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Silviculture at establishment of hardwood plantations is relatively ineffective in the presence of deer browsing

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ABSTRACT

Ungulate browsing limits forest regeneration on many reforestation and restoration sites. Silviculture can be used to mitigate the effects of ungulate damage by promoting rapid early growth of planted seedlings, but benefits may depend upon site characteristics and ungulate browse pressure. We studied the interactions among browsing by white-tailed deer (*Odocoileus virginianus*), use of genetically select seed sources, controlled-release fertilization (CRF) at planting, and site type (harvest openings and plantations) in a nine-year hardwood forest regeneration study. The experiment consisted of paired deer exclosure and control plots, with fertilization and seed source, established at two reforested clearcut sites and three afforested agricultural field sites in Indiana, USA. Our objectives were to examine treatment effects on growth (height and diameter), survival, and stem quality of four temperate deciduous hardwood species (northern red oak, white oak, black walnut, and black cherry). For all species, fencing had the greatest significant positive influence on survival (non-fenced: 50–72%, fenced: 71–75% by year 8) and growth (81–178% greater height and 90–167% greater diameter by year 8), as well as stem quality ratings. Fencing also increased (by 50–78%) the probability that black cherry and black walnut at afforested sites (as well as northern red oak at both site types) would reach free-to-grow status by year 5. We observed gains in height and diameter from CRF only during the first three years for fenced black cherry (11% greater height and 14% greater diameter in year 3), and for white oak regardless of fencing (13% greater height and 10% greater diameter in year 3). Genetically select seed sources had the greatest and most consistent growth benefit for black walnut (81% greater height and 50% greater diameter by year 8). Early growth was improved in genetically select *P. serotina* vs. non-select sources (11% greater height in year 3) but differences faded by the fifth growing season, while superior growth of genetically select *Q. rubra* began to manifest only after year 5 (16% greater height 21% greater diameter by year 8). In addition, select northern red oaks had an 8% greater probability of reaching free-to-grow status by year 5 and black walnuts at afforested sites had a 13% greater probability of reaching free-to-grow status. Without protection from herbivory, genetically improved sources did not realize their full potential for enhanced growth. Our results from this nine-year-long hardwood plantation experiment confirm that without browse protection, additional silvicultural treatments are unlikely to improve regeneration performance.

1. Introduction

Regenerating forests face many challenges, including herbivory, poor nutrition, and competing vegetation, which typically vary across sites. Browse damage caused by high native populations or novel introductions of ungulates limit the function, diversity, and resilience of temperate hardwood ecosystems (Côté et al., 2004; Tanentzap, 2012; Murray et al., 2013; Bachand et al., 2014). Deer populations have increased in many regions over the last century due to reduced hunting pressures, loss of predators, the adaptability of deer to anthropogenic landscapes, and increases in available forage due to increasing early-successional habitats (Côté et al., 2004; Whitaker, 2009). Though deer herbivory often does not directly kill hardwood regeneration, it stunts growth, allows neighboring, more browse-tolerant vegetation to dominate, and limits the recruitment of new stems into the overstory (Götmark et al., 2005; Putman and Moore, 1998). In addition, deer browse often results in loss of the terminal bud (Götmark et al., 2005), which can reduce timber quality by encouraging trees to grow multiple

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leaders (Jacobs et al., 2004). Marquis et al. (1992) suggested that shifts in species composition can occur under densities of 12–48 deer km^{-2} at low food availability, and total regeneration failure may occur between 30 and 48 deer km^{-2} (Marquis et al., 1992). Alternatively, Hanberry and Abrams (2019) showed that deer densities are not consistently associated with understocking in forests of the eastern USA on a regional scale, suggesting that density-dependent mortality has a greater influence on the density of adult trees. However, deer remain a challenge in many forests and have broad ranging effects on herbaceous communities (Webster et al., 2005; Heckel et al., 2010). Csigi and Holzemueller (2015) observed that deer densities as low as 6 to 12 deer km^{-2} can limit the growth of desirable hardwood seedlings. Due to lowered food resources, reduced plant population densities, and seed dispersal limitations some plant populations may be more sensitive to herbivory after a history of over-browsing, even following deer population reductions (Aronson and Handel, 2011; Jenkins et al., 2014; Csigi and Holzemueller, 2015).

Various methods of reducing the impacts of ungulate herbivory have been studied (Beguin et al., 2016; Sage et al., 2003). Fertilization is a silvicultural treatment that may allow seedlings to reach free-to-grow status above the browse line (i.e., a height above which deer cannot stunt tree growth; ca. 150 cm) sooner than non-fertilized seedlings. Controlled-release fertilizer (CRF) applied to the seedling root zone is particularly beneficial because, unlike broadcast fertilizer, it limits the extent to which competing vegetation can acquire the applied fertilizer (Sloan and Jacobs, 2013). It also moderates the release of nutrients to the tree, thus reducing leaching and providing seedlings more opportunity to uptake nutrients (Jacobs et al., 2005; Sloan et al., 2016). However, fertilizer also increases the palatability of some seedlings to deer (Burney and Jacobs, 2013; Tripler et al., 2002), and deer may increasingly target palatable genera, such as oak (*Quercus* spp.; Tripler et al., 2002; Wakeland and Swihart, 2009). While studies have examined short-term responses of hardwood regeneration to CRF application (Burney and Jacobs, 2018; Jacobs et al., 2005), few longer-term studies have been published.

Artificial forest regeneration with the goal of improved timber production may benefit from the use of superior seed sources that have been selected for improved growth, stem form, and pest resistance (Beineke, 1989; Zobel and Talbert, 1984). While rapid compensatory growth or production of secondary metabolites may infer increased tolerance of (or resistance to) ungulate browse (Wooley et al., 2008; Miller et al., 2009; Burney and Jacobs, 2011; O'Reilly-Wapstra et al., 2014), few seed sources or cultivars have been identified with these traits. However, trees selected for fast growth may reach free-to-grow status more rapidly than non-selected sources (Burney and Jacobs, 2013; Salifu et al., 2009; Vila et al., 2003). While tree improvement programs exist for many commercial conifers, seed for reforestation of most temperate hardwood species originates from unimproved sources (Jacobs and Davis, 2005; Merkle and Nairn, 2005), despite demonstrated positive effects of genetic selection on hardwood forest development (Beineke, 1989; Rink and Coggeshall, 1995; Woeste et al., 2011). In areas with high ungulate populations, however, silvicultural methods to aid regeneration are unlikely to be successful if herbivory is not directly addressed (Sage et al., 2003).

Conditions for hardwood plantings differ between abandoned agricultural fields and reforested clearcuts. At afforested sites previously used for agriculture, there is less competition for light than in forests. Old fields are low stress environments for regenerating oaks when large herbivores are absent or excluded (Pons and Pausas, 2006). Reforestation sites may also have greater diversity of shrubs and trees than afforestation sites, which has been shown to reduce the negative effects of herbivores due to positive interspecific interactions between plants, though positive effects are dependent on the relative palatability and abundance of the species involved, as well as the abundance of herbivores (Brown and Ewel, 1987; Baraza et al., 2006; Cook-Patton et al., 2014). However, such positive interspecific interactions may be outweighed by competitive interactions in the absence of herbivory (Cook-Patton et al., 2014; Gorchov and Trisel, 2003; Murray et al., 2016).

