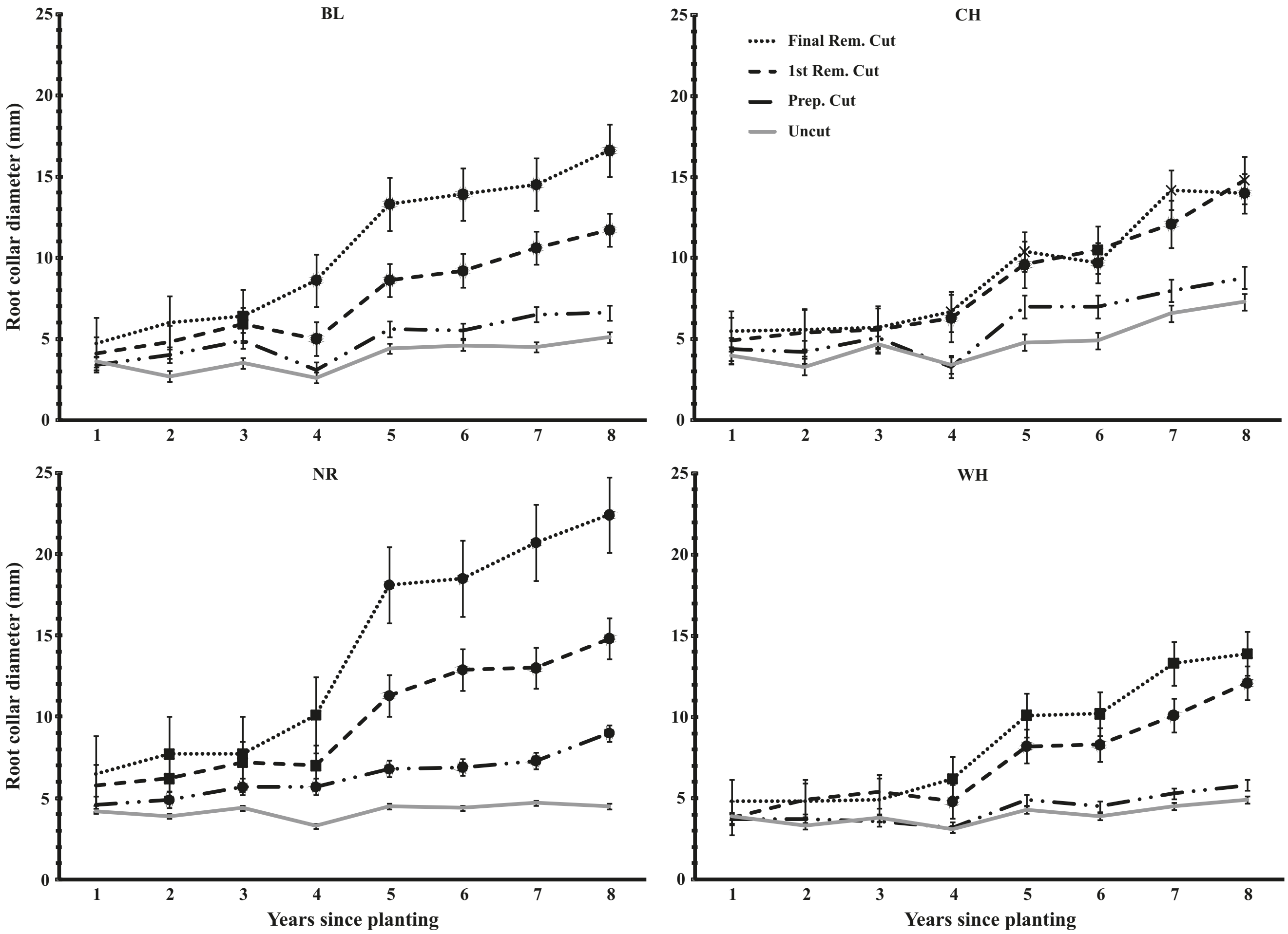
Responses of other tree species

The four treatments caused common hardwood associate species to regenerate and grow during the course of the study (Table 3). The uncut treatment contained approximately 7500 stems·ha^{-1}, and the maples, especially red maple, comprised nearly 60% of this total. Heights varied from <1 to 4 m (the tallest red maple) due to the pre-existence of saplings, whereas the tallest oaks ranged from 0.29 to 0.39 m. The preparatory cut contained more than 12 000 stems·ha^{-1}, and red maple was the dominant species. Regeneration heights were less variable in the preparatory cut due to the removal of the saplings at the beginning of the study. Also, the heights of the tallest non-oaks were reduced to between 2.0 and 2.5 m, whereas the tallest oaks ranged from approximately 0.5 to 1.0 m. In the first removal cuts, densities of non-oak also averaged more than 12 000 stems·ha^{-1}, and composition was a mix of black birch, black cherry, pin cherry (*Prunus pensylvanica* L.f.), red