

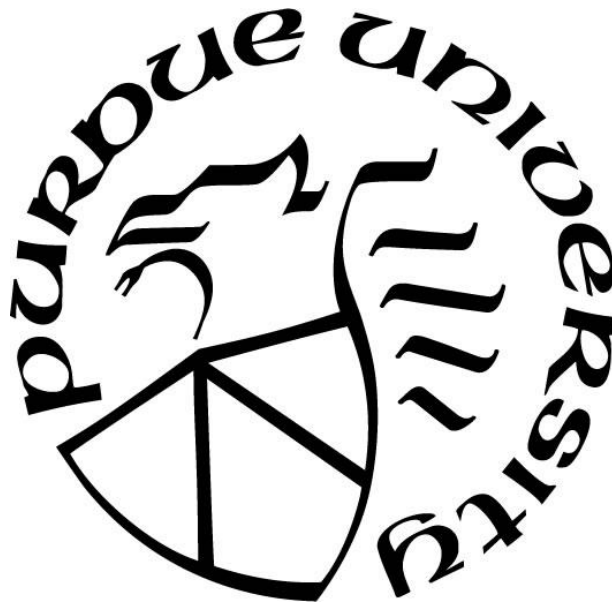
QUANTIFYING IMPACTS OF DEER BROWSING AND MITIGATION EFFORTS ON HARDWOOD FOREST REGENERATION

by
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Dedicated to my grandparents: Joseph Howell, Jr., who taught me patience, frugality, and the beauty of plants; Mary-Ann Hanson, who has always supported me in all of my undertakings; to Jack and Lucy Redick; and, lastly, to John “Dick” Hanson.

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CHAPTER 1. INTRODUCTION

1.1 Temperate hardwood forests in the eastern United States

Temperate hardwood forests provide food and habitat for wildlife as well as valuable wood products. These forests contain a wide diversity of species, with some of the most important ecological and commercial species including oaks, hickories, cherries, and walnuts. Oaks, in particular, are a foundational species for many temperate forest types, which grow in dry and mesic environments (van de Gevel et al., 2012). In the Midwestern USA, oak-hickory forests are the most prominent forest type, making up to 71% of Indiana forests (Gormanson and Kurtz, 2017). Northern red oak and white oak are important timber species in the eastern USA. Black cherry is a minor component of many northern hardwood forest types and has valuable wood (Burns and Honkala, 1990).

1.2 Limiting factors to hardwood regeneration

Oak forests across the eastern USA are shifting to a mixed mesophytic species composition dominated by maples and beeches (*Acer-Fagus*) (van de Gevel et al., 2012; Hart et al., 2008). A combination of factors has led to decline of oak and hickory regeneration in the Midwest, including reduced frequency of fire, changes in harvest practices, and herbivory by white-tailed deer (*Odocoileus virginianus*) (Csigi and Holzmueller, 2015; McEwan et al., 2011). The decline of oak is present in other countries as well, including Sweden and Japan (Petersson et al., 2019; Takatsuki, 2009). Disturbances that create canopy openings and reduce competition release light resources for the understory and benefit regeneration of fire-tolerant and moderately shade-tolerant and intolerant species. For example, oaks and American chestnuts both historically relied on disturbances such as wind or ice storms to create canopy gaps (van de Gevel et al., 2012). A lack of surface fires and single-tree selection harvesting practices have both contributed to the establishment of understory sugar maple and American beech, which are late-successional shade-tolerant species (Holzmueller et al., 2011). Even disturbance is reintroduced, however, invasive plants and deer herbivory present additional challenges to temperate forest regeneration and management.

1.3 The threat of damage by deer

Animal herbivory, resulting from high populations of native ungulates or novel introductions of deer, goats, or cattle, poses a problem in forest regeneration globally (Kuijper et al., 2010; Petersson et al., 2019; Takatsuki, 2009; Whitaker, 2009). Silvicultural techniques that produce small clearcuts and sharp forest edges create attractive habitat for herbivores, but often lead to a concentration of food resources insufficient to satiate the animals without resorting to woody seedlings (Reimoser and Gossow, 1996). For example, in southern Sweden, an increase in deer and moose populations and a concomitant increase in basal area (due to changes in harvesting practices) have caused a regional decline in oak sapling density (Petersson et al., 2019). Similarly, in Japan increasing Sitka deer populations threaten to change plant communities (Takatsuki, 2009). In the eastern USA, reduced hunting pressure, loss of predators, and the adaptability of deer to anthropogenic landscapes and structures have contributed to an increase in white-tailed deer populations (Whitaker, 2009). Deer herbivory stunts tree growth, hindering seedlings from growing into the overstory and allowing herbaceous species to overtop them (McKenna and Woeste, 2004; Putman and Moore, 1998; Webster et al., 2008). In addition, browsing of terminal buds reduces the quality of timber by encouraging trees to grow multiple leaders, which lead to split, crooked trunks (McKenna and Woeste, 2004). Browsing favors some tree species over others, changing composition (Owings et al., 2017; Strole and Anderson, 1992; Stromayer and Warren, 1997) and favoring unpalatable competitive species such as ferns and grasses (Stromayer and Warren, 1997; Takatsuki, 2009). Sugar maples, in addition to being more shade-tolerant than oaks, show an ability to recover from frequent browsing, meaning that they are favored over less tolerant species under heavy browse pressure (Stromayer and Warren, 1997). Oaks are preferred by deer (Strole and Anderson, 1992; Wakeland and Swihart, 2009), while black cherry and black walnut are moderately preferred by deer in Indiana, though preference of black cherry greatly varies by site (Wakeland and Swihart, 2009).

It has been suggested that deer may shift eastern forest ecosystems to alternative stable states (Stromayer and Warren, 1997). This shift in stable states can begin after long term suppression of regeneration, or in a short period after a disturbance such as fire or clearcutting (Stromayer and Warren, 1997). Mid- and late-successional forests are particularly at risk from a change in stable state. Long-term deer herbivory can remove the understory, and when combined with other disturbances that remove the overstory, ecosystems can shift to an early-successional state (Frelich

et al., 2002). A forest will need more than reductions in deer populations to recover from an alternative stable state; it will need other forms of management as well (Stromayer and Warren, 1997), such as vegetation control and deer exclusion or shelters. The strength of effect a deer population has on a forest depends on the food available and the density of the deer population; low populations of deer are ecologically beneficial (Parker et al., 2010; Takatsuki, 2009). For example, deer that reduce woody competition, increase survival or growth of unpalatable tree seedlings and herbaceous plants (Itô and Hino, 2005). Marquis et al. (Marquis et al., 1992) created a deer impact index with a range of deer populations and food availabilities under which various forest regeneration outcomes occur. According to this index, species shifts can occur under densities of 12-48 deer per square kilometer at low food availability, and total regeneration failure will occur between 30 and 48 deer per square kilometer. Csigi and Holzmüller (2015), however, found that deer densities lower than this (6-12 per square kilometer) can have an unfavorable effect on the height of desired hardwood seedlings, such as oak and hickory species.

1.4 Management options for deer control

Many studies have evaluated the impact of deer on forest ecosystems and various methods of overcoming deer browse. There is a need for long-term studies, however, showing the relative impacts of management methods on forest regeneration. There is also a need for reviews of research comparing browse management methods so researchers and landowners can compare method costs and effectiveness. One commonly used silvicultural method is fencing (Csigi and Holzmüller, 2015; Frigoletto et al., 2017) to reduce herbivore damage, which is frequently used in restoration work, as well as research to examine the impact of deer on plant communities. There are several types of fencing; plastic mesh fences are relatively cheap and easy to repair, and are also popular with landowners because they have low visibility, reducing the effect on aesthetics (McKenna and Woeste, 2004). Other fences include wire mesh, barbed wire, and electric fences, which have varying costs and effectiveness.

Fertilization is another silvicultural treatment that may help to promote free-to-grow status of planted trees. Controlled-release fertilizer gradually releases nutrients to target trees, improving nutrient use efficiency, as well as limiting the extent to which competing vegetation takes advantage of the applied fertilizer (Jacobs et al., 2005). Fertilization using this method may encourage trees to reach free-to-grow status (a height above which deer cannot stunt growth;

usually 120-150 cm), however, it may also increase the palatability of seedlings to deer (Burney and Jacobs, 2013; Tripler et al., 2002). In addition, the adaptation of oaks to nutrient-poor environments may preclude their ability to take advantage of fertilizers (Rebbeck et al., 2011).

Forest tree improvement, defined by Zobel and Talbert (1984) as “control of parentage... combined with other forest management activities... to improve the overall yield and quality of products from forestlands” is increasingly important in contemporary forestry. Current attempts at breeding range from first-generation select seed sources to progeny-tested improved lines. Quick growth and good form in selected progeny may allow trees to reach free-to-grow status earlier and compensate for the deer problem. However, herbivory may prevent the gains one would expect of select trees from being realized. Forest tree improvement cannot compensate for poor silviculture (Zobel and Talbert, 1984).

Protection of seedlings by shrubs has been explored as an option for managing deer herbivory without a direct financial cost (Baraza et al., 2006; Jensen et al., 2012). Allowing shrubs to grow alongside seedlings has been suggested for invasive shrubs, such as Amur honeysuckle (Peebles-Spencer and Gorchov, 2017). However, such facilitation depends on the relative palatability of the species involved, and effects of shrubs on some tree species can be negative (Baraza et al., 2006). Competing vegetation is, in itself, a challenge to forest regeneration.

1.5 Competing Vegetation: Amur honeysuckle

Recent work on the interaction of deer and invasive species has been published (Aronson and Handel, 2011; Owings et al., 2017; Loomis et al., 2015; Peebles-Spencer and Gorchov, 2017), but more is needed because a range of responses have been found in different studies, from synergistically negative, to antagonistic interactions. Invasive plants become prominent due to disturbances, a lack of natural enemies (herbivores, for example) (Pimentel et al., 2005), and the ability to form pure stands that exclude competitors (Webster et al., 2006). Competing vegetation, along with herbivory, are two of the biggest challenges to hardwood seedling success (Jacobs et al., 2005). Invasive shrubs in particular are challenging to forest regeneration because they often form monocultures that shade out seedlings (Webster et al., 2006).

There are approximately 138 invasive shrub and tree species in the USA, which often displace native species (Pimentel et al., 2005). Amur honeysuckle (*Lonicera maackii*) is an allelopathic invasive shrub in the eastern U.S.A. that monopolizes light in the understory, especially due to its

early bud-break and late senescence of leaves (Webster et al., 2006; Cipollini et al., 2008). As a result of heavy shading produced by invasive shrubs, moderately shade-tolerant species may be suppressed and unable to take advantage of openings in the canopy. In addition, this shrub may interact with herbivores either by providing habitat for deer (Allan et al., 2010), or alternatively, by sheltering some plants from deer herbivory by restricting movement and access (Christopher et al., 2014). Indirect interactions between invasive plants and native plants may lead to a form of apparent competition in which two species together support greater populations of a predator than they would alone, which adds to the negative effects of (or even gives a false impression of) direct competition between the plants (Holt, 1977; Meiners, 2007). Amur honeysuckle has been confirmed to provide habitat for seed predators (Meiners, 2007), and to provide food to deer in resource-poor times of year due to extended leaf phenology (Martinod and Gorchov, 2017). In stands where honeysuckle has become established, shrub removal may be a necessary step in management for reforestation to succeed.

Honeysuckle and deer both have negative effects on seedlings, as well as diversity and coverage of native herbaceous vegetation, and present a challenge to reforestation. However, the interactions remain poorly understood (Haffey and Gorchov, 2019). Gould and Gorchov (2000) showed that Amur honeysuckle reduced the survival of native annuals, especially at disturbed sites where densities of the shrub tend to be greater. However, removal of honeysuckle resulted in the survival of annuals plants on these plots equivalent to survival on plots where it was never present, and fecundity of annual plants was actually greater at removal sites, likely due to the absence of other competitors (Gould and Gorchov, 2000). In addition to their value as unique species, native herbaceous plants are important in regulating ecosystems.

There is no simple solution to the problem of intensive deer herbivory. For political and economic reasons, the present populations of deer are often favored and hunting is controlled to prevent population reduction. In addition, deer harvest is not possible in all areas due to lack of access or the urban-wildland interface. In these cases, browse control methods including, but not limited to, culls are required. If ecosystems have shifted to alternative stable states, multiple management methods will be required to return desirable states (Stromayer and Warren, 1997). Even in areas with healthy populations of deer, effective browse control is still desirable. For example, even at populations of 6-12 deer per square kilometer, usually considered as moderate, deer can still reduce seedling height of hardwood species (Csigi and Holzmueller, 2015). Indeed,

regenerating seedlings may need protection even after population reduction has been implemented due to the fact that they have lower density after long-term subsection to herbivory (Tanentzap et al., 2011).