There is no simple solution to the problem of intensive deer herbivory on forest regeneration, particularly if social and economic drivers continue to prevent cull reductions in deer herds (Phillip et al., 2009; Tanentzap, 2012). While effective browse control methods are expensive, several solutions are cost-effective in some situations. For example, the number of seedlings that must be planted to reach stocking targets may be reduced if browse management is used (Ward et al., 2000). Additionally, once ecosystems have shifted to alternative stable states (for example, when ferns have dominated a site, or desired plant populations have been extirpated), more intensive management techniques are required to return desired function and species composition (Stromayer and Warren, 1997), suggesting that the use of silviculture to prevent such shifts from occurring is economically desirable (Stanturf et al., 2014). Even after ungulate populations are reduced, regeneration may still require protection to adequately restore areas that have been subject to long-term herbivory (Tanentzap et al., 2011). In addition, other herbivores may continue to browse seedlings after their competitors are removed (Belovsky, 1984; Hough, 1949).

Long-term studies are needed to evaluate the relative impacts of silvicultural treatments on hardwood plantation development in the presence of varying browse pressure. By employing a planting-exclosure study, we measured the growth performance and stem quality of four hardwood tree species in response to individual and interactive effects of browse control, fertilization at planting, and genetic seed source across reforestation and afforestation sites in Indiana, USA. We hypothesized that: (i) deer exclusion via fencing would have the greatest positive effect on hardwood tree performance attributes; (ii) fertilization at planting and use of genetically select seed sources would positively affect growth across all treatment and site combinations, yet show the strongest synergistic interaction with fencing; and (iii) less competition with other plants on afforestation vs. reforestation sites would result in greater survival and growth, yet browse damage would be higher on non-fenced afforestation sites.

2. Materials and methods

2.1. Location, planting materials, and treatment establishment

Between 2007 and early 2008, the Department of Forestry and Natural Resources (FNR) at Purdue University harvested timber on two properties in Indiana, USA within the Central Hardwood Forest Region:

Table 1
Site locations and characteristics of experimental sites in Indiana. Soil type information is from the USDA Web Soil Survey (Natural Resource Conservation Service, 2019).

Site	Site Type	Location	No. Trees	8-Year Survival	Coordinates	Soil Type
Stephens	reforestation	Carroll County	591	41.6%	N 40°40′48″ W 86°37′32″	Hennepin loam and Miami-Crosier complex
Darlington	reforestation	Montgomery County	721	25.7%	N 40°07′13″ W 86°48′40″	Starks silt loam and Martinsville-Ockley silt loam
SEPAC	afforestation	Jennings County	1489	27.0%	N 39°02′27″ W 75°32′05″	Ryker-Muscatatuck silt loam
Martell	afforestation	Tippecanoe County	1139	36.0%	N 40°26′36″ W 87°01′58″	Starks-Fincastle complex and Rainsville silt loam
Lugar Farm	afforestation	Tippecanoe County	1147	32.0%	N 40°25′43″ W 86°57′29″	Starks-Fincastle complex and Richardville silt loam

Stephens Forest (hereafter Stephens) and Darlington Woods (hereafter Darlington; Table 1). The harvest sites were mature oak-hickory forests succeeding to maple-beech with a lack of disturbance. The mature timber was > 100 years in age and both sites appeared to have never been farmed (Brian Beheler, Purdue FNR, personal communication). In 2008, after removing all residual trees and debris, the sites were planted for this study. In addition, three afforestation sites were established at other FNR properties: Southeastern Purdue Agricultural Center (hereafter SEPAC), Martell Forest (hereafter Martell), and Richard G. Lugar Forestry Farm (hereafter Lugar Farm; Table 1). The sites at SEPAC and Martell have been under cultivation for at least fifty years. Lugar Farm was an apple orchard from ca. 1950–2002, when the orchard was removed and the ground left fallow. Each planted site was approximately 0.81 ha in size. A total of 5,077 seedlings from four species: white oak (*Quercus alba* L., n = 1277), northern red oak (*Quercus rubra* L., n = 1255), black cherry. (*Prunus serotina* Ehrh, n = 1277), and black walnut. (*Juglans nigra* L., n = 1268) were obtained from Indiana Department of Natural Resources (DNR) Vallonia Nursery (Vallonia, IN, USA; Table A1). These species are commonly planted, commercially valuable hardwoods in the Central Hardwood Region. Black cherry, black walnut, and northern red oak all have active improvement programs. Among these species, northern red oak is most highly preferred by deer, followed by white oak (Strole and Anderson, 1992; Wakeland and Swihart, 2009). Black cherry varies in palatability depending on the region and leaf nitrogen concentration, while black walnut is one of the least preferred of high-value timber species in the Central Hardwood Region (Tripler et al., 2002; Wakeland and Swihart, 2009). All seedlings were 1 + 0 bareroot and were grown following operational production protocols (Jacobs, 2003). Seedlings were planted using an auger to drill holes at 2.45 × 2.45 m spacing.

Seed was collected in the fall of 2006. Select seed sources from the Indiana DNR Division of Forestry were used for black cherry, black walnut, and northern red oak from grafted seed orchards (IDNR Division of Forestry, 2006). Orchard clones were selected for superior timber form and growth, and each orchard contained 30 or more clones. Non-select (bed-run) seed for northern red oak and white oak was purchased from commercial seed collectors from accessible, open-grown trees as is customary for this region (Jacobs and Davis, 2005). Non-select black walnut seed was obtained from the Mason State tree nursery in Illinois (Topeka, IL, USA), and black cherry seed was obtained from the Jasper-Pulaski Indiana DNR Nursery (Medaryville, IN, USA); all seed was fall sown and grown at the Indiana DNR Vallonia Nursery. In total, seven seed sources were planted at each of the five sites. Mean initial height (± SE) of the non-select seedlings was 45.5 ± 13.0 cm for northern red oak, 60.6 ± 22.1 cm for black cherry, 27.9 ± 8.9 cm for black walnut, and 26.6 ± 9.4 cm for white oak. Mean initial height (± SE) of the select seedlings was 45.0 ± 13 for northern red oak, 77.2 ± 29.2 cm for black cherry, and 29.9 ± 13.2 cm for black walnut.

A 2-m tall plastic mesh deer fence was erected around half of the trees on each site, creating two paired blocks at each site. The fence was repaired when breaches occurred and was maintained until the end of the third growing season. Half of the trees were systematically fertilized with controlled-release fertilizer (CRF) in blocks of four rows at each site. Fifty grams of Osmocote® Exact Lo-Start 15 N-9P-10 K plus minor nutrients (O.M. Scotts Co., Marysville, OH, USA) was applied using a potapuki one to two weeks after planting (Jacobs et al., 2005). Competing vegetation in all treatments was controlled with herbicide applications in 2008, 2009, and 2010 (Appendix 1). Mowing was done between rows in 2008 and 2009 at all sites and until 2012 at afforested sites for consistent weed control. Tree height and survival were assessed on all sites in years 1, 2, 3, 5 and 8. Basal diameter was measured in year 3, and diameter at breast height (DBH, 1.37 m above groundline) was measured in years 5 and 8. Incidence of deer browse was noted in years 1, 2, 3, and 5. In year 9, the quality of all trees was assessed by the same two technicians who assigned a single rating score to each tree using a qualitative scale based on a combination of timber quality traits including: straightness, apical dominance, self-pruning, depressed knots, crooks, sweep, number of lateral branches, and branch angles. A score of 1 was considered poor, 3 average, and 5 excellent (Mckenna and O'Connor, 2013).