maple, and sassafras (*Sassafras albidum* (Nutt.) Nees). The heights of the tallest stems of these species ranged from 4.0 to 5.5 m. The tallest oaks ranged from approximately 2.0 to 2.5 m. The final removal cuts contained nearly 14 000 stems·ha^{-1}. Black birch and pin cherry dominated numerically and in height, with the tallest stems of these two species measuring 7.5 and 11.0 m, respectively. The tallest oaks in the final removal cuts were from 2 to 4.3 m in height. In all treatments, the tallest oak was always a northern red oak.

Discussion

Regenerating upland oak forests on intermediate and mesic sites requires skillfully establishing oak seedlings and growing them to a competitive size while retarding the development of reproduction of other hardwood species. To meet

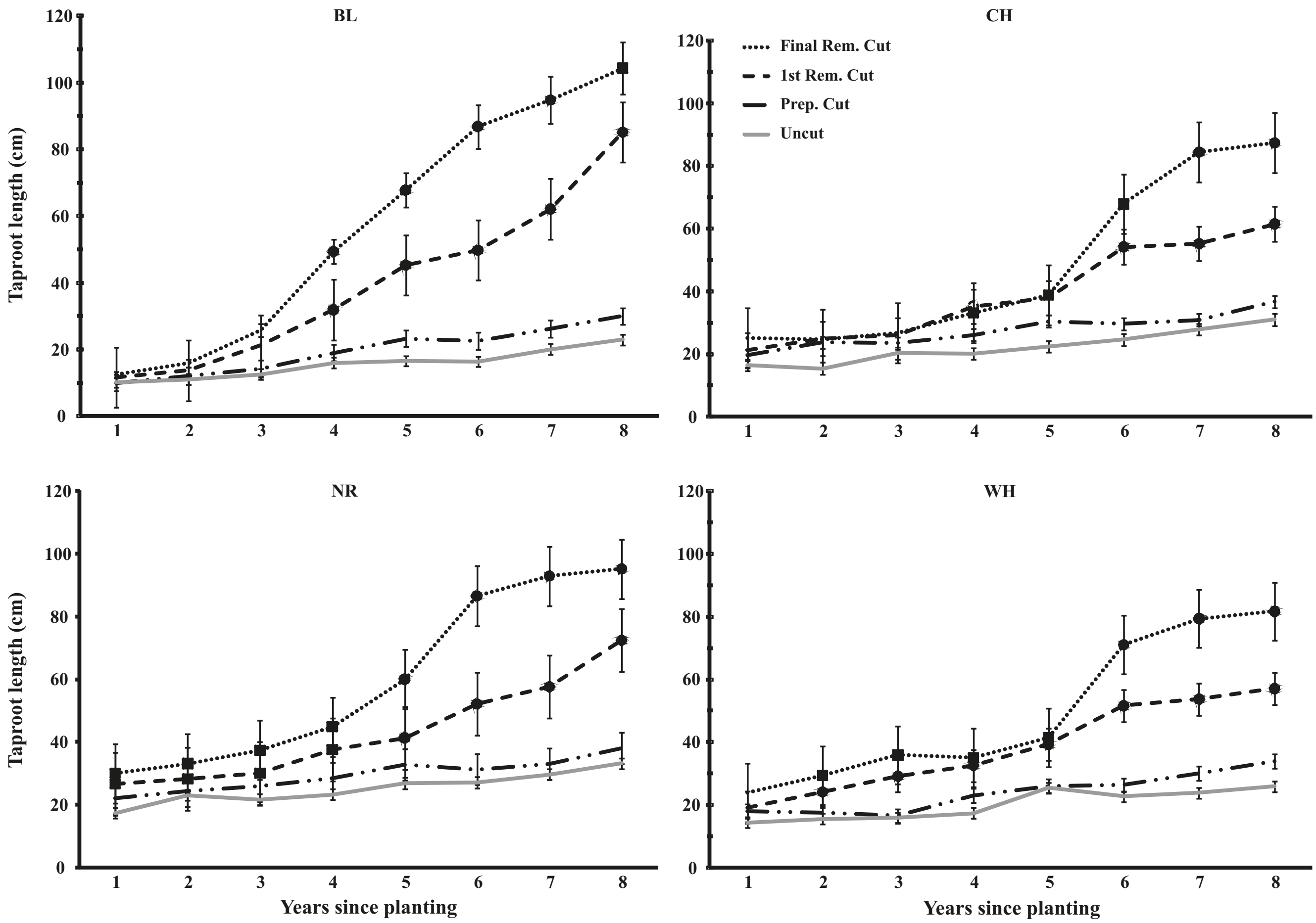
Fig. 4. Mean root collar diameters (mm) of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings grown for 8 years in four different shelterwood treatments in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.