1.6 Objectives of Study

In this thesis, I studied management strategies to aid hardwood regeneration. Specifically, my research focused on the following areas: 1) fencing, fertilizer, and seed sources as methods to overcome deer herbivory and encourage tree growth; 2) the effects of deer herbivory and Amur honeysuckle (*Lonicera maackii*) invasion and their interactive effects on underplanted seedlings as well as on natural regeneration and plant communities; 3) past studies on the relative effectiveness and cost of browse control methods available to forest landowners. This research is, thus, divided into three projects: two experimental studies in Indiana and a literature review. All projects study damage by deer to regenerating or afforested temperate hardwood forests. The first and second projects compare the relative effect of fencing to other management practices such as invasive plant removal, fertilization, and selection of improved seedlings.

Study 1: Enhancing Hardwood Regeneration with Select Seedlings, Fertilization and Deer Exclusion

The purpose of this study was to determine whether deer fencing, controlled-release fertilization, and select seed sources affect the survival, growth, or quality of planted trees and how fencing interacts with these other factors. In addition, we sought to determine how survival, growth, and stem quality (rated as a function of timber quality) differ at afforested vs. reforested site types, and how site type interacted with fencing. We hypothesized that: (1) fencing prevents deer from browsing seedlings, thus fencing should increase survival, height and diameter growth, and timber quality relative to non-fenced sites. (2) We predicted that the fertilized treatments would increase survival, height, and diameter growth inside fenced treatments, but that there would be an interaction between fencing and fertilizer such that no increase outside of fenced treatments occurs. (3) We predicted that height and diameter growth, as well as quality would be greater for select seedlings than non-select seedlings; and that the effect size would be smaller in non-fenced and unfertilized treatments. We predicted no differences in survival between select seedlings and non-select seedlings. (4) Trees on afforested sites are likely to be subjected to higher levels of deer

herbivory due to their high visibility to deer. We predicted that higher browse pressure would result in lower height and diameter growth and lower quality outside fenced treatments on afforestation plantings compared to reforestation plantings. Within fenced treatments we predicted greater growth and survival at afforestation plantings, particularly for shade-intolerant species, due to lower competition for light and other resources.

Study 2: Response of underplanted trees and plant community to fencing and invasive removal

The purpose of this study was to determine the individual and interactive effects of fencing and invasive shrub removal on herbaceous species cover and woody regeneration. We hypothesized that: (1) fencing would reduce deer browse and invasive plant removal would release woody seedlings from competition and herbivory.

Individually, these treatments would increase herbaceous-layer cover, and richness, as well as the density of woody seedlings. (2) Deer and honeysuckle would interact synergistically (a positive interaction) to suppress the growth of natural regeneration and herbaceous vegetation due to browse and competition. Honeysuckle may provide cover for deer, as well as rabbits, increasing use of invaded sites. Richness, diversity, density of seedlings, and native plant cover would be lowest in the non-fenced, reference areas. (3) Due to reduced herbivore pressure, fencing would prevent native plants from being outcompeted by invasive species. This would result in lower invasive cover, as well as higher species richness and diversity in fenced removal areas.

Study 3: Review of research on browse control methods

The purpose of this study was to determine the most effective research-based management options for deer browse of hardwood forest trees. Many empirical studies have been conducted over the past century on the impacts of deer on plant communities and ecosystems (Côté et al., 2004), including those involving fencing and exclosures, tree shelters, cages and repellents (Kochenderfer and Ford, 2008). However, few literature reviews of such studies have been conducted specific to ecology and management of hardwood forest regeneration.

CHAPTER 2. SILVICULTURE AT ESTABLISHMENT OF HARDWOOD PLANTATIONS IS RELATIVELY INEFFECTIVE IN THE PRESENCE OF DEER BROWSING

2.1 Abstract

Ungulate browsing is limiting to 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 the benefits from these methods may depend upon site characteristics and ungulate browse pressure. We studied the interactions among browsing by deer (*Odocoileus virginianus*), use of genetically select seed sources, applications of controlled-release fertilization (CRF) at planting, and site type 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 clear-cut 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 (*Quercus rubra*, *Quercus alba*, *Juglans nigra*, and *Prunus serotina*). Fencing had the greatest significant, positive influence on survival and growth, and had a pronounced effect on stem quality ratings for all species. We only observed gains in height and diameter from CRF up to the first three years for fenced *P. serotina*, and for *Q. alba* regardless of fencing. Genetically select seed sources had the greatest and most consistent growth benefit for *J. nigra*. Early growth was improved in genetically select *P. serotina* vs non-select sources but differences faded by the fifth growing season, while superior growth of genetically select *Q. rubra* began to manifest only after year 5. Without protection from herbivory, genetically improved sources did not realize their full potential for enhanced growth. Our results from this long-term hardwood regeneration experiment confirm that without browse protection, additional silvicultural treatments are unlikely to improve tree growth and survival.

2.2 Introduction

Regenerating forests face many challenges, including herbivory, poor nutrition, and competing vegetation, which typically vary among sites. Browsing damage caused by high native populations or novel introductions of ungulates are a limiting factor within temperate hardwood ecosystems.

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 leaders (Jacobs et al., 2004). Marquis et al. (1992) suggested that shifts in species composition can occur under densities of 12 to 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). Other studies have observed that deer densities as low as 6 to 12 deer km⁻² can limit the height of desirable hardwood seedlings (Csigi and Holzmüller, 2015). Due to lowered food resources and plant population densities, browse-sensitive plant populations may be more sensitive to herbivory after a history of over-browsing, even following deer population reductions (Aronson and Handel, 2011; Csigi and Holzmüller, 2015; Royo et al., 2010).

Various methods of reducing the impacts of ungulate herbivory have been studied (Beguín et al., 2016; Sage et al., 2003). Fertilization is a silvicultural treatment that may allow seedlings to reach free-to-grow status sooner than an unfertilized tree (i.e., a height above which deer cannot stunt tree growth; usually 120-150 cm). 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 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 may also increase the palatability of seedlings to deer (Burney and Jacobs, 2013; Tripler et al., 2002), and deer may increasingly target palatable species, such as oak (*Quercus* spp.; Tripler et al., 2002; Wakeland and Swihart, 2009). While studies have examined short-term responses of hardwood seedlings to CRF application (Burney and Jacobs, 2018; Jacobs et al., 2005), few long-term studies have been published.

Artificial forest regeneration may benefit from the use of superior seed sources that have been selected for improvement of growth, stem form, and pest resistance (Beineke, 1989; Zobel and Talbert, 1984). While few seed sources or cultivars have been identified with increased tolerance

to ungulate browsing (Kimball, 2005; Wooley et al., 2008), 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 demonstration of 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 old 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 herbivores such as large grazers are absent (Pons and Pausas, 2006). Larger gap sizes are associated with greater tree growth (Kern et al. 2013). In addition, the lack of a surrounding forest, and the lower vegetation, makes trees more apparent to deer, especially when little other palatable food is present. Feeny proposed that plants with greater apparency to herbivores are exposed to a greater adaptive pressure (1976). While Feeny proposed this in regard to insect herbivores, apparency and concealment are important factors for mammalian herbivores as well (Kellner and Swihart, 2017; Jensen et al., 2012). Plant diversity has been shown to reduce the negative effects of herbivores due to positive interspecific interactions, though positive effects are dependent on the relative palatability and abundance of the species involved (Cook-Patton et al., 2014; Brown and Ewel, 1987; Baraza et al., 2006). 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).

There is no simple solution to the problem of intensive deer herbivory on forest regeneration, particularly if political and economic drivers continue to prevent cull reductions in deer herds (Phillip et al., 2009; Tanentzap, 2012). While effective browse control methods may be 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 may be required to return desired function and species (Stromayer and Warren, 1997), suggesting that the use of silviculture to prevent such shifts from occurring may be 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).

There is a need for long-term studies to evaluate the relative impacts of silvicultural treatments on hardwood plantation development in the presence of varying browse pressure. 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 source across five reforestation or afforestation sites in Indiana. We hypothesized that: (i) 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 vegetative competition on afforestation vs. reforestation sites would result in greater survival and growth, yet browse damage would be higher on non-fenced afforestation sites.

2.3 Methods

2.3.1 Location, Planting Materials, and Treatment Establishment

Between 2006 and 2007, 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 including: Stephens Forest (Stephens) and Darlington Woods (Table 2.1). Both of these sites were mature oak-hickory forests succeeding to maple-beech. They are >100 years of age and appear to have never been farmed other than on upland flats (Brian Beheler, personal communication). Neither forest had been harvested previous to 2006. 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 (SEPAC), Martell Forest (Martell), and Lugar Forestry Farm (Lugar Farm; Table 2.1). The sites at SEPAC and Martell have been under cultivation for at least fifty years. Lugar Forestry Farm was an apple orchard from circa 1950-2002, when the orchard was removed and the ground left fallow. Each site was approximately 0.81 ha in size. 5,083 seedlings of four species, including

Quercus alba L. (white oak), *Quercus rubra* L. (northern red oak), *Prunus serotina* Ehrh. (black cherry), and *Juglans nigra* L. (black walnut). All seedlings were grown as 1+0 bareroot seedlings (obtained from Indiana Department of Natural Resources (DNR) Vallonia Nursery (Vallonia, IN, USA) following operational production protocols (Jacobs, 2003). Seedlings were planted using an auger to drill holes at 2.4 x 2.4 m spacing.

Table 2. 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	Delphi	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	West Lafayette	1139	36.0%	N 40°26'36" W 87°01'58"	Starks-Fincastle complex and Rainsville silt loam
Lugar Farm	afforestation	West Lafayette	1147	32.0%	N 40°25'43" W 86°57'29"	Starks-Fincastle complex and Richardville silt loam

A “select” seed source was collected for black cherry, black walnut, and northern red oak by the Indiana DNR (IDNR Division of Forestry, 2006); select trees that displayed superior form and height and diameter growth traits were selected from grafted seed orchards. In addition, a non-select (woods-run) source was acquired for black cherry, black walnut, northern red oak, and white oak following collection from accessible, open-pollinated 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 other seed was obtained from the Indiana DNR Vallonia Nursery. In total, seven seed sources were planted at each of five sites.

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. Half of the trees were fertilized with CRF (Osmocote® Exact Lo-Start 15N-9P-10K plus minors; O.M. Scotts Co., Marysville, OH, USA) applied directly in the planting hole (Jacobs et al., 2005). Vegetative competition in all treatments was controlled through the use of herbicide applications in 2008, 2009, and 2010. Herbicide applications included glyphosate (Razor Pro, Burr Ridge, IL, USA) at 2.05-2.63 L/ha (depending on the vegetation on site) pre-planting, pendimethalin (Pendulum Aqua Cap, Research Triangle Park, NC, USA) at 2.63 L/ha with 1% glyphosate post-planting, clopyralid (Transline, Indianapolis, IN, USA) at 1.90 L/ha in June 2008 at afforested sites, clethodim (Envoy, Walnut Creek, CA, USA) at 1.75 L/ha in July 2008 at afforested sites, pendimethalin at 1.90 L/ha with 1.5% glyphosate in spring 2009, clopyralid and clethodim on patches of grass on afforested sites in June and July 2009, respectively, pendimethalin at 7.02 L/ha with 1% glyphosate and simazine (Drexel Simazine 90 DF, Memphis, TN, USA) at 4.48 kg/ha in spring 2010 on afforested sites, and clopyralid at 1.90 L/ha on afforested sites during the 2010 growing season. Reforested sites were sprayed via a backpack sprayer and afforested sites were sprayed using a tractor. Tree height and survival were measured on all sites after planting and in years 1 (2009), 2, 3, 5, and 8. Survival, measured in years 5 and 8, was calculated indirectly from empty planting locations for the interceding years. Basal diameter was measured in year 3, and diameter at breast height (DBH, 1.3 m above groundline) was measured in years 5 and 8. In year 9, quality was assessed visually using a qualitative scale based on a combination of straightness, apical dominance, self-pruning, depressed knots, crooks in the stem, and the angle, size, and number of lateral branches: 1 was considered poor, 3 was average, and 5 was excellent (Mckenna and O’Connor, 2013).

2.3.2 Statistical Analyses

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.