2.2. Statistical analyses

Logistic regression was used to analyze survival across treatments and produce survival probabilities for year 1, 2, 3, 5, and 8, and also analyze the probability of seedlings reaching free-to-grow status (here defined as > 150 cm) by year 5. Linear mixed model analyses were conducted separately for each species to evaluate height at multiple years (1, 2, 3, 5, and 8), seedling basal diameter for year 3, and DBH for years 5 and 8. The quality scoring system yields an ordinal variable (i.e., the distance between ordered scores was not equal); therefore, parametric analyses could not be used. Instead, ordinal logistic regression was used to analyze quality for trees > 150 cm height at year 9. This analysis used a series of logistic regression models to produce log odds ratios, which were used to predict the probability of the response variable being over or under specific thresholds (Liao, 1994). Within each analysis, the effects of the independent variables and their interactions (fencing, fertilizer, site type, and seed source) were compared for each dependent variable (height, DBH, or survival, quality, or free-to-grow status). No interactions were considered for the quality analysis and seed source was not used as a factor for white oak. Each tree was considered a replicate, while site was used as a random intercept for all models. Factors were nested within the random location term when they resulted in a better fit for the model (Table A2). Stepwise regression using backwards elimination was used for model selection, using t-tests as the criteria for fixed interaction terms and the Akaike Information Criterion (AIC) for nested random terms. Main effects were never dropped. The models took the following general form:

$$y = (Fence + Fertilizer + SeedSource + SiteType)^2 + (1|Site) + \varepsilon$$

Height and diameter were square-root transformed (except in year 1) to better meet the assumptions of homogeneity of variance and linearity of error. The logit transformation was used on the survival, quality, and free-to-grow status data prior to the use of logistic regression. All means reported were back-transformed and standard errors were back-transformed using the delta method. Tukey's test was used for pairwise comparisons for all significant effects. The proportional odds assumption was checked by comparing the difference between predicted values of adjacent ordinal values for each level of each factor; if the differences were similar across the ordinal scale, the assumption held.

All statistical analyses were conducted using R statistical software (R Core Team, 2018). Differences were considered significant at $\alpha = 0.05$. Restricted maximum likelihood (REML) was used for the estimation of likelihood in height and diameter analyses. REML gives slightly biased results for fixed effects; thus, any marginally significant results (p-values between 0.04 and 0.05) were subjected to bootstrapping for a more accurate p-value (Faraway, 2006). The "lme4" R statistical package was used to determine the fixed effects of fencing, fertilizer, site type, and seed source, as well as the random effect of site (random slope and intercept) on the height and diameter growth of seedlings of each species over time (Bates et al., 2015). The "lme4" package was also used to perform logistic regression for the survival analysis. The "lmeTest" package was used to obtain p-values for all analyses done in "lme4" (Kuznetsova et al., 2017). The "ordinal" package was used to analyze the effects of each treatment on tree quality using cumulative link mixed models (Christensen, 2019). Least square means and standard errors were obtained using "lsmeans" and "emmeans" (Lenth, 2018, 2016). The "MuMIn" package (Barton, 2019) was used to calculate R^2 values for each model. Theoretical R^2 values were computed for logistic models.

Table 2
Proportion of surviving black cherry (BC), black walnut (BW), northern red oak (NRO), and white oak (WO) trees browsed by level of each fencing treatment after one and five growing seasons. Browse inside fences was due to occasional breaches.

Species	Treatment	Browsed (%)	
		Year 1	Year 5
NRO	fenced	7.0	8.5
NRO	non-fenced	56.4	75.6
WO	fenced	6.2	11.5
WO	non-fenced	46.2	86.1
BC	fenced	9.0	2.2
BC	non-fenced	52.3	83.2
BW	fenced	5.3	3.0
BW	non-fenced	26	80.6

3. Results

3.1. Fencing

Fencing successfully reduced browse, though breaches did occasionally occur (Table 2). Fenced trees had a greater probability of survival than non-fenced trees at afforested sites in year 5 ($p = 0.049$) for northern red oak; years 3 ($p = 0.046$) and 5 ($p < 0.001$) for white oak; years 2 ($p = 0.004$), 5 ($p < 0.001$), and 8 ($p = 0.024$; Table 3) for black cherry; and year 5 ($p < 0.001$) for black walnut. Survival probability was 28% greater for fenced northern red oaks at afforested sites in year 5 ($p = 0.003$ for the interaction; Fig. 1), 13% greater for fenced white oak at afforested sites in year 5 ($p < 0.001$ for the interaction; Fig. 1), 28% greater for fenced black cherry at afforested sites in year 8, and 14% greater for fenced black walnut at afforested sites in year 5 ($p < 0.001$ for the interaction). In year 5, fenced black cherry, northern red oak, and black walnut trees at afforested sites had greater probabilities of survival than any other treatment (Figs. 1 and 2). Fenced northern red oak had a greater probability of survival than non-fenced northern red oak grown from the select seed source in years 3–8 ($p = 0.043$ for the interaction in year 8; Fig. 3). Fenced, select northern red oak had greater survival probability than all other northern red oak in year 5 ($p = 0.003$; Fig. 3). In year 8, fenced northern red oak had a greater probability of survival than non-fenced northern red oak when non-fertilized ($p = 0.015$ for the interaction; Fig. 3). Fencing, as a main effect, increased the probability of survival for northern red oak seedlings in for the first two years post-planting ($p < 0.030$), white oak in years 2 ($p < 0.001$) and 8 (Table 3; $p = 0.023$), and black cherry in years 1 ($p = 0.006$) and 3 ($p = 0.005$). Fencing positively affected black walnut survival for the first five years, though by year 5 this was only the case at afforested sites (Fig. 2).

Table 3
Mean (± SE) probability of survival of black cherry (BC), black walnut (BW), northern red oak (NRO), and white oak (WO) trees by level of each treatment after eight growing seasons. Select or non-select seedlings were planted with or without controlled-release fertilizer at reforested or afforested sites with or without fencing. Means for each treatment are averaged across the other treatments. Bold indicates significant differences among treatments (α = 0.05). Asterisks indicate involvement with interactions.