this goal, foresters often use the shelterwood system, but results are not consistently positive (Schlesinger et al. 1993; Schuler and Miller 1995). The findings of this study help explain how and when to apply the shelterwood system in mixed-oak forests to meet the competing and conflicting silvical characteristics of oak seedlings and associated hardwood reproduction.

Hypothesis 1, the shelterwood cuts would create distinct understory light regimes and these would remain relatively stable for at least 5 years, was partly validated. The treatments clearly created four different residual stands with RDs of 98%, 80%, 59%, and 12%. Corresponding PAR levels were 4%, 14%, 50%, and 90%, but only the two lowest levels remained largely unchanged during the study. The 4% PAR level of the uncut stands (98% RD) doubled during 2003 and 2004 due to an anthracnose outbreak, but PARs reverted to their initial levels once the trees refoliated and remained at 4% to 5% through the rest of the study. These values are within the range of PAR levels reported for other mixed hardwood forests (Hutchison and Matt 1977; Baldocchi et al. 1986; Miller et al. 2004). In general, closed-canopy multistrata hardwood forests permit between 2% and 8% of full sunlight to reach the forest floor, with the species composition and minor canopy disturbances probably causing much of this variation. The preparatory cuts (80% RD) removed the suppressed and smaller intermediate trees, creating an open understory with diffuse shade and 14% PAR, a level comparable with that found by Miller et al. (2004) in similarly treated mixed oak stands in West Virginia. The 14% PAR remained unchanged for the entire study, suggesting that removing these understory and midstory trees creates a diffuse shade environment that endures for at least 8 years and, quite likely, for considerably longer. The first removal cuts (59% RD) increased forest-floor PAR to 50%. These levels gradually declined to approximately 30% in 2009 because of canopy expansion of the residual trees and development of the non-oak seedlings in and near the plots casting shade onto the plots. The proportion of understory light will continue to gradually decline in the future because many of the residual trees are northern red oaks, a species capable of rapid canopy enlargement (Miller et al. 2006). In 2002, the final removal cut stands (12% RD) had virtually no overstory left standing after these harvests. However, growth of non-oak seedlings in and near the plots was rapid and began influencing the light meter readings by the third year (2004). By 2009, some of these seedlings had grown into saplings,

Fig. 5. Mean taproot length (cm) of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings grown for 8 years in four different shelterwood treatments in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.