Logistic regression was used to analyze survival among treatments for year 1, 2, 3, 5, and 8. The quality scoring system was considered to be an ordinal variable (i.e., the distance between ordered scores was not equal); therefore, parametric analyses could not be used. Therefore, ordinal logistic regression was used to analyze quality for year 9. This analysis uses a series of logistic regression models to produce log odds ratios, which can be 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 application, site type, and seed source)) were compared for each dependent variable (height, DBH, survival or quality)). 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. Random slopes were used on models when they resulted in a better fit (Table 2.2). The models took the following general form:

$$y = (Fence + Fertilizer + Seed Source + Site Type)^2 + (1|Site) + \varepsilon$$

Table 2. 2 Factors used as random slopes for each model by species and year

Random Slope	Species	Response Variable	Years
Fencing	NRO	Height	All
Fencing	NRO	Diameter	3,8
Fencing	NRO	Survival	2,3,5,8
Fencing	WO	Height	All
Fencing	WO	Diameter	All
Fencing	WO	Survival	8
Fencing	BC	Height	1,2,5,8
Fencing	BC	Diameter	3,8
Fencing	BC	Survival	3,8
Fencing	BW	Height	2,3,5,8
Fencing	BW	Diameter	3,5,8
Fencing	BW	Survival	1,2,3
Fertilizer	WO	Survival	8
Fertilizer	BC	Height	1
Fertilizer	BC	Survival	8
Fertilizer	BW	Height	2,3,5
Fertilizer	BW	Diameter	3,5
Fertilizer	BW	Survival	3
Seed Source	NRO	Height	3
Seed Source	NRO	Diameter	3
Seed Source	BC	Height	1
Seed Source	BW	Height	1

Height and diameter were square-root transformed to better meet the assumptions of homogeneity of variance and linearity of error. The logit transformation was used on the survival and quality 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; because REML gives slightly biased results for fixed effects, 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 same package was 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 “MASS” package was used to analyze the effects of each treatment on tree quality using proportional odds models (Venables and Ripley, 2002). Least square means and standard errors were obtained using “lsmeans” and “emmeans” (Lenth, 2018; Lenth, 2016).

2.4 Results

2.4.1 Fencing

Fencing interacted with site type on northern red oak survival in years 1 and 5, on white oak survival in years 3 and 5, on black cherry survival in years 1, 2, 5, and 8, and on walnut survival in year 5. Fenced trees had a greater probability of survival than non-fenced trees at afforested sites. Survival was 27.6% greater for fenced northern red oaks at afforested sites in year 5 ($p = 0.003$ for the interaction; Figure 2.1), 13.1% greater for fenced white oak at afforested sites in year 5 ($p < 0.001$ for the interaction; Figure 2.1), and 27.7% greater for fenced black cherry at afforested sites in year 8 ($p = 0.023$ for the interaction). In year 5, fenced black cherries, northern red oaks, and black walnuts at afforested sites had higher probabilities of survival than any other treatment (Figures 2.1 and 2.4). Fencing interacted with seed source on northern red oak in years 3, 5, and 8. Fenced northern red oaks had a greater probability of survival than non-fenced northern red oaks within the select seed source ($p = 0.043$ for the interaction in year 8; Figure 2.2). Fenced, select northern red oaks had higher survival than all other northern red oaks in year 5. In year 8, fenced northern red oaks had a greater probability of survival than non-fenced northern red oaks when non-fertilized ($p = 0.015$ for the interaction; Figure 2.3). Fencing, as a main effect, increased the probability of survival for northern red oak in year 2, white oak in years 2 and 8, black cherries in year 3, and black walnuts in years 1, 2, and 3. In year 8, fenced white oaks had a 2.8% greater probability of survival (Table 2.3). Fencing positively affected black walnut survival in years 1-5, though by year 5 this was only the case at afforested sites and by year 8 the difference between fence treatments was no longer significant for any site type (Figure 2.4).

Fencing increased the height of both oak species and black cherry in every year. After year 8, fenced northern red oaks were >2.5 times the height of non-fenced northern red oaks on average and fenced white oaks were almost twice the height of non-fenced white oaks on average (Figure 2.5). Fenced black cherries were over twice the height of non-fenced black cherries on average (Figure 2.5). Fencing increased the height of black walnut seedlings in years 2 ($p = 0.029$) and 3 ($p = 0.027$). Though fenced black walnuts were still almost twice as tall in year 5, the difference was not significant, and, similarly, in year 8, when fenced trees were 1.8 times taller than their non-fenced counterparts on average (Table 2.4).

After year 8, both oak species had greater diameters in the fenced treatments than the non-fenced treatments. Fenced northern red oaks were over 2.5 times the diameter of non-fenced trees on average (Figure 2.5), and fenced white oak diameters were over 2 times the diameter of non-fenced white oaks (Figure 2.5). These same trends were present, but nonsignificant, for black cherry and black walnut in year 8; for both species fenced trees had about twice the diameter of non-fenced trees on average (Table 2.5). In year 3, the fenced black cherries were significantly larger within and across each fertilizer treatment ($p = 0.038$), and the fenced black walnuts were larger within each seed source treatment ($p = 0.039$), but that was the only year these trends were significant.

Fencing had a significant positive effect on quality of all species. The probability of quality being average or better was 60% or more for all fenced species (ranging from 60% for black cherries to 76% for northern red oaks), while the probability of being average or better was less than 22% for all non-fenced species (ranging from 22% for black walnuts to 6% for white oaks; Table 2.6).

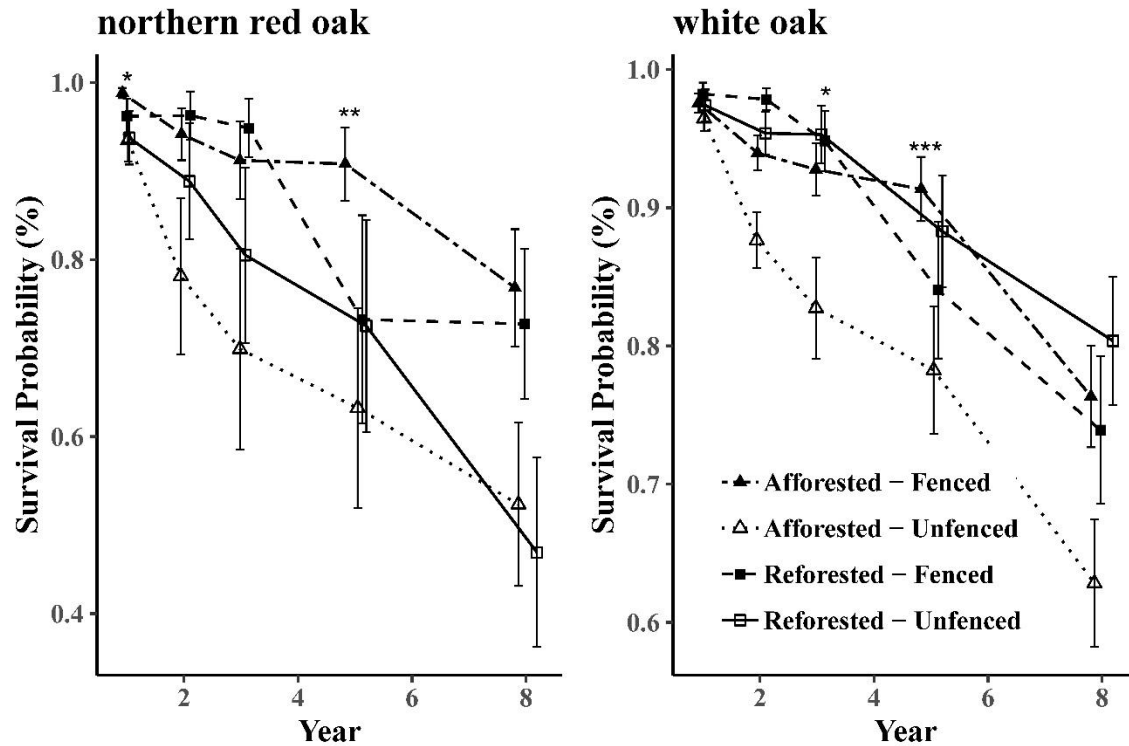


Figure 2. 1: Proportion of surviving fenced and non-fenced northern red oaks and white oaks over time on reforested or afforested sites. Asterisks represent significant interactions (* <0.05 , ** <0.01 , *** <0.001), which occurred for northern red oak in years 1 and 5 whereby fenced seedlings had a greater probability of survival than non-fenced seedlings only within the afforested sites, and for white oak in year 3 whereby non-fenced seedlings at afforested sites had a lower probability of survival than all other treatments, as well as year 5 whereby fenced seedlings had a greater probability of survival at afforested sites only.

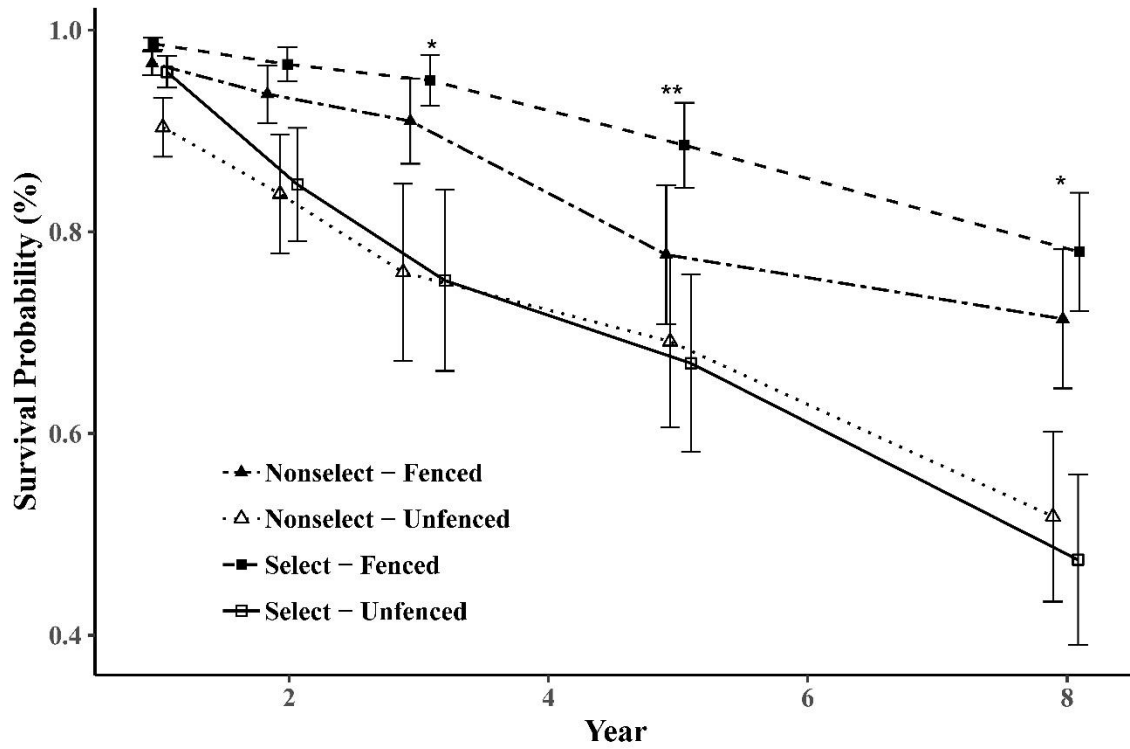


Figure 2. 2: Proportion of surviving northern red oaks for fencing and select treatments across all sites. Asterisks represent significant interactions ($* < 0.05$, $** < 0.01$, $*** < 0.001$), which occurred in years 3 and 8 whereby only select fenced trees had a greater probability of survival than select non-fenced trees, as well as in year 5 whereby select, fenced trees had a higher probability of survival than all other treatments.