Species	Treatment	Survival (%)	Standard Error	P-value
NRO	fenced	0.75	0.06	**0.018***
NRO	non-fenced	0.50	0.08	
NRO	fertilized	0.63	0.06	0.907*
NRO	non-fertilized	0.63	0.06	
NRO	select	0.64	0.06	0.335*
NRO	non-select	0.62	0.06	
NRO	afforested	0.66	0.07	0.271
NRO	reforested	0.61	0.09	
WO	fenced	0.75	0.03	**0.023**
WO	non-fenced	0.72	0.04	
WO	non-fertilized	0.75	0.03	0.409
WO	fertilized	0.73	0.03	
WO	reforested	0.77	0.04	**0.013**
WO	afforested	0.70	0.03	
BC	fenced	0.75	0.05	**0.002***
BC	non-fenced	0.63	0.06	
BC	fertilized	0.71	0.05	0.376
BC	non-fertilized	0.67	0.05	
BC	non-select	0.73	0.04	**0.003**
BC	select	0.65	0.05	
BC	reforested	0.73	0.06	0.119*
BC	afforested	0.69	0.05	
BW	fenced	0.71	0.09	**0.036**
BW	non-fenced	0.70	0.09	
BW	non-fertilized	0.29	0.09	0.801
BW	fertilized	0.30	0.09	
BW	non-select	0.75	0.08	0.844*
BW	select	0.65	0.09	
BW	afforested	0.76	0.09	0.832*
BW	reforested	0.64	0.15	

Fencing increased the height of both oak species and black cherry in every year. After year 8, fenced northern red oak trees were > 2.5 times the height of non-fenced northern red oak and fenced white oak trees were almost twice the height of non-fenced white oak (Fig. 4). On average, fenced black cherry trees were over twice the height of non-fenced black cherry (Fig. 4). Fencing increased the height of black walnut seedlings in year 1 ($p = 0.016$ after bootstrapping; $p = 0.05$ before bootstrapping), year 2 ($p = 0.029$) and year 3 ($p = 0.027$). Though fenced black walnut trees were almost twice as tall in year 5, the difference was not significant after bootstrapping ($p = 0.067$). By year 8, fenced walnut trees were 1.8 times taller than their non-fenced counterparts on average (Table 4).

Fenced trees had 54% and 55% greater probabilities of reaching free-to-grow status by year 5 than non-fenced trees for northern red oak ($p < 0.001$) and white oak ($p < 0.001$), respectively. Probability of reaching free-to-grow status by year 5 was 78% greater for fenced black cherry at afforested sites ($p = 0.018$ for the interaction), and 70% greater for fenced black walnut at afforested sites in year 5 ($p = 0.005$ for the interaction).

Fencing increased the DBH of northern red oak by 6 mm ($p < 0.001$) in year 5. After year 8, both oak species had greater diameter measurements in the fenced treatments than the non-fenced treatments (Table 5). On average, fenced northern red oaks were over 2.5 times the diameter of non-fenced trees ($p = 0.003$; Fig. 4), and fenced white oak diameters were over 2 times the diameter of non-fenced white oaks ($p = 0.004$; Fig. 4). We observed similar, but non-significant, trends for black cherry ($p = 0.107$) and black walnut ($p = 0.163$) in year 8; fenced trees of both species were approximately twice the diameter of non-fenced trees (Fig. 4). In year 3, fenced black cherry trees were significantly larger within and across each fertilizer treatment ($p = 0.038$), and fenced black walnut trees were larger within each seed source treatment ($p = 0.039$), but these trends did not last into later years (Table 5).

Fencing had a significant positive effect on timber quality for all species ($p < 0.001$). The probability of quality being average or better was 58% or more for all fenced trees (ranging from 58 ± 2% for black cherries to 76 ± 2% for northern red oaks), while the probability of being average or better was < 33% for all non-fenced trees (ranging from 32 ± 4% for black walnuts to 13 ± 3% for white oaks).

3.2. Fertilizer

The effects of fertilizer treatments on growth were mixed. Application of CRF had no effect on northern red oak growth. Fertilizer increased the height of fenced black cherry seedlings in year 1 by 9.9 cm ($p = 0.003$ for the interaction) and in year 2 by 17.8 cm ($p = 0.009$ for the interaction). Outside the fence, however, fertilized seedlings showed no differences. This interaction between fencing and CRF held in the third year when the difference between fertilized and

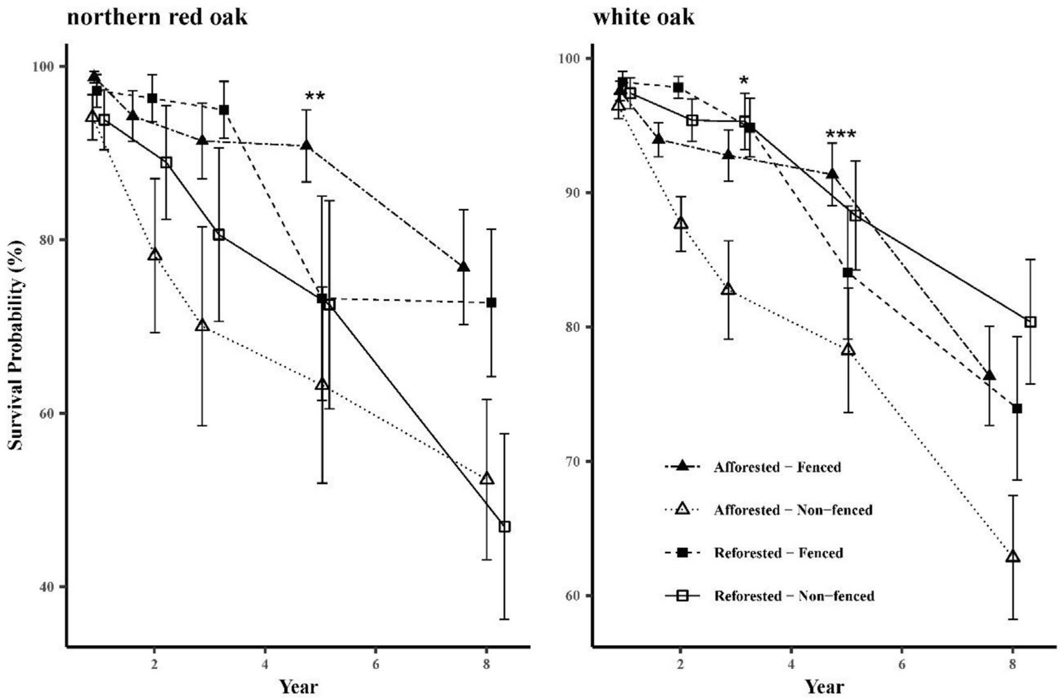

Fig. 1. Mean (± SE) proportion of surviving fenced and non-fenced northern red oaks and white oaks over time on reforested or afforested sites. Asterisks represent significant interactions (* < 0.05,** < 0.01,*** < 0.001), which occurred for northern red oak in year 5, and for white oak in years 3 and 5.