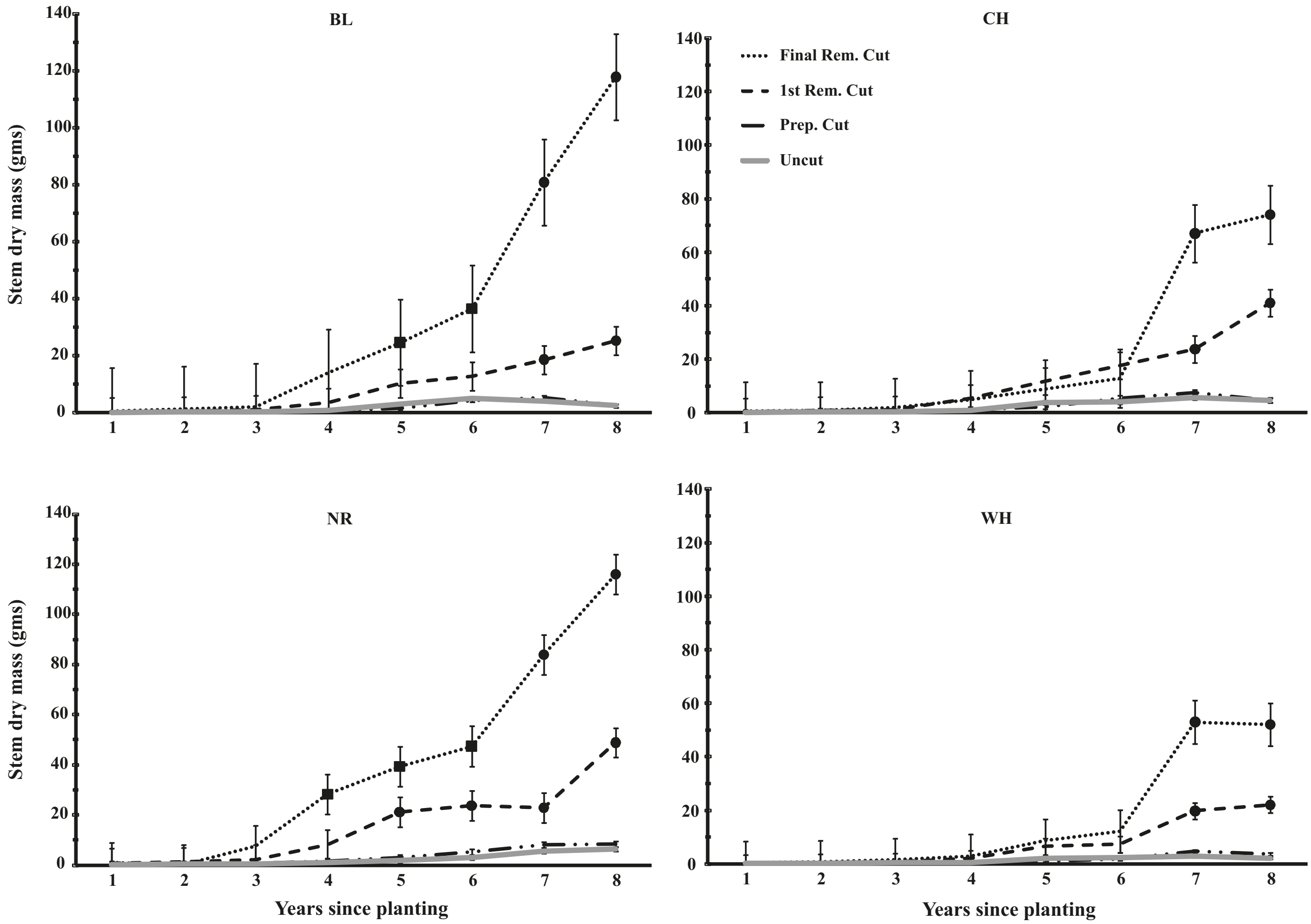
causing understory light to decline to less than 60% for the smaller oaks. PAR will continue to rapidly decline, and in a few years, understory light levels will be less for the oaks than they are in the first removal cut treatment.

Hypothesis 2, oak seedling survival will differ between uncut and the three shelterwood treatments, but not among the three shelterwood treatments, was partly validated. There were fewer black, chestnut, and white oak seedlings in the uncut controls than in any of the other treatments. Also, there were always fewer seedlings of these species in the preparatory cut than in the first and final removal cut, especially in the latter half of the study. Conversely, the number of northern red oak seedlings in the uncut stands was not different from the shelterwood harvest treatments until year 7, but this difference probably was not ecologically meaningful. The pertinent literature indicates that white oak is the most shade tolerant of these species (Johnson et al. 2009), but these data show that more northern red oak seedlings survived in the uncut treatment than any of the other species, suggesting that it is more shade tolerant than the others. The use of single mother trees as the acorn source for each species maybe the reason for this discrepancy (McGee 1968). The shade-tolerance ranking of these specific mother trees may have been northern red > black = chestnut = white.

The small increase in understory light between the uncut and preparatory cut treatments (4% to 14%) significantly improved survival for black, chestnut, and white oak and generally benefitted northern red oak. This is consistent with previous research (Loftis 1990*b*; Lorimer et al. 1994; Miller et al. 2004) and indicates the importance of controlling low shade early in the oak regeneration process via a preparatory cut or other silvicultural treatment.