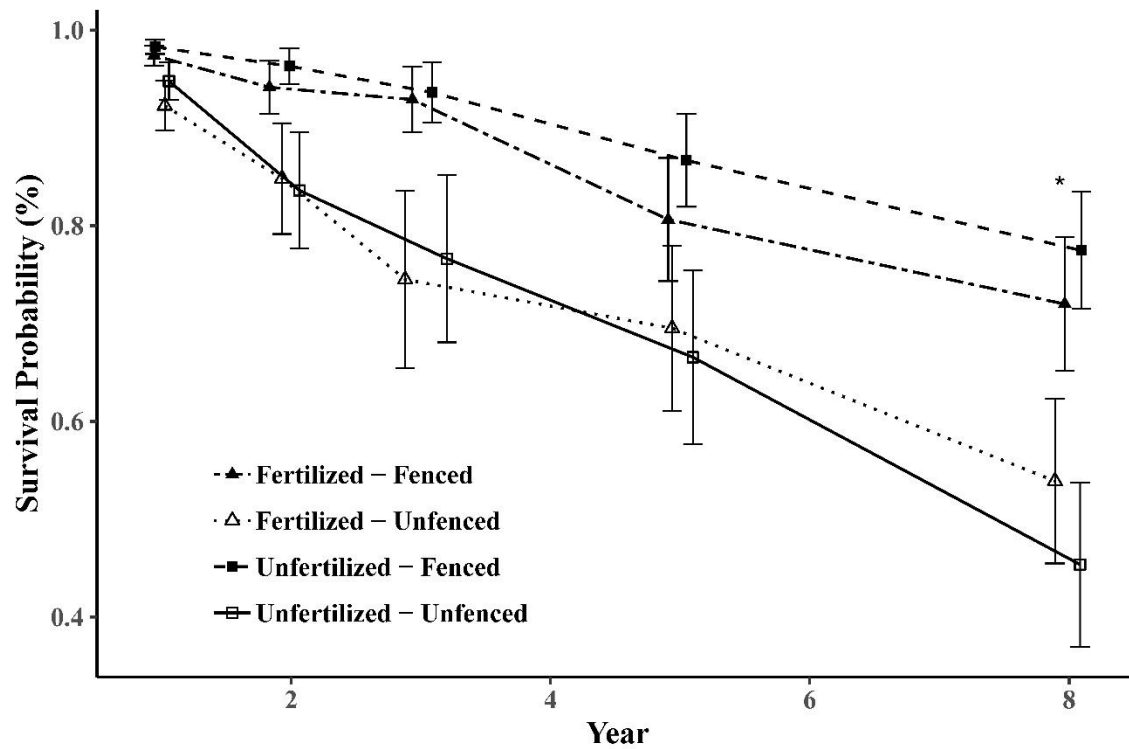


Figure 2. 3: Proportion of surviving northern red oak over time for fencing and fertilizer treatments across all sites. Asterisks represent significant interactions (* <0.05 , ** <0.01 , *** <0.001), which occurred in the year 8 whereby fenced trees had a greater probability of survival than non-fenced trees in the non-fertilized treatment only.

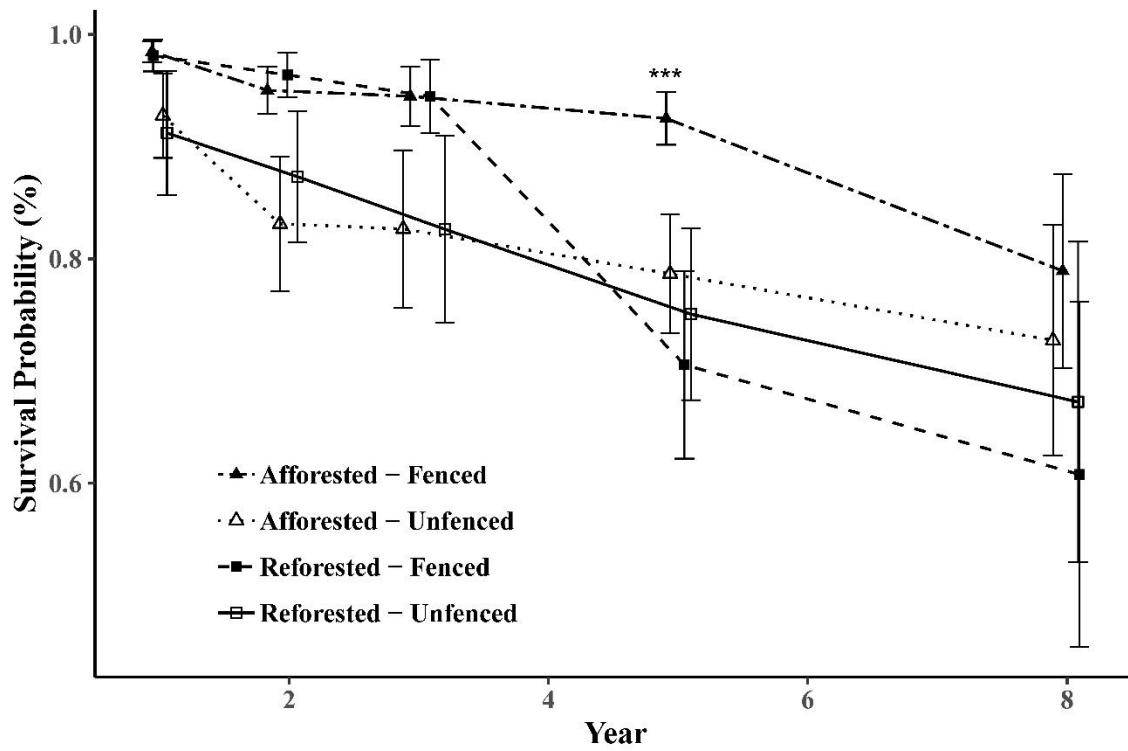


Figure 2. 4: Proportion of surviving black walnuts over time for fencing and site type. Asterisks represent significant interactions (* <0.05 , ** <0.01 , *** <0.001), which occurred in year 5 whereby fenced trees on afforested sites had a greater probability of survival than any other treatment.

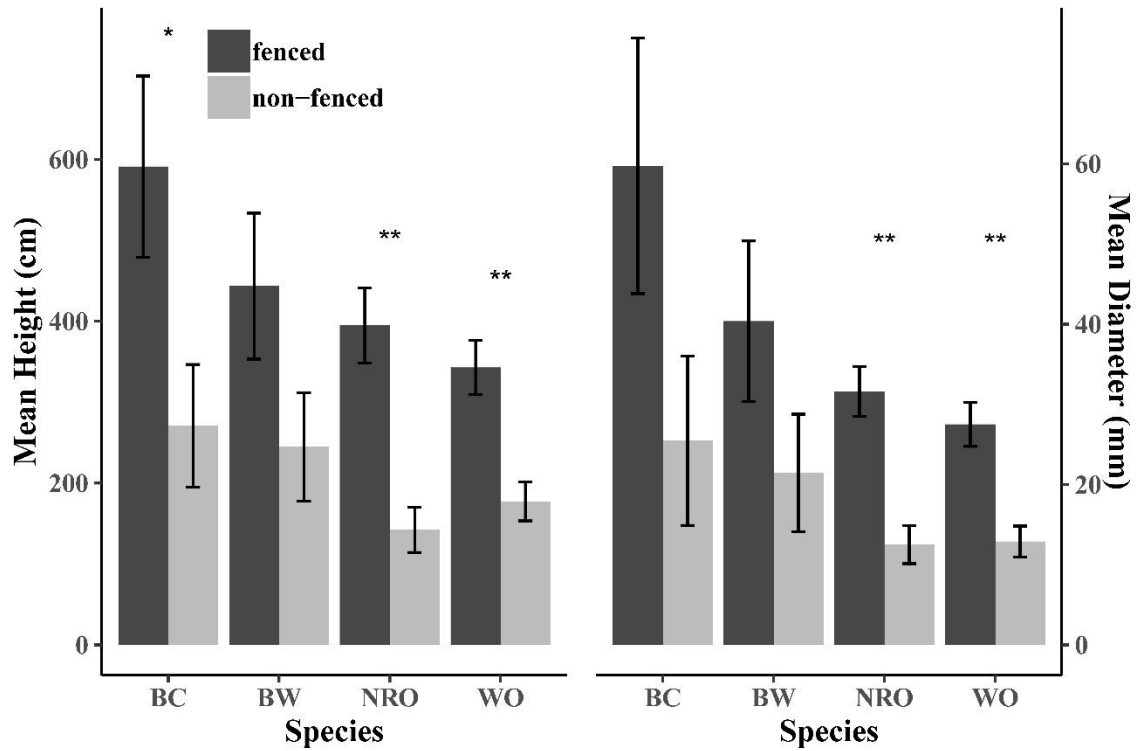


Figure 2. 5: Mean (\pm SE) height (cm) and diameter (mm) of black cherry (BC), black walnut (BW, northern red oak (NRO), white oak (WO) after eight growing seasons in fenced or non-fenced treatments across all sites. Asterisks represent significant differences between treatments within a species (* <0.05 , ** <0.01 , *** <0.001).

Table 2. 3: Mean (\pm 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 ($\alpha = 0.05$). Asterisks indicate factors involved in 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	0.003*
BC	non-fenced	0.63	0.06	
BC	fertilized	0.71	0.04	0.141
BC	non-fertilized	0.67	0.04	
BC	non-select	0.73	0.04	0.002
BC	select	0.65	0.04	
BC	reforested	0.70	0.06	0.108*
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	

Table 2. 4: Mean height (\pm 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 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 ($\alpha = 0.05$).

Species	Treatment	Height		p-value
		(cm)	standard error	
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 2. 5: Mean DBH (\pm 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 ($\alpha = 0.05$).

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	AFS	22	2.8	0.549
NRO	RGN	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	AFS	21	2.2	0.461
WO	RGN	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	AFS	47	12.9	0.551
BC	RGN	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	RGN	31	9.8	0.852
BW	AFS	28.	7.7	

Table 2. 6: Mean (\pm SE) probability that quality is ≥ 3 (average or greater) for black cherry (BC), black walnut (BW), northern red oak (NRO), and white oak (WO) trees by fencing treatments after nine growing seasons. P-values represent the significance of the effect of the treatment on quality.

Species	Treatment	Probability	Standard Error	P-value
NRO	fenced	0.76	0.02	<0.001
NRO	non-fenced	0.07	0.02	
WO	fenced	0.66	0.06	<0.001
WO	non-fenced	0.06	0.02	
BC	fenced	0.60	0.03	<0.001
BC	non-fenced	0.20	0.03	
BW	fenced	0.66	0.05	<0.001
BW	non-fenced	0.22	0.04	

2.4.2 Fertilizer

In year 1, fertilizer decreased the probability of survival of black cherry by 3% and northern red oak (at afforested sites) by 4%. As stated previously, there was an interaction between fencing and fertilizer in year 8, whereby fencing increased the probability of survival for unfertilized northern red oaks. In year 2, fertilizer decreased the probability of survival of white oak by 4% ($p = 0.002$) and fenced black cherry by 5% ($p = 0.023$).

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 2 by 17.8 cm. Outside the fence, however, fertilized seedlings showed no differences. This interaction between fencing and CRF held in third year; the difference between fertilized and non-fertilized seedlings increased to 25.1 cm inside the fences (Figure 2.6). Fertilized black cherries also had greater basal diameter than non-fertilized cherries within the fences that year. White oak height was greater in the fertilized treatments in years 2 and 3; basal diameter was also greater in fertilized treatments in year 3. By year 5, fertilized white oaks were only taller than unfertilized white oaks at the reforested sites (Figure 2.7), but there were no significant height differences by the end of the experiment (Table 2.4). Fertilizer had no effect on quality of any species.

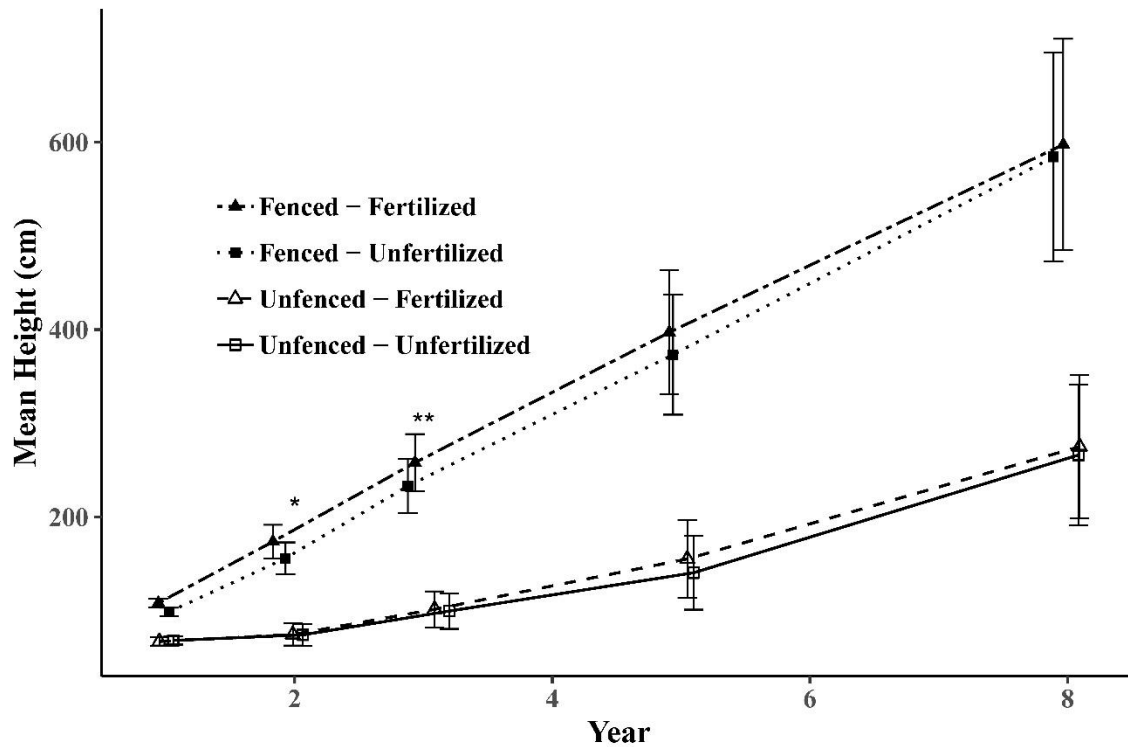


Figure 2. 6: Mean (\pm SE) height (cm) of black cherry seedlings for fencing and fertilizer treatments across all sites. Fenced trees were significantly taller than trees in every year. Asterisks represent significant interactions (* <0.05 , ** <0.01 , *** <0.001), which occurred in years 2 and 3 whereby fertilized trees were taller than trees in fenced treatments only.