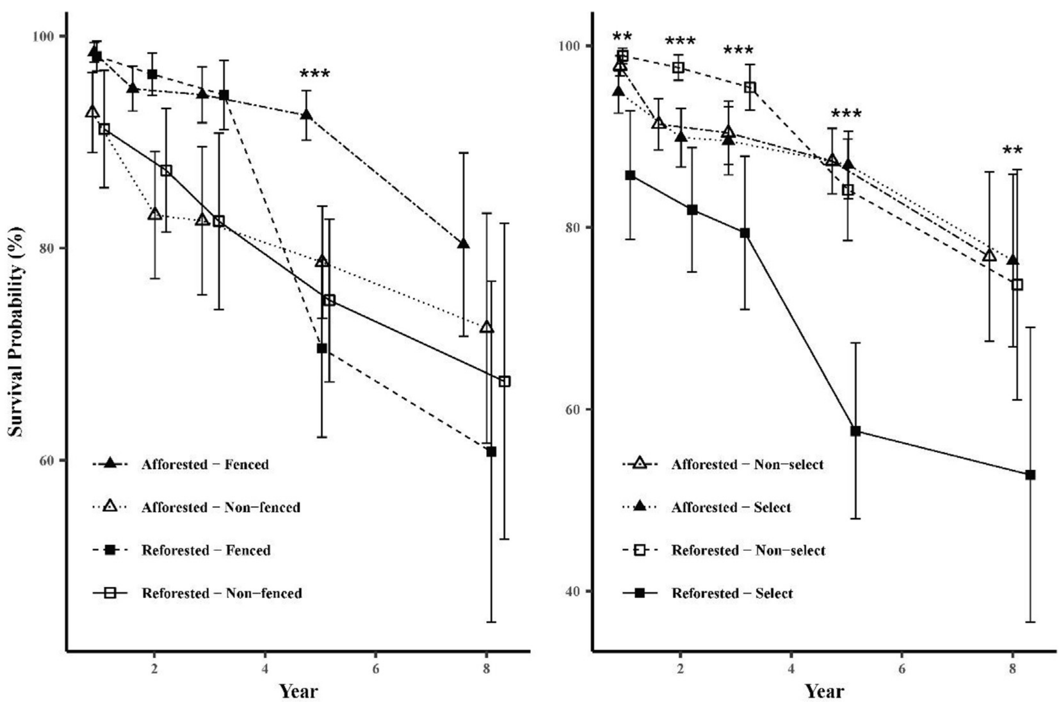

Fig. 2. Interactive effects of site type with fencing (left panel) and site type with seed source (right panel) on black walnut survival probability (mean ± SE). Asterisks represent significant interactions (* < 0.05, ** < 0.01, *** < 0.001), which occurred only in year 5 for site type and fencing, and in years 2, 3, and 8 for site type and seed source.

non-fertilized seedlings increased to 25.1 cm inside the fences ($p = 0.020$ for the interaction; Fig. 5). Fertilized black cherry displayed greater basal diameter than non-fertilized cherry within the fences in the third year ($p = 0.038$), and by year 5 fertilizer had a positive main effect on black cherry diameter ($p = 0.034$). White oak height was 2.6 cm and 5.8 cm greater in the fertilized treatments in years 2 and 3, respectively ($p < 0.040$); basal diameter was also greater (but only by 1 mm) in fertilized treatments in year 3 ($p < 0.001$). By year 5, fertilized white oak trees were only taller than non-fertilized white oak at the reforested sites (Fig. 5), but there were no significant height differences by the end of the experiment, though fertilized white oak trees were slightly taller on average (Table 4). Fertilizer had no effect on the timber quality of any species.

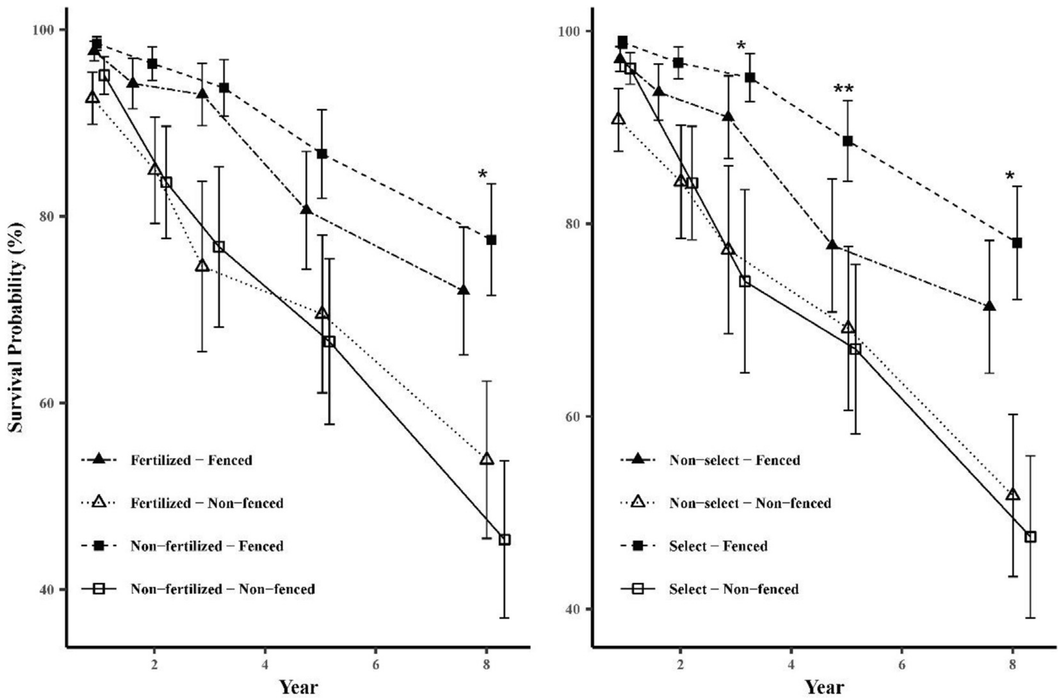

Fig. 3. Interactive effects of fertilizer with fencing (left panel) and seed source with fencing (right panel) on northern red oak survival probability (mean ± SE) across all sites. Asterisks represent significant interactions (* < 0.05, ** < 0.01, *** < 0.001) between seed source and fencing, which occurred in years 3, 5, and 8.

3.3. Seed source

In year 1, select black cherry had a 4.9% lower probability of survival than non-select black cherry ($p = 0.009$); this effect was present in every year up to the end of the study period (Table 3). In every year, select black walnut at the reforested sites had a lower probability of survival than non-select black walnut (Fig. 2).

Differences in growth between seed sources were present for all species during some years. Within the fenced treatments, select black cherry trees were 26 cm taller on average than non-select black cherries in year 1 ($p < 0.001$ for the interaction). In addition, despite the fact that most fenced treatments resulted in greater heights than non-fenced