Hypothesis 3 was that oak seedling root development, stem growth, and biomass allocation would differ among the four treatments based on whether the treatment provided less or more than 30% sunlight. This hypothesis was partly confirmed. All four oak species clearly showed a two-way split (uncut – preparatory cut and first–final removal cut) based on the 30% threshold for all response variables. This is consistent with previous research that showed oak seedlings to be light saturated between 30% and 50% of full sun (Bourdeau 1954; Phares 1971; Kolb et al. 1990). However, black and northern red oak also showed a difference in root and stem growth between the first and final removal cuts, indicating that more sunlight translates into more growth. This discrepancy with the literature may be due to those studies occurring under tightly controlled conditions for 1 to 2 years, while this study used ambient forest conditions for 8 years. Also for

Fig. 6. Mean stem dry masses (gm) of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings grown for 8 years in four different shelterwood treatments in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.

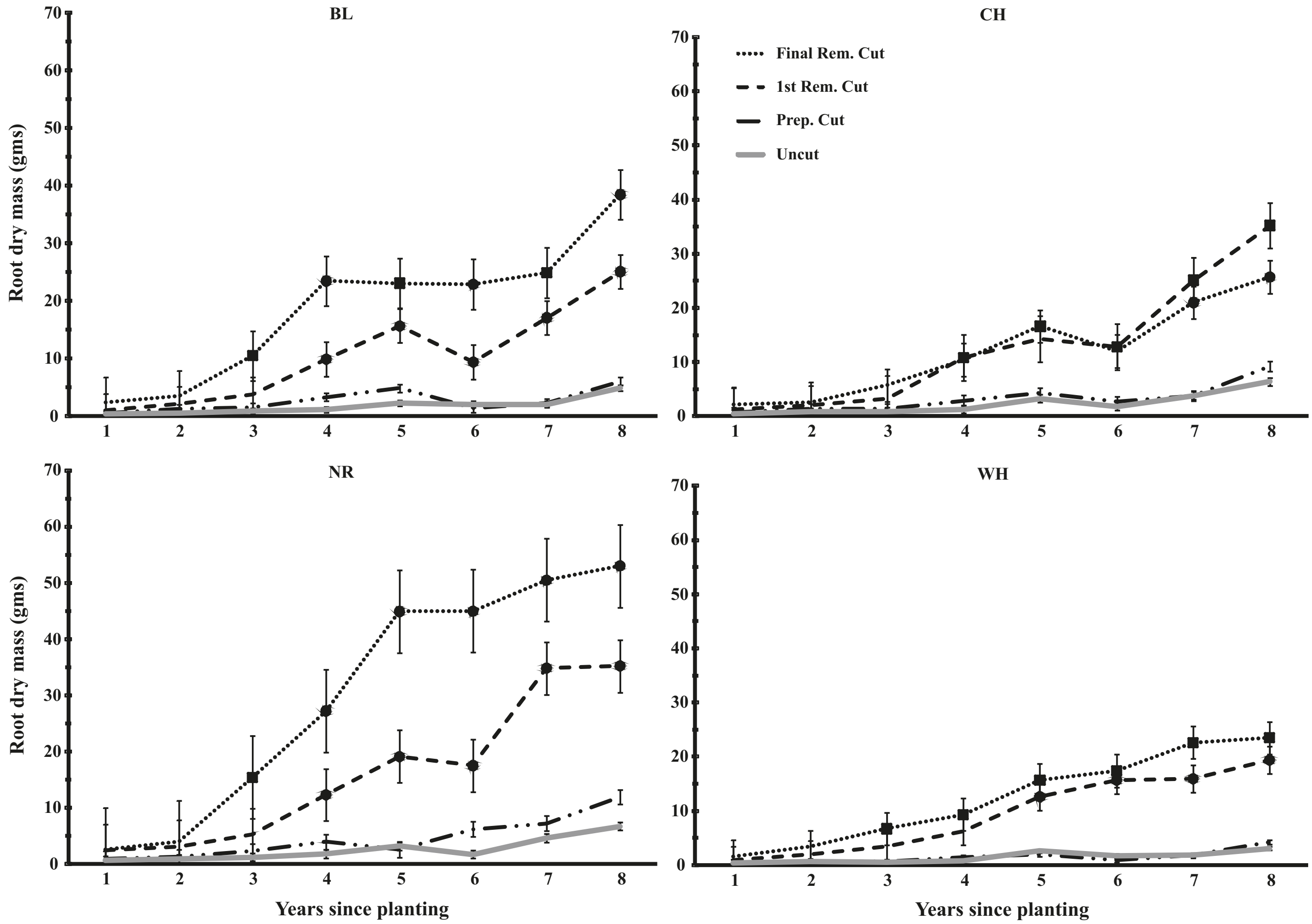


northern red oak, the uncut differed from the preparatory cut depending on the response variable. For example, BD and RCD increased significantly between the uncut and preparatory cut, but STH and STM did not. The fact that northern red oak seedlings responded positively to this diffuse shade regime while the other three species showed little improvement is consistent with results from other studies (Loftis 1990*b*; Kass and Boyette 1998; Miller et al. 2004) and suggests that small increases in understory lighting favor northern red oak seedlings but provide negligible benefit for black, chestnut, and white oak seedlings.