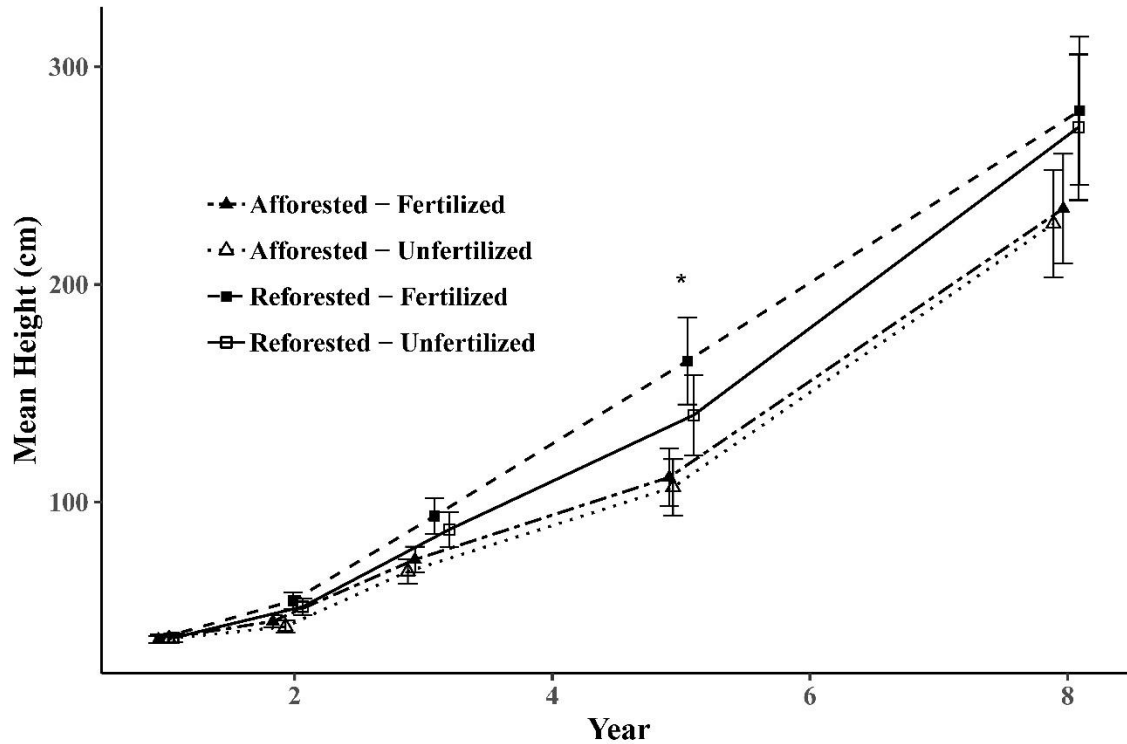


Figure 2. 7: Mean (\pm SE) height (cm) of white oak seedlings on afforested or reforested sites. Asterisks represent significant interactions (* <0.05 , ** <0.01 , *** <0.001), which occurred in year 5 whereby fertilized trees were taller than non-fertilized trees at reforested sites only.

2.4.3 Seed Source

During year 1, select northern red oak had a 6% greater probability of survival than non-select sources when not fertilized ($p = 0.003$); this interaction remained in year 2, and by year 3 the difference increased to 7% ($p = 0.021$ for the interaction). In year 1, select black cherries had a lower probability of survival than non-select black cherries; this effect was present in every year up to the end of the study period (Table 2.3). As stated previously, there was an interaction between fencing and seed source in years 3, 5, and 8, whereby fencing increased select northern red oak survival. In year 1, select black walnuts had a lower probability of survival within both site types. In year 2, select black walnuts at the reforested site had a 15.7% lower probability of survival. In year 3, non-select black walnuts at the reforested site had a 16% higher probability of survival than select black walnuts at the reforested site. In year 5, select black walnuts at reforested sites had a lower probability of survival than black walnuts in any other treatment. In year 8, select black

walnuts had a 21% lower probability of survival than non-select black walnuts at reforested sites (Figure 2.8).

Differences in growth between seed sources were present for all species during some years. Within the fenced treatments, select black cherries were taller than non-select black cherries in year 1 ($p < 0.001$ for the interaction). In addition, non-fenced, select black cherries did not have significantly different heights than fenced, non-select black cherries, while every other fenced treatment had greater heights than non-fenced treatments. In years 2 and 3, select black cherries were taller on average than non-select black cherries. By year 5, however, differences were non-significant. In year 2, select black walnuts were taller on average than non-select black walnuts within afforested sites. Reforested sites exhibited a similar, but nonsignificant, trend. By year 3, select black walnuts were 27 cm taller than non-select black walnuts on average, and remained 46 cm and 72 cm (over 1.2 times) taller on average in years 5 and 8, respectively (Table 2.4). In year 2, select northern red oaks were taller on average than non-select northern red oaks within the fenced treatments. The select northern red oaks were 13 cm taller on average by year 5 and remained 38 cm (16%) taller on average in year 8 (Table 2.4). Select northern red oaks also had greater diameters on average in year 5 and in year 8 (Table 2.5). Seed source interacted with fencing as well as site type on black walnut basal diameter in year 3; select black walnuts had greater diameters on average at the afforested sites. In addition, select black walnuts at reforested sites were not significantly shorter on average than non-select black walnuts at afforested sites; in contrast, every other species on afforested treatments had taller trees on average compared to all other reforested treatments. Seed source also interacted with fencing for black walnut diameters in year 3; fenced select seedlings were the largest on average, followed by fenced, non-select and non-fenced, select seedlings, while non-fenced, non-select seedlings were the shortest on average. In year 5, select seedlings had greater DBH on average across all species (excluding white oak). These differences remained for black walnut and northern red oak into year 8, but they were not significantly different for black cherry. Select northern red oaks were 23% larger in diameter on average, and select black walnuts were 49% larger in diameter on average (Table 2.5).

Seed source had a significant effect on quality of black cherry and black walnut ($p < 0.001$). Select trees had greater likelihood of displaying better quality. The probability that black cherry quality would be average or better was 0.49 ± 0.03 for select trees, but only 0.31 ± 0.03 for non-

select trees. The probability that black walnut quality would be average or better was 0.54 ± 0.05 for select trees, but only 0.33 ± 0.04 for non-select trees.

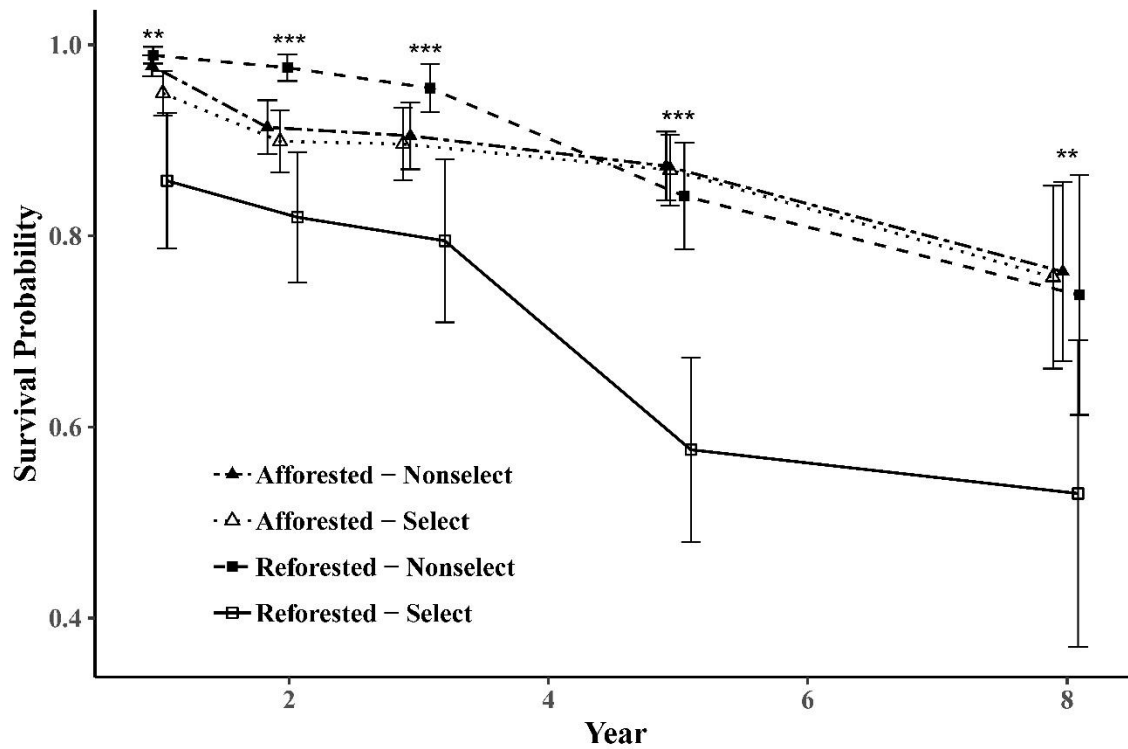


Figure 2. 8: Proportion of surviving black walnuts over time for site type and seed source across all sites. Asterisks represent significant interactions (* <0.05 , ** <0.01 , *** <0.001), which occurred in year 1 whereby non-select trees had a greater probability of survival within each site type (and select trees at the reforested site had lower probability of survival than non-select trees at both site types), as well as in years 2, 3, and 8 whereby non-select trees had a greater probability of survival at reforested sites only, and in year 5 whereby non-select trees at the reforested site had a lower probability of survival than trees in any other group.

2.4.4 Site Type

There were no main effects of site type on survival, except that northern red oak had 22% lower probability of survival at afforested sites than reforested sites in year 3. In addition, white oak had a 5.5% lower probability of survival at afforested sites than reforested sites ($p = 0.005$) in year 2, although higher mortality at reforested sites in later years erased this difference.

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. There was an interaction between seed source and site type for black walnut diameters ($p = 0.009$) in year 3, whereby the trees at afforested sites had larger diameters within each seed source, but the non-select trees at afforested sites did not differ

from the select trees at reforested sites. By year 5, none of these effects were significant. Oaks and black walnuts tended to be taller at reforested sites, but differences were not significant.

Quality of northern red oak and black cherry was greater at reforested sites ($p < 0.001$). The probability that their quality would be average or better was 0.46 ± 0.02 for northern red oak and 0.49 ± 0.04 for black cherry at reforested sites, but only 0.38 ± 0.02 for northern red oak and 0.31 ± 0.03 for black cherry at afforested sites. Black walnut also had a tendency towards greater quality at reforested sites, but the effect was non-significant.

2.4.5 Species

By year 8, black cherry was the tallest species, followed by black walnut, northern red oak (when fenced), and, finally, white oak; non-fenced northern red oaks were the shortest (Figure 2.5). By year 8, average diameter was largest for black cherry, followed by black walnut, northern red oak, and white oak. The trends were the same across site type and seed source, but not fencing. Northern red oak had the smallest diameter of any species outside of fencing treatments (Figure 2.5).

2.5 Discussion

2.5.1 Fencing Drives Hardwood Performance

The positive effect of fencing on growth performance of artificially-regenerated hardwood trees in our study is well supported by past research (Burney and Jacobs, 2018). Another deer enclosure study found that native hardwood natural regeneration occurred exclusively inside enclosures, and that relative diameter growth rates for fenced seedlings was double that of seedlings outside the enclosures (Shelton et al., 2014). These results were present for enclosures that were in place for as little as 2-3 years (Shelton et al., 2014). Another study that examined the tallest seedlings of each species reported that the height of northern red and white oaks, among other species, were significantly taller inside vs. outside enclosures (Csigi and Holzmüller, 2015). This result occurred despite reportedly low deer populations, 6 to 12 deer per km², which is usually considered acceptable for the purposes of forest regeneration in the eastern USA (Csigi and Holzmüller, 2015).