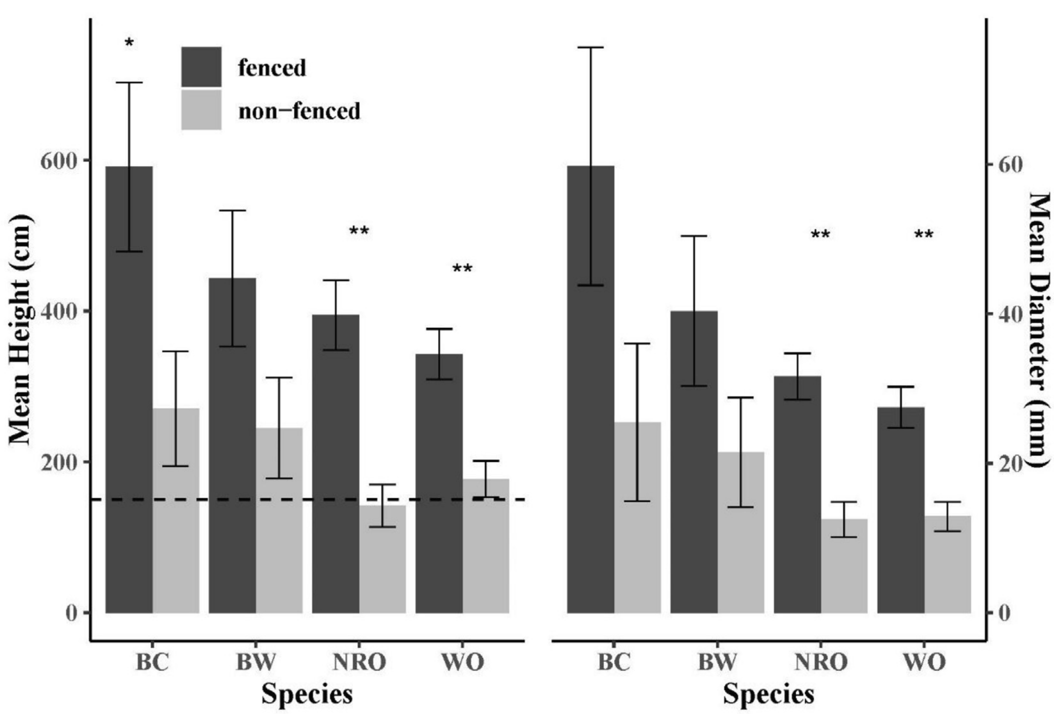

Fig. 4. Mean (± SE) height (cm) and diameter (mm) of black cherry (BC), black walnut (BW, northern red oak (NRO), white oak (WO) after eight growing seasons in fenced or non-fenced treatments across all sites. Asterisks represent significant differences between treatments within a species (* < 0.05, ** < 0.01, *** < 0.001). The dotted baseline represents the free-to-grow line above which deer have limited capacity to browse. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Mean height (± SE) of black cherry (BC), black walnut (BW), northern red oak (NRO), and white oak (WO) trees by level of each treatment after eight growing seasons. Select or non-select seedlings were planted with or without CRF at reforested or afforested sites with or without fencing. Means for each treatment are averaged across the other treatments. Bold indicates significant differences among treatments (α = 0.05).

Species	Treatment	Height (cm)	standard error	p-value
NRO	fenced	395	46	**0.002**
NRO	non-fenced	142	28	
NRO	non-fertilized	255	27	0.531
NRO	fertilized	250	27	
NRO	select	272	28	< **0.001**
NRO	non-select	234	26	
NRO	reforested	282	44	0.314
NRO	afforested	225	32	
WO	fenced	343	33	**0.006**
WO	non-fenced	177	24	
WO	fertilized	257	21	0.092
WO	non-fertilized	250	21	
WO	reforested	276	33	0.348
WO	afforested	231	25	
BC	fenced	591	112	**0.045**
BC	non-fenced	271	76	
BC	fertilized	421	68	0.345
BC	non-fertilized	410	67	
BC	select	423	68	0.191
BC	non-select	408	67	
BC	reforested	431	106	0.818
BC	afforested	399	83	
BW	fenced	443	90	0.099
BW	non-fenced	245	67	
BW	fertilized	337	56	0.973
BW	non-fertilized	336	56	
BW	select	374	59	< **0.001**
BW	non-select	301	53	
BW	reforested	399	95	0.386
BW	afforested	279	65	

Table 5
Mean DBH (± SE) of black cherry (BC), black walnut (BW), northern red oak (NRO), and white oak (WO) trees by level of each treatment after eight growing seasons. Select or non-select seedlings were planted with or without CRF at reforested or afforested sites with or without fencing. Means for each treatment are averaged across the other treatments. Bold indicates significant differences among treatments (α = 0.05).

Species	Treatment	Diameter (mm)	Standard Error	P-value
NRO	fenced	32	3.1	**0.003**
NRO	non-fenced	12	2.4	
NRO	non-fertilized	22	2.1	0.185
NRO	fertilized	20	2.0	
NRO	select	23	2.2	< **0.001**
NRO	non-select	19	1.9	
NRO	afforested	22	2.8	0.549
NRO	reforested	20	2.8	
WO	fenced	27	2.7	**0.004**
WO	non-fenced	13	1.9	
WO	fertilized	20	0.2	0.148
WO	non-fertilized	19	0.2	
WO	afforested	21	2.2	0.461
WO	reforested	18	2.5	
BC	fenced	60	15.9	0.107
BC	non-fenced	25	10.6	
BC	fertilized	42	9.6	0.175
BC	non-fertilized	40	9.4	
BC	select	42	9.7	0.140
BC	non-select	40	9.4	
BC	afforested	47	12.9	0.551
BC	reforested	35	13.5	
BW	fenced	40	10.0	0.163
BW	non-fenced	21	7.3	
BW	non-fertilized	30	6.3	0.660
BW	fertilized	30	6.2	
BW	select	36	6.9	< **0.001**
BW	non-select	24	5.6	
BW	reforested	31	9.8	0.852
BW	afforested	28	7.7	

treatments, select black cherry trees outside the fences had heights comparable to non-select black cherry inside the fences. In years 2 and 3, select black cherry trees were 17.7 cm and 16.5 cm ($p < 0.001$ both years) taller on average than non-select black cherry. By year 5, however, differences were non-significant. In year 2, select black walnut trees were 17.3 cm taller than non-select black walnut within afforested sites ($p = 0.010$ for the interaction). Reforested sites exhibited a similar, but nonsignificant, trend. By year 3, select black walnut trees were 27 cm taller than non-select black walnut on average ($p < 0.001$), and remained 46 cm and 72 cm (over 1.2 times) taller in years 5 and 8 ($p < 0.001$), respectively (Table 4). In year 2, select northern red oak trees were 9.0 cm taller on average than non-select northern red oak within the fenced treatments ($p = 0.003$). On average, select northern red oak trees were 8.6 cm taller by year 3 ($p = 0.005$), 13 cm taller by year 5 and remained 38 cm taller in year 8 (Table 4). There was an interaction between seed source and site type for black walnut diameter ($p = 0.009$) in year 3, whereby the trees at afforested sites had larger diameters within each seed source, but the select trees at reforested sites were comparable to non-select trees at afforested sites; in contrast, every other species tended to have larger diameters on average on afforested treatments compared to reforested treatments in year 3. Seed source also interacted with fencing for black walnut diameter in year 3 ($p = 0.039$); fenced select seedlings were the largest on average (27 ± 3 mm), followed by fenced, non-select (21 ± 2 mm) and non-fenced, select seedlings (14 ± 2 mm, while non-fenced, non-select seedlings were the smallest on average (12 ± 2 mm). In year 5, select seedlings had greater DBH on average across all species other than white oak (which had no select seed sources): northern red oak ($p = 0.011$), black cherry ($p = 0.011$), and black walnut ($p < 0.001$). These differences remained for black walnut and northern red oak into year 8, but they were not significant for black cherry (Table 5). By year 5, select black walnuts had a 13% greater probability of reaching free-to-grow status ($p = 0.001$).

Seed source had a significant effect on timber quality of northern red oak ($p = 0.005$), black cherry and black walnut ($p < 0.001$), all of which displayed better quality. The probability that northern red oak quality would be average or better was 54 ± 3% for select trees, but only 45 ± 3% for non-select trees. The probability that black cherry quality would be average or better was 55 ± 3% for select trees, but only 33 ± 2% for non-select trees. The probability that black walnut quality would be average or better was 60 ± 4% for select trees, but only 37 ± 4% for non-select trees.