Hypothesis 4 was that the oak seedlings' root-to-stem ratios would decline through time more quickly and to a greater degree in treatments providing abundant sunlight relative to those treatments providing little sunlight. This hypothesis was rejected. The RSRs began relatively high (3:1 to 4:1) regardless of treatment, and this is consistent with previous oak research (Gottschalk 1987; Kolb and Steiner 1990; Sung et al. 1998). In the third year, they peaked for each species. This was likely a weather-related effect. The summers of 2003 and 2004 were exceptionally wet in Pennsylvania and soil moisture has a direct affect on root development (Larson and Whitmore 1970; Reich et al. 1980), so the spike in RSR was likely due to the weather, although it may be an inherent growth pattern in oaks. After the peak, RSR gradually declined for all species in all treatments with no differences detected among the treatments. By the sixth year of the study, RSR reached 1:1 for all species in all treatments, indicating that root and stem growth were balanced despite vast differences in available lighting. This suggests that the shift from root development to stem growth is a function of seedling age and not seedling size. This finding also suggests that foresters have a 6-year window in which they must control competing vegetation so that oak seedlings can develop their roots.

Hypothesis 5 was that the oak seedlings of all four species would be in a stronger competitive position in the first removal cut than in any of the other treatments at the end of the study. This hypothesis was partly validated. The oak seedlings in the first removal cut were in a stronger competitive position than those in the uncut control based on the height of the tallest remaining oak seedling (2.20 vs. 0.33 m) and the number of plots dominated by oak (4 vs. 0). The contrast between the first removal cut and the prepara-

Fig. 7. Mean taproot dry masses (gm) of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings grown for 8 years in four different shelterwood treatments in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.