Though not quantified in our study, it is important to note that exclosures may also increase vegetative competition within fences associated with the absence of browsing, 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 was 30 times greater than the growth of native shrubs within fences. 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.

Fencing interacted with site type to positively affect survival in some cases. Black walnuts had lower survival rates outside the fences at afforested sites in the first two years, and in year 5, indicating browse effects (Figure 2.4), despite black walnut being of low browse preference (Wakeland and Swihart, 2009). This difference between fenced and non-fenced treatments was significant at the afforested sites for all species in many years, suggesting that browse pressure was higher at afforested sites (Figures 2.1 and 2.4). Trees at reforested sites were often surrounded by neighboring shrubs and naturally regenerating seedlings, thus making individual trees less likely to be browsed compared to those in open fields. According to the plant apparency hypothesis (Feeny, 1976; Kellner and Swihart, 2017), susceptibility to browse pressure increases with increasing visibility to herbivores. Shrubs, species mixtures, and understory vegetation can protect or obscure susceptible seedlings from herbivores (Brown and Ewel, 1987; Harmer et al., 2010; Jensen et al., 2012; Cook-Patton et al., 2014). By year 8, the interaction between fencing and site type was only significant for black cherry. Northern red oak and white oak had greater probability of survival inside fences, without any site type interaction. Select northern red oaks growing inside exclosures displayed higher survival than their non-fenced counterparts (Figure 2.2), suggesting that protection from deer browse is needed for genetically select northern red oaks to reach their potential. Northern red oaks, black cherries, black walnuts at afforested sites not only displayed greater risk when exposed to herbivory; but, in year 5, they had greater probability of survival than trees at reforested sites when protected from herbivory (Figures 2.1 and 2.4). Improved survival, in the absence of herbivory, on afforested sites may have been associated with lower woody competition; none of the species used in this study were shade-tolerant. Oaks are not highly

competitive in clear-cuts (Burns and Honkala, 1990; Swaim et al., 2016; Swaim et al. 2018), but a study in Spain found that old fields provide a low-stress environment for them and reduce the occurrence of dieback (Pons and Pausas, 2006). Though black cherry has proven competitive in clearcuts in the central hardwood region (Swaim et al. 2016; Swaim et al. 2018), it also benefited from the conditions on afforested sites when protected from herbivory, as did black walnut.

Some studies indicate that herbivory affects growth, but not survival of plants (Kellner and Swihart, 2016). Our results did reveal a negative effect of herbivory on survival, specifically for trees planted in old agricultural fields. Reports of decreased survival may be less common because many studies do not repeatedly measure individuals over time, and thus mortality due to cumulative stress is not quantified (Russell et al., 2001). Studies that do measure the effects of cumulative browse have shown reduced survival when compared to seedlings protected from browse. For example, Cook-Patton et al. (2014) found that browse resulted in decreased hardwood survival of seedlings three years after planting. Sugar maple (*Acer saccharum* Marshall) had lower survival outside exclosures after only one year (Peebles-Spencer and Gorchov, 2017), whereas black cherry had lower survival inside exclosures after 2 years (Burney and Jacobs, 2018). Such contrasting findings suggest interactions between browsing, species, and site that make predicting the results of specific management practices difficult. However, our results suggest that fencing may improve survival at afforested agricultural sites.

There are few studies on the long-term effects of browsing by deer on timber quality of hardwoods. We found that non-fenced trees, across all species, had only a 22% chance or less at average or greater quality after nine years, while those inside fences had a 60% chance or greater at the same quality scores. Future growth may compensate for the current lack of quality in many of the trees, but trees at some of the sites had still not achieved free-to-grow status after nine years. In a 32-year-old stand in northern Michigan dominated by sugar maple, trees that regenerated in a heavily-browsed area had 26% more crook than trees in a reference area (Switzenberg et al., 1955), yet 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 did increase forking and decrease height, but the authors determined that other factors, such as competition and light, were more important in affecting regeneration and quality (Jacobs, 1969). Considering the expenses of protecting trees from browse early in life, understanding the effects of these efforts on stem quality is important if commercial production is an objective.

2.5.2 Fertilization interacts with fencing

Black cherry growth may benefit from fertilizer during the establishment phase of regeneration, but only when browsing by deer is controlled. Fertilizer had a positive effect on black cherry height and diameter in the first three years (Figure 2.6), similar to results reported by Burney and Jacobs (2018). The fact that fertilizer only had a positive effect inside fences may be explained by plant chemistry responses. 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 were much more likely to be browsed, which may account for some of the inconsistent species preference results among studies on white-tailed deer (*Odocoileus virginianus* Zimm.) preferences (Tripler et al., 2002). Burney and Jacobs (2018) also found that fertilizer significantly increased nitrogen concentration of black cherry.

Though 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 after the second growing season, whereas unfertilized 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 the findings of Burney and Jacobs (2018), in which diameter of black cherry and bur oak (*Quercus macrocarpa* Michx.) were only increased by fertilizer inside fenced treatments. Contrary to their results, however, we did find 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; Figure 2.7).

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 (Figure 2.3), suggesting that CRF may aid the survival of northern red oak under herbivore pressure. Our study suggested that the gains in growth from CRF were discernible beyond the two years of controlled 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.

2.5.3 Seed Source

We observed greater quality black walnuts and black cherries, and greater growth in select black walnuts and northern red oaks when 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 quality. 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 explains that the most limiting factor to growth and survival (for example, the nutrient that is in lowest supply) must be addressed before other factors affect performance (Liebig, 1855; Dumroese et al., 2016). In this case, this means that 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 8, seed source was the only factor significantly affecting black walnut size (Tables 2.4 and 2.5). 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.

2.6 Conclusions

In regions where ungulate browsing limits temperate hardwood regeneration, fencing is not only effective on its own (especially on afforested sites), but can interact synergistically to allow or enhance expression of growth benefits from CRF and select seed sources. For some species, such as black cherry, investing in fertilizer 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 and planted on optimal site types. Further improvement of seed sources through progeny testing, may produce greater gains in growth and quality. By itself, fencing improved survival for afforestation plantings in old agricultural fields, and increased quality of all species examined.

CHAPTER 3. RESPONSE OF NATURAL REGENERATION TO FENCING AND INVASIVE SHRUB REMOVAL

3.1 Abstract

Ungulate browse and invasive plants threaten forest regeneration and plant communities globally. Invasive plants may interact with ungulates in various ways, ranging from synergistic interactions in which the negative effects of both are additive, to antagonistic effects associated with protection and reduction of plant apparency. Recent research has focused on such interactions, but long-term studies are lacking. We used factorial treatments of deer fencing and invasive shrub (Amur honeysuckle, *Lonicera maackii*) removal plots established at three mature forests sites in Indiana, USA. Our objectives were to examine treatment effects on the density and composition of natural tree regeneration as well as richness and cover of native plants at the herbaceous-layer. Honeysuckle had the greatest influence on regeneration of tree seedlings and plant cover in the herbaceous-layer, but the effects varied by tree species with negative effects most pronounced on shade-intolerant and moderately shade-tolerant species. Interactive effects of honeysuckle and deer tended to be antagonistic when they were present, suggesting that when deer are excluded, honeysuckle should be removed. Our results from this hardwood regeneration experiment confirm that deer browse control must be accompanied by control of competing vegetation to be successful.

3.2 Introduction

A combination of factors has led to widespread decline of oak and hickory regeneration in the eastern USA, and a shift towards mixed mesophytic species, though there are regional and species-specific exceptions and the causes are dependent on location (Fei et al. 2011). Some of these factors include reduced frequency of fire, changes in harvest practices, climate change, and herbivory by white-tailed deer (*Odocoileus virginianus*) (Csigi and Holzmüller, 2015; McEwan et al., 2011). Factors reducing canopy gaps, increasing moisture, and decreasing fire have favored the growth of late-successional shade-tolerant species, such as sugar maple and American beech (*Fagus grandifolia*; Abrams, 2003; Holzmüller et al., 2011; Nowacki and Abrams, 2008). In addition to oak, forests in the eastern USA are losing ash (*Fraxinus*) as a widespread component due to emerald ash borer (Goins et al., 2013). White ash (*Fraxinus americana*, the most common native

American ash) is shade-tolerant when young, but becomes shade-intolerant as it ages (Burns and Honkala, 1990). It has been observed at high densities in understories (Goins et al., 2013). How the forest will respond to the loss of adults from the canopy is yet to be seen, and how such disturbance will interact with the invasion of Amur honeysuckle (*Lonicera maackii*) is a pertinent question.

Over-browsing of desired regeneration by deer and other ungulates is a global problem (Beguin et al., 2016). A range of solutions to the browse problem have been produced with greatly varying effectiveness. One commonly used method is fencing (Csigi and Holzmueller, 2015; Frigoletto et al., 2017); plastic mesh fences have proven to be effective (Burney and Jacobs, 2018; Shelton et al., 2014), however, the high cost inhibits many landowners from using them. Facilitation by neighboring vegetation has been proposed as an alternative method of protecting regeneration from deer browse. Certain plants can restrict physical access of deer to seedlings, or deter deer with spines or unpalatable foliage (Beguin et al., 2016). However, protection provided by surrounding vegetation must be balanced with the negative effects of competition. For example, Amur honeysuckle has been shown to have positive protective effects on otherwise unprotected seedlings, but negative, competitive effects on seedlings that were caged (Gorchov and Trisel, 2003). However, other studies have shown no protective effects of Amur honeysuckle on planted seedlings, and very few on naturally regenerating species (Owings et al., 2017).

Invasive plants, often introduced intentionally for ornamental plantings or other purposes, can inhibit forest regeneration. Disturbances in ecosystems, a lack of natural enemies (for example, herbivores may be less likely to browse them; Pimentel et al., 2005), bird dispersal of seeds, and the ability to form pure stands that exclude competitors (Webster et al., 2006) allow invasive species to establish and thrive. Invasive shrubs, in particular, are challenging in regard to forest regeneration because they may form dense monocultures that shade out seedlings (Webster et al., 2006). Such shrub canopies reduce the effects of canopy disturbance that would otherwise allow for the release of shade-intolerant species.

Amur honeysuckle, a widespread shrub in the eastern USA, shades the understory during the entire length of the growing season due to its early production and late senescence of foliage (Webster et al., 2006), and prevents even moderately shade-tolerant plants from taking advantage of canopy openings.

Rehabilitation of forested ecosystems may require removal of non-native shrubs as part of timber stand improvement to favor regeneration of desired species that are already in the overstory (Stanturf et al., 2014). In addition, Amur honeysuckle may interact synergistically with deer by providing habitat (Allan et al., 2010), or by slowing the growth of trees, compounding the stunting effect that deer browse has on trees (Vila et al., 2003). Herbivores may also contribute to the success of invasive shrubs and other competing vegetation by preferentially browsing native seedlings. For example, ferns have a negative effect on tree regeneration (Gilliam, 2007), and may form dense monocultures when deer select against other plants, such as raspberry (Stromayer and Warren, 1997). Competing vegetation may still need to be removed in order to create enough light for seedlings to establish after deer have been culled (Engelman and Nyland, 2006; Tanentzap, 2012). Alternatively, shrubs may interact antagonistically with deer by restricting movement and access (Christopher et al., 2014), and deer may keep honeysuckle in check through herbivory (Martinod and Gorchov, 2017).

Herbaceous-layer vegetation has value to wildlife, recreationists, and landowners, and functions as part of a balanced ecosystem. In addition to effects on woody seedlings, honeysuckle and deer also reduce coverage of native herbaceous vegetation, as well as affecting composition and richness of the herbaceous-layer (Haffey and Gorchov, 2019). Herbaceous-layer vegetation contains an average of 80% of the species richness of a temperate forest, contributes to leaf litter and nutrient cycling, and affects tree regeneration (Gilliam, 2007). Previous research from short-term studies (three years) in the central hardwood region did not find any significant differences in richness and diversity between deer enclosure treatments, or interactive effects with honeysuckle (Owings et al., 2017), or only found interactions on annuals and spring perennials (Christopher et al., 2014). However, a longer study (five years) found more differences and interactions, as well as main effects from deer on annuals that contradicted previous studies (Haffey and Gorchov, 2019;

Studies are needed to evaluate interactive effects of deer exclusion and invasive shrub removal on restoration of seedlings, saplings, and forest communities. We measured the effects of invasive shrubs and deer over five years on natural regeneration and plant communities that arose in response to individual and interactive effects of browse control and invasive shrub removal across three forested sites. We hypothesized that: (i) fencing would reduce deer browse, and invasive plant removal would release trees from competition; both factors increasing density

of natural regeneration, as well as herbaceous-layer species richness and cover; and (ii) deer and honeysuckle would interact synergistically (a positive interaction) to suppress natural regeneration and herbaceous vegetation due to browse and competition, resulting in the lowest density of natural regeneration, species richness, and cover in unfenced, reference areas.