3.4. Site type

White oak had a 5.5% lower probability of survival at afforested sites than reforested sites ($p = 0.005$) in year 2, and by year 8 this difference had increased to 7% (Table 3). However, in the intervening years this effect was only present outside the fences (Fig. 4). Site type affected the basal diameter of all species in year 3. Red and white oaks and black cherry had larger diameters at afforested sites. Quality of black cherry was greater at reforested sites ($p < 0.001$). The probability that black cherry quality would be average or better was 50 ± 3% at reforested sites, but only 37 ± 2% at afforested sites. Black walnut also had a tendency towards greater quality at reforested sites, but the effect was non-significant.

4. Discussion

4.1. Fencing drives hardwood performance

We found that fencing had the greatest significant positive effect on

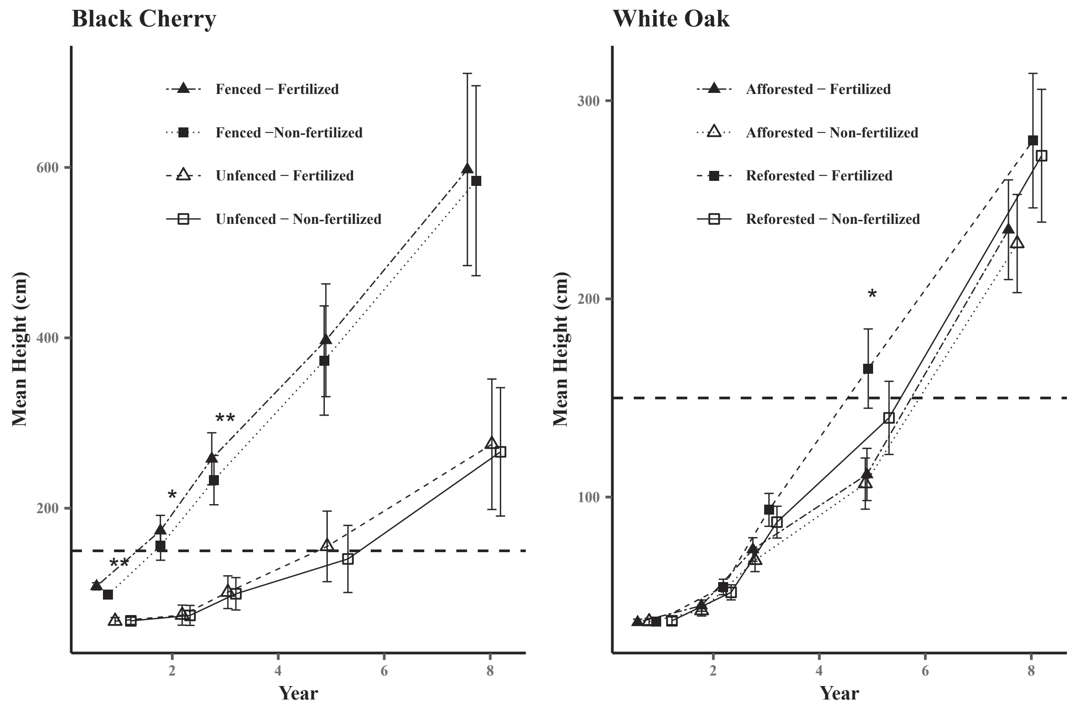

Fig. 5. Mean (± SE) height (cm) of black cherry seedlings for fencing and fertilizer treatments across all sites (left panel); and of white oak seedlings on afforested or reforested sites (right panel). Fenced black cherry trees were significantly taller than unfenced black cherry in every year. Asterisks represent significant interactions (* < 0.05, ** < 0.01, *** < 0.001), which occurred in years 1, 2, and 3 for black cherry, and in year 5 for white oak. The dotted baseline represents the free-to-grow line above which deer have limited capacity to browse. Inside the fences, fertilized black cherry reached free-to-grow status one year earlier than unfertilized black cherry.

survival, growth, and timber quality ratings for all species. In addition to its effect on growth, our results revealed a negative effect of herbivory on survival that was measurable until year 8 for three of our four species. Fences were only maintained for the first three years. Thus, much of the residual effects are due to improved survival and growth in earlier years; however, even at year 8, > 50% of the living non-fenced trees remained below free-to-grow height, suggesting that deer will continue to exert a negative effect on their growth and survival. Thus, fencing not only increased vigor by directly protecting the trees, but also allowed the trees to reach free-to-grow height so that they were not affected by browsing after fencing was removed. Other studies have shown that herbivory reduces the survival of planted seedlings (Tripler et al. 2005; Dickinson and Van Auken, 2016; Owings et al. 2017), but survival differs across species based on the abundance of deer, the palatability and browse tolerance of planted species, and the composition and structure of the understory (Aronson and Handel, 2011; Peebles-Spencer and Gorchov, 2017; Kellner and Swihart, 2016). In our study, the positive effects of fencing on survival and growth were more pronounced for trees planted in old agricultural fields. An interaction between fencing and site type, in which fencing positively affected survival at afforested sites, was present for all species in many years (Figs. 1 and 2). Even black walnut had lower survival rates outside the fences in the first three years, despite this species being of relatively low browse preference (Wakeland and Swihart, 2009). However, by year 5, black walnut survival inside fences at reforested sites was reduced to similar levels as the unfenced treatments (Fig. 2). Interactions between browsing, species, and site make predicting the results of specific management practices difficult, but our results suggest that fencing improves seedling survival at afforested agricultural sites.

The lower survival of non-fenced seedlings at afforested sites was apparently not due to greater incidence of deer browse. Contrary to our hypothesis, browse rates were higher at reforested sites (Table A1). Though not quantified in our study, fencing may increase competition within exclosures due to the absence of browsing (Murray et al., 2016), and these differences are likely intensified in areas with heavy browse pressure. For example, Shelton et al. (2014) found that the relative diameter growth rate of invasive shrubs within exclosures was 30 times greater than the growth of native shrubs. We applied herbicide to competing vegetation for the first three years to reduce competition, although woody competition, particularly black locust (*Robinia pseudoacacia* L.) and tulip-poplar (*Liriodendron tulipifera* L.), were abundant at the reforested sites. Despite this, our results are consistent with findings that show benefits of fencing on growth (and often survival) of regenerating hardwoods and highlight the importance of preventing browsing by deer to increase the effectiveness of forestry plantings.

Compared to trees at reforested sites, northern red oak, black cherry, and black walnut at afforested sites had greater risk of mortality when exposed to herbivory; and in year 5, they showed greater survival when protected from herbivory (Figs. 1 and 2). Improved survival, in the absence of herbivory, on afforested sites may have been associated with reduced competition from woody vegetation compared to reforested sites. Oak species are not highly competitive in clearcuts (Swaim et al., 2016, 2018; Burns and Honkala, 1990), but old fields may provide a low-competition environment that reduces the occurrence of mortality and dieback when trees are protected from browse (Pons and Pausas, 2006). Though black cherry is competitive in clearcuts (Swaim et al., 2016, 2018), it also benefited from the conditions on afforested sites when protected from herbivory, as did black walnut.