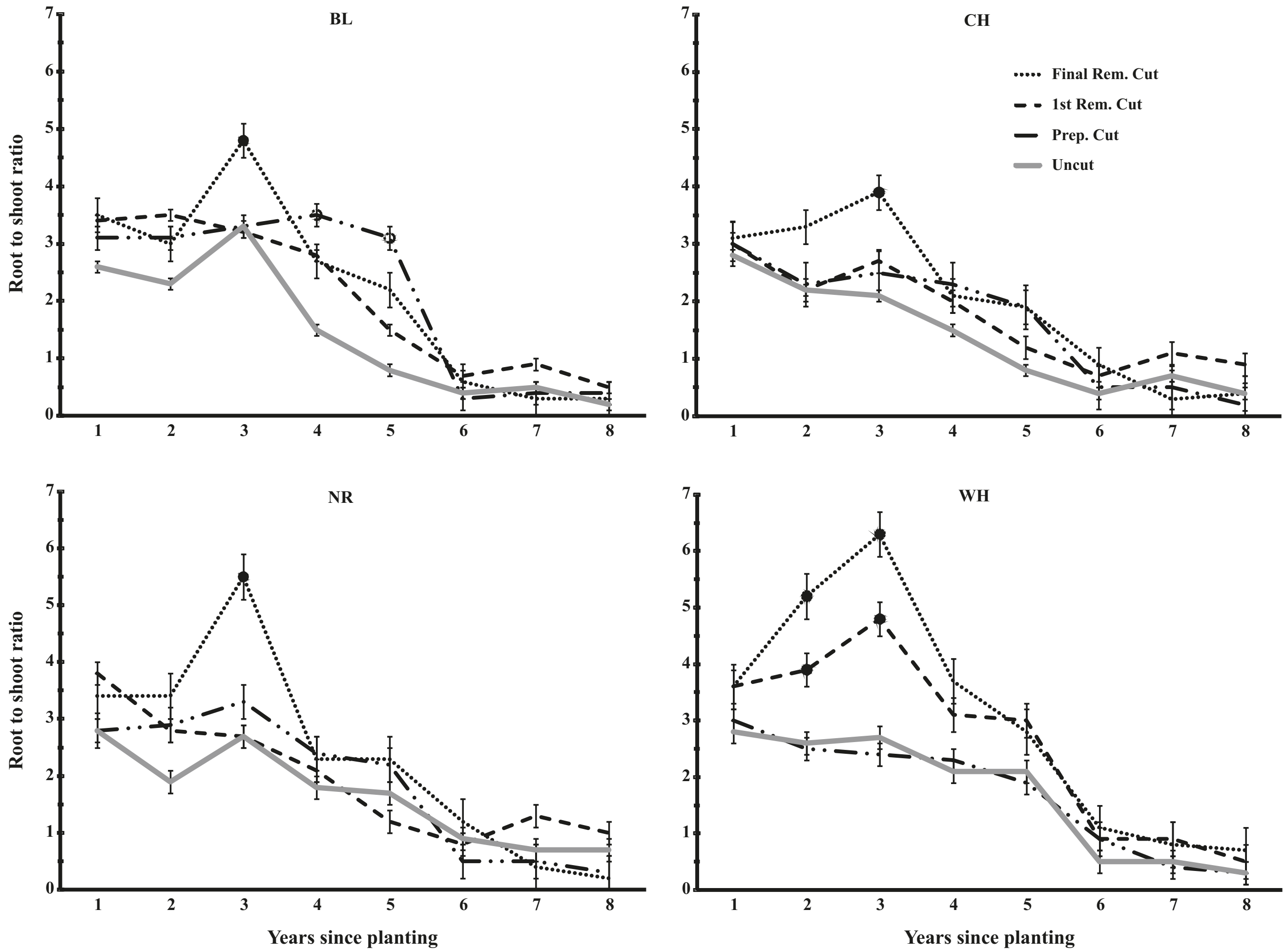


tory cut was less clear. Oaks in the former were taller than in the latter (2.20 vs. 0.75 m), but plot dominance was only 4 to 3 in favor of the first removal cut. Also, heights of the non-oak competitors in the preparatory cut were less than half those in the first removal cut. In comparing the first and final removal cuts, it is also unclear as to which treatment has the more competitive oak seedlings. The tallest black and northern red oak seedlings were found in the final removal cut, and the heights of the tallest chestnut and white oak seedlings were essentially equal between the two treatments. However, the heights of the non-oak competitors in the final removal cut were nearly twice as tall as those in the first removal cut, resulting in none of the plots being dominated by oak even though their seedlings were 2 to 4 m tall. These findings indicate that controlling competing vegetation after first and final removal cuts via herbicides or prescribed fire is an absolute necessity in regenerating oak stands on intermediate and mesic sites.

Based on this study, how should a forester proceed with the shelterwood system when desiring to regenerate an upland oak forest? First, begin a shelterwood sequence only when there is an adequate density of oak seedlings to create a new oak forest. In this project, pre-existing oak regeneration was absent or too sparse to conduct the study, so cohorts of new oak seedlings had to be created via intensive site preparation, planting of acorns, small mammal control, and deer fencing. Collectively, those measures are likely uneconomical on an operational basis, so waiting for a suitable acorn crop to establish seedlings is probably the wisest course of action for stands lacking sufficient numbers of oak seedlings to begin the regeneration process. Removal of low shade via herbicides or prescribed fire are potential treatments in lieu of no action as both create the diffuse shade that will increase survival of new oak seedlings when an acorn crop occurs, as well as stimulate modest height growth in those seedlings.

When it is time to proceed with the shelterwood sequence, the forester needs to determine whether controlling the reproduction of other hardwoods with herbicides or prescribed fire will be feasible in the near future. If controlling competing vegetation will not be possible, then a preparatory cut may avoid or minimize the interference problem (Loftis 1990*b*; Lorimer et al. 1994). The key feature of this treatment is changing the dense shade to a diffuse shade by removal of

Fig. 8. Root-to-shoot ratios of black (BL), chestnut (CH), northern red (NR), and white (WH) oak seedlings grown for 8 years in four different shelterwood treatments in Pennsylvania. Circles indicate treatment means that are greater than all smaller treatment means in that year at $p < 0.05$. Squares indicate treatment means that are greater than all the nonadjacent treatment means in that year at $p < 0.05$. Error bars indicate one standard error. Rem., removal; Prep., preparatory.