3.3 Methods

3.3.1 Location, Planting Materials, and Establishment of Treatments

Between November 2010 and March 2011 two 80 x 80 m areas were established for invasive shrub removal at each of two sites in Tippecanoe County, Indiana, U.S.A.: (1) Ross Biological Reserve (N 40°24'43" W 87°03'58") with Camden silt loam soils, (2) Lugar Forestry Farm (N 40°25'34" W 87°03'58") with Crosby-Miami silt loam, Miami silt loam, and Starks-Fincastle complex soils (where invasive shrubs were removed) and Richardville silt loam and Crosby-Miami silt loam soils (where invasive shrubs were not removed; Table 3.1; Shields et al., 2015b; Natural Resources Conservation Service, 2019). Two 80 x 80 m areas were established for invasive shrub removal at a third site (Martell Experimental Research Forest) in 2013. Martell Experimental Research Forest had Richardville silt loam and Strawn-Rodman complex soils (Table 3.1; Owings et al., 2017; Natural Resources Conservation Service, 2019). The Lugar Forestry Farm and Martell sites were both open to deer hunting, but Ross Biological Reserve was not. Each site contained a well-developed population of Amur honeysuckle, which was the most common woody invasive (Table 3.1). One of the areas at each site was selected for invasive plant removal. Honeysuckle and other woody invasive plants were removed by cutting the shrub at the base and applying cut-stump treatments of herbicide (20% triclopyr [Garlon 4®, Indianapolis, IN USA], 1% imazapyr [Stalker®, Research Triangle Park, NC, USA], and 79% Ax-it® basal oil). Herbaceous invasive species and small shrubs were removed by hand. Large shrubs were removed from the site after cutting. Follow-up cut-stump and hand-pulling treatments were implemented in the summer of 2014 and fall of 2017 to remove new invasive plants within 1 m of the transects.

In spring of 2013, half of each 80 x 80 m plot was fenced to exclude deer. The fences consisted of 2-m tall plastic mesh, which allowed small mammals to enter underneath. Fences were periodically checked and repaired (Owings et al., 2017). A severe windstorm in November 2013 felled trees in the forest canopy where shrubs had been removed at Lugar Farm. Debris was cut

and removed and trees in the reference area were selectively girdled in spring 2014 to equalize the living basal area between removal and non-removal areas (Owings et al., 2017).

Transects were established to sample natural regeneration and herbaceous vegetation. Three 10 m transects were established in each treatment unit at least 5 m apart (Owings et al., 2017).

Table 3. 1: Site names, dominant overstory species, age of *L. maackii* invasion, *L. maackii* density (mean \pm 1 SE is for stems > 1.37 m tall), and total deer visits for three study sites in IN, USA. The dominant overstory species were obtained from Shields et al. (2015a), and age of invasion was determined from counting the rings of stem cross-sections from *L. maackii* shrubs harvested to create the removal areas, or, in the case of Martell, using a linear mixed effects model and harvested stem cross sections to create an age model to predict the age of the oldest *L. maackii* shrub (Shields et al. 2014; Owings et al. 2017). Deer visits represent the combined number of deer photographed by four cameras for a total of four weeks (two weeks in June and two weeks in September 2014) for each study site. These numbers were obtained from Owings et al. (2017).

Site	Dominant overstory species	Invasion Age (Years)	Honeysuckle density (stems/ha)	Deer Visits	% PAR (mmol/m ² s)
Ross	<i>Q. velutina</i> , <i>L. tulipifera</i>	18	1042 \pm 1134	86	3.0 \pm 1.2 (reference)
					2.9 \pm 1.4 (removal)
					1.4 \pm 0.6 (reference)
Martell	<i>Q. alba</i> , <i>Q. velutina</i>	13	854 \pm 1677	47	2.5 \pm 0.4 (removal)
					0.5 \pm 3.6 (reference)
Lugar	<i>R. pseudoacacia</i> , <i>J. nigra</i>	35	3135 \pm 863	19	9.5 \pm 1.3 (removal)

3.3.2 Measurements

Five 1-m² quadrats were placed every other 1 m along one side of each transect for seedling sampling. Seedlings and shrubs below 50 cm in height (seedlings) were counted by species within these quadrats to determine density and species richness in the fall of 2013, 2014, 2015, and 2018. Trees and woody shrubs between 50 and 200 cm (saplings) were counted by species within a 2-meter wide band along each transect in the fall of 2018. All vegetation under 50 cm was sampled in late summer of 2013, 2014, 2015, and 2018. Each species was identified (to the lowest possible taxonomic level). Cover (defined as the proportion of total transect line covered by plants) was estimated for plants below 50 cm in 2018.

In June and September of 2014 two trail cameras (HC600 Hypefire, RECONYX, Inc., Holmen, Wisconsin) were used in each of the two honeysuckle treatments outside the fence at each site to collect images over two-weeks. The number of deer visits was determined by tallying the number of deer captured on camera during this time. A light ceptometer was used in July 2015 to measure

photosynthetically active radiation (PAR). Measurements were made on cloudless days within one hour of solar noon both in a field next to each study site and at eight places within the study site.

3.3.2 Statistical Analyses

Total species richness was calculated from the transect cover data. Species richness was defined as the number of unique species per transect. Generalized linear model analyses were conducted to evaluate total seedling density, seedling density separately for each genus, total species richness, as well as total sapling count, sapling counts separately for each genus, and total plant cover in 2018. A gaussian link function was used to model total seedling and sapling counts, total plant cover, and the tree genera that did not fit a Poisson distribution. A Poisson link function was used to model species richness, as well as the tree genera that fit a Poisson distribution. Within each analysis the dependent variables were compared to examine the effects of fencing and honeysuckle removal and their interaction. Site was used as a blocking factor and interactions between treatments and site were kept if they resulted in a better model. The models took the following general form:

$$y = (Fence + Removal + Site)^2 + \varepsilon$$

The fourth root transformation was used on stem counts that were modeled using the gaussian distribution. All means reported were calculated from the raw data, except seedling and sapling counts were converted to densities (stems/m²) first. If interactions were detected, pairwise comparisons were conducted using Tukey tests.

All statistical analyses were conducted using R statistical software (R Core Team, 2018); differences were considered significant at $\alpha=0.05$. The “lme4” R statistical package was used to determine the fixed effects of fencing and honeysuckle removal on density, cover, and richness (Bates et al., 2015). Post-hoc Tukey tests were performed using “emmeans” (Lenth, 2018).

3.4 Results

3.4.1 Fencing

Fencing interacted with site to affect total native seedling counts in 2013, 2014, and 2015, and with honeysuckle in 2015 (Table 3.2). Despite the significant interaction, a post-hoc Tukey test revealed no differences within sites in 2013. In 2014, total seedling density was higher outside the

fences than inside at Martell, according to a Tukey test ($p < 0.001$ for the interaction, Figure 3.1). This difference was largely due to *Fraxinus* seedlings, which had a higher density outside the fences at Martell (4.7 ± 1.9 stems/ m^2) than inside (0.3 ± 0.2 stems/ m^2 ; $p = 0.003$ for the interaction). *Fraxinus* and *Acer* species made up $45.6 \pm 18.2\%$ and $32.9 \pm 14.5\%$ of the seedlings outside the fences at Martell, but only $11.7 \pm 6.5\%$ and $13.4 \pm 9.1\%$ inside.

Table 3. 2: P-values from ANOVAs for native tree seedling and sapling densities across years. Bold indicates significant differences among treatments ($\alpha = 0.05$).

Year	Measure	Honeysuckle Removal	Deer	Removal: Deer	Removal: Site	Deer: Site
2013	Seedling density	<0.001	0.191	0.651	<0.001	0.021
2014	Seedling density	0.020	0.079	0.940	0.147	<0.001
2015	Seedling density	0.836	<0.001	0.040	0.008	<0.001
2018	Seedling density	0.156	0.745	0.214	0.119	0.078
2018	Sapling density	0.487	0.180	0.514	<0.001	0.122

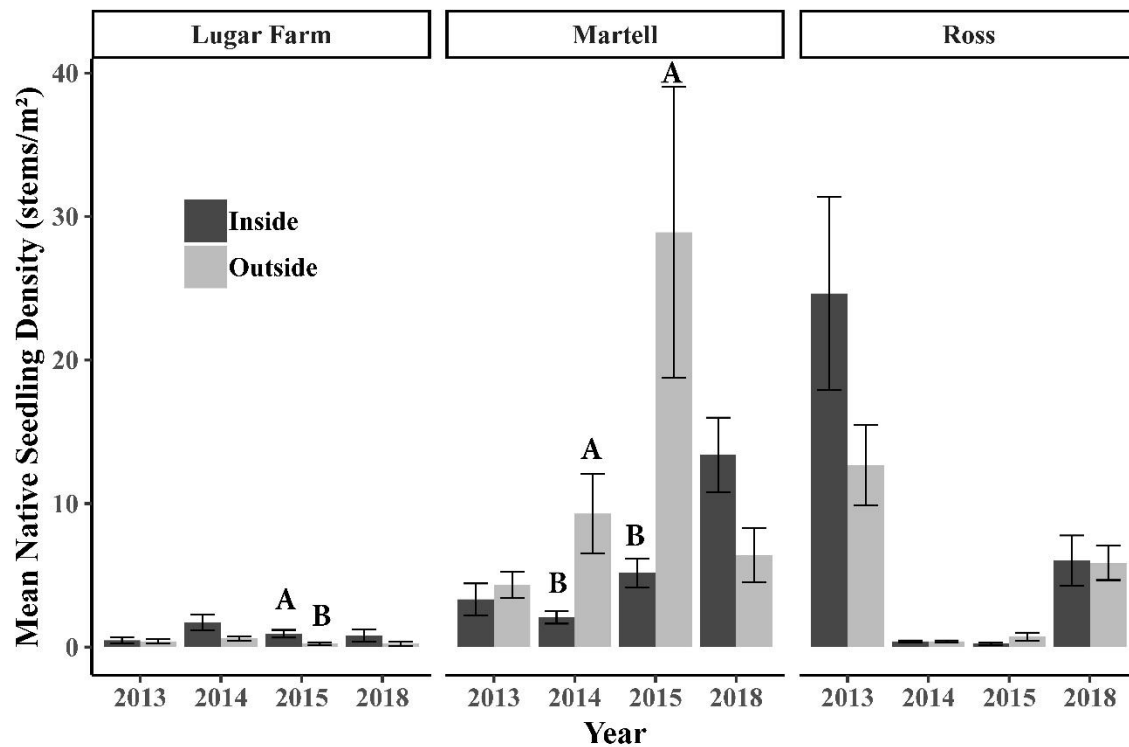


Figure 3. 1: Density (stems/ $m^2 \pm SE$) of all naturally regenerating native seedlings inside and outside deer exclusion fences at three sites.

In 2015, seedling density was higher outside the fences than inside at Martell, but higher inside fences than outside at Lugar Farm ($p < 0.001$ for the interaction, Figure 3.1). *Fraxinus* seedlings had the same interaction ($p < 0.001$), whereby density was greater outside the fences (1.8 ± 0.13 stems/ m²) than inside (1.1 ± 0.13 stems/ m²) at Martell. By 2015, *Fraxinus* and *Acer* species comprised $55.0 \pm 18.8\%$ and $26.7 \pm 11.9\%$ of the seedlings outside the fences at Martell and $43.3 \pm 13.5\%$ and $26.8 \pm 11.9\%$ inside.

In addition, there was an interaction in 2015 ($p = 0.040$) between fencing and honeysuckle, whereby total seedling density was higher outside the fences where honeysuckle was removed (17.5 ± 8.51 stems/ m²) than in reference areas outside (2.42 ± 1.03 stems/ m²) or inside (1.58 ± 0.76 stems/ m²) the fences.

There were no effects of deer exclosures on total seedling counts in 2018. However, *Celtis occidentalis* seedling density was higher inside fences at Martell than outside ($p=0.002$ for the interaction; Table 3.3). The opposite interaction occurred between site and fencing for *Ulmus* ($p < 0.001$). *Ulmus* density was greater outside the fences at Martell than inside (Table 3.3). In addition, there was an interaction between honeysuckle and fencing on *Ulmus* seedling counts in 2018 ($p < 0.001$). Density was greater inside the fences where honeysuckle was removed (0.4 ± 0.2 stems/ m²) than inside the fences where honeysuckle was left intact (0.09 ± 0.04 stems/ m²). It was also greater outside the fences where honeysuckle was left intact (0.6 ± 0.3 stems/ m²). *Prunus serotina* seedling density was higher inside fences (0.9 ± 0.3 stems/ m²) than outside (0.6 ± 0.4 stems/ m²; $p = 0.005$).