Fencing had long lasting significant effects on the growth of oaks and black cherry, and increased black walnut height in the first three years (which remained as a nonsignificant trend until the end of the experiment; Fig. 4). By the fifth year, the probability of reaching free-to-grow status inside fences was > 50% for both oak species, while, outside the fences, the probability was < 10%. Jacobs et al. (2004) found that a large increase in the proportion of trees reaching free-to-grow status occurred between the fourth and fifth year in hardwood plantations, with 49% of trees surveyed reaching free-to-grow status by year 5. In our study, fencing interacted with site type to affect free-to-grow status of black cherry and black walnut in year 5, in a similar fashion to survival. The probability that trees would reach free to grow height was much greater inside fences at afforested sites (> 90% inside fences for black cherry and > 70% for black walnut, < 3% outside the fences for both species). The positive effect of fencing on the growth of planted hardwood seedlings observed in our study is well supported by past research (Owings et al., 2017; Burney and Jacobs, 2018; Blossey et al., 2019). The positive effect of fencing on natural regeneration of native hardwood species has also been well documented (Horsley et al., 2003; Côté et al., 2004; Griggs et al., 2006; Shelton et al., 2014). Under extreme browse pressure, Shelton et al. (2014) observed no new recruitment of seedlings over a three-year study period, and two-times greater diameter growth of pre-existing seedlings inside exclosures compared to outside. Csigi and Holzmueller (2015) reported that seedlings of northern red and white oak, among other species, were significantly taller inside vs. outside exclosures, despite reportedly low deer populations of 6 to 12 deer per km^2, which is usually considered acceptable for the purposes of forest regeneration in the eastern USA.

There are few studies that have examined the long-term effects of browsing by deer on the quality of hardwood trees. We found that non-fenced trees, across all species, had a 22% or less chance of being average or greater in timber quality after nine years, while trees inside fences had a 60% chance or greater of being average or greater in quality. Future growth may compensate for the current low quality of many of the trees, but many trees in our study had still not achieved free-to-grow status when the last measurements were taken after eight growing seasons. In a 32-year-old stand in northern Michigan dominated by sugar maple, trees that regenerated in a heavily-browsed area had 26% more crooks than trees in a reference area with lower browse (Switzenberg et al., 1955), however, the authors suggested that the crooks would not affect the subsequent merchantable value of the trees. Another study of five-year-old sugar maple trees in northeastern Wisconsin found that browse increased forking and decreased height, but other factors, such as competition and light, more greatly affected timber quality (Jacobs, 1969). Considering the expenses of protecting trees from browse early in life, understanding the effects of these efforts on timber quality, and how this may or may not equate to future stumpage value, is important if commercial production is the objective.

4.2. Fertilization interacts with fencing

Fertilizer had a positive effect on growth, but the effect depended on species and the presence of fencing. Black cherry height and diameter during the first five years (Fig. 5) showed a positive response to fertilization when browsing was excluded. Tripler et al. (2002) showed that black cherry is a luxury nitrogen consumer under low light conditions; thus, it increases its nitrogen concentration in response to fertilization when light limits growth. Luxury nitrogen consumers are much more likely to be browsed, which may account for some of the inconsistent species preference results among studies of browse selection by white-tailed deer (Tripler et al., 2002), and may explain why fertilized black cherry did not grow faster outside fences, despite low ratings for browse preference for this species (Wakeland and Swihart, 2009).

Although size differences between fertilized and non-fertilized black cherry faded by the end of the experiment, average height of fertilized cherry exceeded the browse line (150 cm) inside fences after the second growing season, whereas non-fertilized cherry did not reach this height until year 5. Thus, faster growth of fertilized black cherry regeneration may allow landowners to stop maintaining fences earlier. Our results are similar to those of Burney and Jacobs (2018), in which diameter growth of black cherry and bur oak (*Quercus macrocarpa* Michx.) only increased with fertilization inside fenced treatments. Contrary to their results, however, we found an early effect of fertilizer on white oak (no interaction with fencing was detected), whereby fertilizer increased height and diameter until year 3 at afforested sites (and height until year 5 at reforested sites; Fig. 5). Despite white oak being a preferred browse species (Wakeland and Swihart, 2009), our evidence suggests that the positive effects of fertilizer are not negated by browse.

We found no effects of fertilizer on northern red oak growth, similar to previous studies (Burney and Jacobs, 2018; Tripler et al., 2002). On the other hand, an interaction between fencing and fertilizer in year 8 for northern red oak revealed that fencing was more important for non-fertilized northern red oaks (Fig. 1), suggesting that CRF may aid the survival of northern red oak under herbivore pressure. Tripler et al. (2002) found that northern red oak was a constant nitrogen consumer (i.e., did not store excess nitrogen in leaf tissues) and that fertilizer did not increase probability of browse. Our study suggested that the gains in growth from CRF were discernible beyond the two years of fertilizer release for black cherry and white oak (and into the final year for northern red oak survival), and that fencing is necessary for the benefits of fertilizer on growth to be realized for black cherry.

4.3. Seed source

We observed greater timber quality in select black walnuts and black cherries, and greater growth in select black walnuts and northern red oaks compared to non-select trees. Greater growth and quality for black walnuts from select seed sources has been found in previous experiments (Beineke, 1989; Geyer and Rink, 1998; Woeste et al., 2011; Woeste, 2002). Geyer and Rink (1998) found a significant effect of provenance on black walnut timber quality. Select northern red oaks growing inside exclosures displayed higher survival than their non-fenced counterparts (Fig. 3), suggesting that protection from deer browse is necessary for genetically select northern red oak seedlings to reach their full potential. In addition, seed source interacted with fencing on third-year black walnut basal diameter and first-year black cherry height, and interacted with site type on second-year black walnut height and third-year black walnut basal diameter, indicating that select seedlings follow the "law of limiting factors" (Zobel and Talbert, 1984). Originally formulated in the context of plant nutrients as "Liebig's law of the minimum," this law indicates that the most limiting factor to growth and survival (e.g., the nutrient that is in lowest supply) must be addressed before other factors affect performance (Liebig, 1855; Dumroese et al., 2016). In this case, genetically improved sources did not realize their full potential for enhanced growth unless protected from herbivory. The exception may be for black walnut where, by year 5, select black walnut trees at afforested sites had 13% greater probability of reaching free-to-grow height than non-select trees (27.9% vs 14.9%). Trees at reforested sites had higher probabilities of reaching free-to-grow status than trees at afforested sites, regardless of seed source (44–50% at reforested sites across species). By year 8, seed source was the only factor significantly affecting black walnut size (Tables 4 and 5). Similar to our results for black cherry in which early height and diameter differences for select sources became non-significant by year 8, Pitcher (1982) found that performance of select black cherry progeny in the field performed no better than non-select sources after 12 years.

5. Conclusions

Fencing interacted synergistically with field fertilization and use of genetically select seed sources to allow improved growth of planted trees. In temperate hardwood forests where deer herbivory poses a challenge for forest managers, especially where commercial timber production is a goal, management of browse is an essential consideration when developing silvicultural prescriptions. While fencing may have considerable up-front costs, it may be necessary to ensure the effectiveness of other costly resources. For some species, such as black cherry, investing in fertilization or select seedlings may only be beneficial if ungulate browse is controlled. Genetically select hardwood seed sources showed improvement in growth when protected from browse. Further improvement of seed sources through breeding may produce greater gains in growth and quality. Nevertheless, fencing was the single most important silvicultural tool across species and sites in this study that significantly improved the growth of oaks and black cherry, the quality of all species examined, and survival of afforestation plantings in agricultural fields.

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Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118339.

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