intermediate or suppressed trees, low-quality stems, and seed sources of undesirable species while not creating large gaps in the canopy (~75% residual relative density). The benefits of a preparatory cut are improved oak seedling survival, longevity of the treatment (at least 8 years and probably much longer), and minimal development of competing hardwood reproduction. The negatives are an extended regeneration period (maybe 10 or more years), slow growth for black, chestnut, and white oak seedlings (Kass and Boyette 1998), slow to moderate growth for northern red oak (Loftis 1990*b*), and that the treatment will likely be noncommercial. Once the oak seedlings reach a competitive size for that site, then the forester can proceed with one or more removal cuts.

If controlling interference is feasible, then a first removal cut that reduces relative density to about 50% is recommended. Wait to control the interference until the oak seedlings are being overtopped by the competing hardwoods (in about 4 to 7 years). After controlling the interference, the forester can proceed with the final removal cut. Benefits to this treatment are sufficient sunlight for relatively rapid oak seedling growth, a commercial harvest, and a shorter regeneration period relative to the preparatory cut. Negatives are rapid development of competing vegetation and the cost and necessity of treating that interference. In either approach, patience is critical and crop tree management commencing 10 to 15 years after the final harvest may be a necessity to ensure maintaining a large oak component in the new stand (Miller et al. 2007).

The heights (3 to 4+ m) attained by some oak seedlings in the final removal cut, especially black and northern red oak, may entice some foresters to forego the shelterwood sequence in favor of a clearcut. This is probably unwise on intermediate and mesic sites because the exceptional height growth of some oak seedlings in this study was likely a result of the site preparation method. The rototilling provided intense competition control that lasted up to two growing seasons for the newly germinating seedlings. Also, rototilling releases nutrients bound in the soil and makes them available (Fisher and Binkley 2000; Brady and Well 2007). Thus, the seedlings benefitted from lack of immediate competition and indirect fertilization because of the site preparation method. It is doubtful that new oak seedlings germinating from acorns

Table 3. Mean densities (stems/ha ± 1 SE) by height class (<1 m, 1 to 2 m, and >2 m) of the non-oak seedlings growing around each planting plot, the tallest oak and non-oak seedling found in each treatment, and the number of plots in each treatment (n = 20) dominated by the different species groups at the end of the study (year 8).

Species	Uncut	Preparatory cut	1st removal cut	Final removal cut
Height class < 1 m				
Birch	11±4	206±25	317±44	317±30
Cherry	33±10	19±5	63±10	16±4
Maple	2 315±128	4 694±200	571±63	159±14
Other	2 268±67	3 711±113	1 269±30	349±28
Height class 1 to 2 m				
Birch	32±11	285±52	507±90	825±80
Cherry	16±6	32±10	270±44	1 284±45
Maple	636±70	1 063±45	680±137	539±44
Other	412±18	1 253±60	1 522±88	1 332±52
Height class > 2 m				
Birch	7±5	0	2 950±95	2 521±210
Cherry	3±3	0	650±147	2 331±306
Maple	1 460±155	587±72	1 475±117	317±34
Other	301±49	396±35	2 029±88	3 870±457
Total	7 494±648	12 246±1500	12 303±1100	13 860±1212
Tallest non-oak (m)				
Birch	0	1.1	4.5	7.5
Cherry	0	0	5.5	11.0
Maple	4.0	2.5	3.5	6.0
Other	2.0	2.2	4.0	6.5
Tallest oak (m)				
Black	0.34	0.73	1.89	3.45
Chestnut	0.32	0.83	2.38	2.36
Northern red	0.39	0.98	2.47	4.33
White	0.29	0.45	2.08	2.03
No. of plots dominated				
Birch	0	4	7	6
Cherry	0	0	5	12
Maple	14	11	3	0
Oak	0	3	4	0
Other	6	2	1	2

under the same light conditions but with little or no site preparation would have grown as quickly or as tall as some of these did in this study.

Furthermore, these tall oak seedlings may entice some foresters to forego controlling competing vegetation. That would be a mistake as none of these tall oak seedlings was dominating a plot by year 8. In all cases, they were under non-oak saplings that were usually 1 to 3 m taller. Controlling competing vegetation with herbicides or prescribed fire is a must when regenerating oak stands on intermediate and mesic sites.

Caution needs to be exercised when applying these results 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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