Table 3. 3: Density (stems/ m²±SE) of naturally regenerating native tree seedlings by genus inside and outside deer exclusion fences at three sites. Bold indicates significant difference between treatments within a site based on a post-hoc Tukey test ($\alpha = 0.05$). Asterisks (*) represent a significant main effect for *Prunus* seedling density, whereby the density was significantly higher inside fences.

Site	Genus	Treatment	Density (stems/m ²)	Standard Error
Farm	<i>Acer</i>	Inside	0.2	0.2
Farm	<i>Acer</i>	Outside	0	0
Farm	<i>Celtis</i>	Inside	0	0
Farm	<i>Celtis</i>	Outside	0.13	0.10
Farm	<i>Fraxinus</i>	Inside	0.47	0.35
Farm	<i>Fraxinus</i>	Outside	0.03	0.03
Farm	<i>Prunus</i>	Inside	0	0*
Farm	<i>Prunus</i>	Outside	0	0*
Farm	<i>Ulmus</i>	Inside	0.07	0.04
Farm	<i>Ulmus</i>	Outside	0.03	0.03
Farm	Other	Inside	0.07	0.07
Farm	Other	Outside	0	0
Martell	<i>Acer</i>	Inside	0.93	0.37
Martell	<i>Acer</i>	Outside	1.43	0.65
Martell	<i>Celtis</i>	Inside	0.80	0.41
Martell	<i>Celtis</i>	Outside	0.17	0.08
Martell	<i>Fraxinus</i>	Inside	1.70	0.75
Martell	<i>Fraxinus</i>	Outside	2.37	1.43
Martell	<i>Prunus</i>	Inside	0.43	0.16*
Martell	<i>Prunus</i>	Outside	0.13	0.07*
Martell	<i>Ulmus</i>	Inside	0.13	0.07
Martell	<i>Ulmus</i>	Outside	1.07	0.33
Martell	Other	Inside	2.03	0.85
Martell	Other	Outside	0.67	0.15
Ross	<i>Acer</i>	Inside	0.27	0.12
Ross	<i>Acer</i>	Outside	0.23	0.13
Ross	<i>Celtis</i>	Inside	0.47	0.12
Ross	<i>Celtis</i>	Outside	0.23	0.10
Ross	<i>Fraxinus</i>	Inside	9.30	2.21
Ross	<i>Fraxinus</i>	Outside	3.77	0.97
Ross	<i>Prunus</i>	Inside	2.20	0.56*
Ross	<i>Prunus</i>	Outside	1.77	1.09*
Ross	<i>Ulmus</i>	Inside	0.47	0.23
Ross	<i>Ulmus</i>	Outside	0.03	0.03
Ross	Other	Inside	0.57	0.21
Ross	Other	Outside	0.33	0.13

There were no significant effects of fencing on total species richness. Honeysuckle interacted with deer to affect total plant cover in 2018 ($p < 0.001$). The proportion of plant cover was lower inside the fences where honeysuckle was left intact ($31.4 \pm 4.0\%$) than in any other treatment (outside reference: $65.0 \pm 7.8\%$, inside removal: $72.3\% \pm 8.5\%$, outside removal: $56.2 \pm 11.2\%$). There was also an interaction between fencing and site ($p = 0.001$) whereby the plant cover was lower inside the fences ($54.3 \pm 13.9\%$) than outside ($88.4 \pm 2.0\%$) at Lugar Farm.

3.4.2 Honeysuckle

Honeysuckle interacted with site to affect total native seedling density in 2013 and 2015, and had a negative main effect on seedling density in 2014 (Table 3.2). In 2018, honeysuckle interacted with site to affect native sapling density, but not native seedling density (Table 3.2).

Total native seedling density in 2013 was higher where honeysuckle was removed than where it was left intact at Lugar Farm ($p < 0.001$ for the interaction, Figure 3.2). However, at Ross in 2013 seedling density was higher where honeysuckle was left intact than where it was removed (Figure 3.2). These results were largely driven by *Fraxinus* species, which had the same interaction between site and honeysuckle in 2013 ($p < 0.001$). *Fraxinus* seedling density was higher where honeysuckle was removed (0.4 ± 0.16 stems/ m^2), than where it was left intact (2.9 ± 0.8 stems/ m^2) at Lugar Farm; however, density was higher where honeysuckle was left intact (18.4 ± 5.66 stems/ m^2) than where it was removed (2.9 ± 0.8 stems/ m^2) at Ross. There were no significant differences at Martell. *Fraxinus* made up over 70% of the relative seedling density where honeysuckle was left intact at Ross, compared to just over 55% where honeysuckle was removed, but had much greater relative density at Lugar Farm where honeysuckle was removed (Table 3.4).

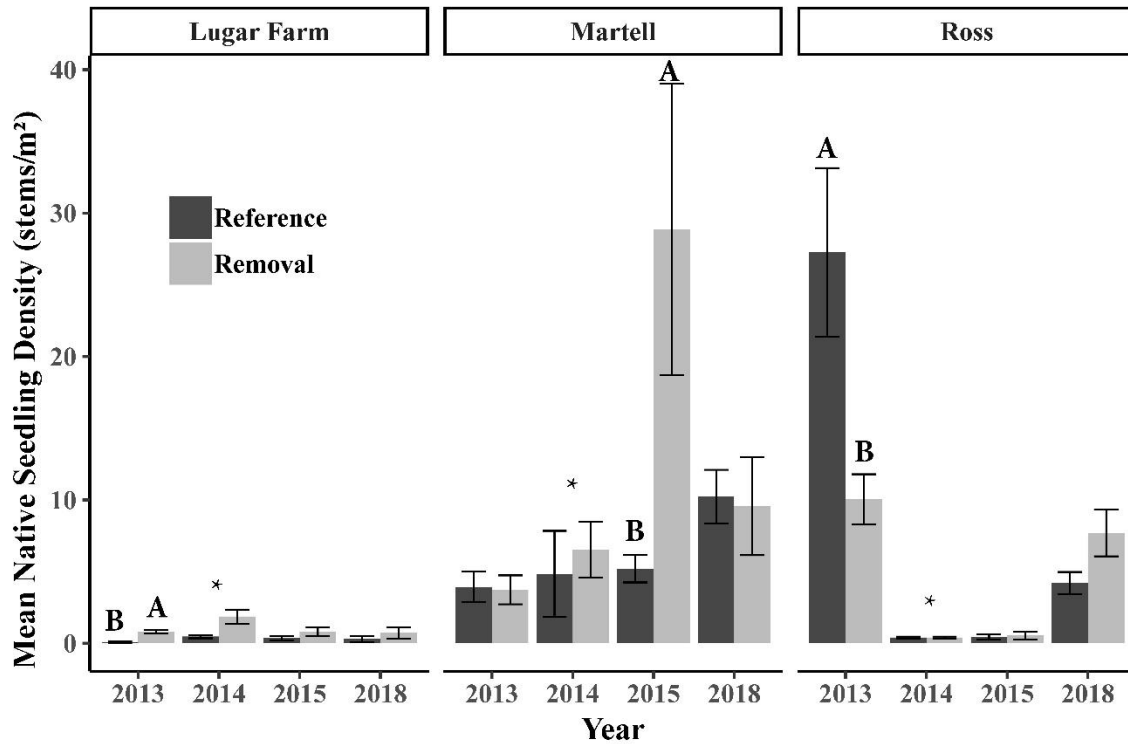


Figure 3. 2: Density of naturally regenerating native seedlings (stems/ m²±SE) in treatments where honeysuckle was removed and in reference treatments where it was left intact at three sites. Letters represent significant difference between treatments within a site and year based on a post-hoc Tukey test ($\alpha = 0.05$). Asterisks (*) represent a significant main effect in 2014, whereby seedling density was higher where honeysuckle was removed.

Table 3. 4: Relative density of selected native tree seedlings by honeysuckle treatments during 2015 at Lugar Forestry Farm and Ross Biological Reserve.

	Lugar Farm		Ross	
Species	Removal	Reference	Removal.	Reference
<i>Celtis occidentalis</i>	7.6 ± 4.8%	0.0 ± 0.0%	2.0 ± 0.8%	1.3 ± 0.5%
<i>Fraxinus spp.</i>	37.7 ± 1.4%	2.4 ± 2.4%	55.7% ± 7.8%	72.9 ± 2.9%
<i>Prunus serotina</i>	40.0 ± 15.3%	0.0 ± 0.0%	28.1 ± 3.8%	12.7 ± 3.0%

In 2014, native seedling density was higher in areas where honeysuckle was removed (2.93 ± 0.90 stems/ m², $39.8 \pm 9.1\%$ of which were *Fraxinus*) than the reference areas (1.90 ± 1.07 stems/ m², $9.9 \pm 4.7\%$ of which were *Fraxinus* and $44.1 \pm 8.8\%$ of which were *Acer*; $p = 0.020$, Figure 3.2). No interaction by site was found. At Lugar Farm, *Fraxinus* seedling density was significantly higher where honeysuckle was removed (1.1 ± 0.4 stems/ m²) than where it was left intact, where there were no *Fraxinus* seedlings ($p = 0.008$ for the interaction). *Acer* species had the opposite trend at Lugar Farm ($p = 0.042$ for the interaction) with greater densities of seedlings under

honeysuckle. At Ross, the density of *Acer* was significantly higher where honeysuckle was left intact (3.1 ± 1.9 stems/ m²) than where it was removed (no *Acer* seedlings were found in this area). This trend was present at the other sites as well, but not significant. *Celtis* ($p = 0.003$) and *Sassafras* ($p = 0.041$) seedlings had a higher density (no interaction with site) where honeysuckle was removed (1.2 ± 0.3 and 0.11 ± 0.05 stems/ m², respectively) than where it was left intact (0.3 ± 0.2 and 0.03 ± 0.02 stems/ m², respectively).

In 2015, total native seedling density was only higher where honeysuckle was removed ($84.5 \pm 6.1\%$ of which were *Fraxinus*) than in reference areas ($13.8 \pm 8.7\%$ of which were *Fraxinus*) at Martell ($p=0.008$ for the interaction, Figure 3.2). *Fraxinus* seedlings had the same interaction ($p < 0.001$). At Martell *Fraxinus* seedlings density was significantly higher where honeysuckle was removed (27.1 ± 10.2 stems/ m²) than the reference area (0.8 ± 0.2 stems/ m²). A honeysuckle by site interaction occurred for *Ulmus* seedlings ($p = 0.039$), which were denser where honeysuckle was left intact (4.3 ± 1.5 stems/ m²) than where it was removed (0.3 ± 0.2 stems/ m²). In addition, the density of *Acer* seedlings was higher where honeysuckle was left intact (1.3 ± 0.3 stems/ m²) than where it was removed (0.1 ± 0.1 stems/ m²; $p=0.001$).

In 2018, there were no honeysuckle effects on total seedling counts. However, at Martell, *Fraxinus* seedling density was higher where honeysuckle was removed than in the reference area ($p<0.001$ for the interaction; Table 3.5). Honeysuckle had an effect on *Celtis occidentalis* ($p = 0.047$) and *Liriodendron tulipifera* ($p = 0.008$) seedling density, whereby density of both species was higher where honeysuckle was removed (0.37 ± 0.15 stems/ m² and 0.08 ± 0.03 stems/ m² respectively) than where it was left intact (0.23 ± 0.07 stems/m² and 0 ± 0 stems/ m² respectively).

Table 3. 5: Density (stems/ m²±SE) of naturally regenerating native tree seedlings by genus in honeysuckle removal and reference areas at three sites. Bold indicates significant difference between treatments within a site based on a post-hoc Tukey test ($\alpha = 0.05$). Asterisks (*) represent a significant main effect for *Celtis* seedling density, whereby the density was significantly higher where honeysuckle was removed.

Site	Genus	Treatment	Density (stems/m ²)	Standard Error
Farm	<i>Acer</i>	Removal	0	0
Farm	<i>Acer</i>	Reference	0.2	0.2
Farm	<i>Celtis</i>	Removal	0.13	0.10*
Farm	<i>Celtis</i>	Reference	0	0*
Farm	<i>Fraxinus</i>	Removal	0.47	0.35
Farm	<i>Fraxinus</i>	Reference	0.03	0.03
Farm	<i>Prunus</i>	Removal	0	0
Farm	<i>Prunus</i>	Reference	0	0
Farm	<i>Ulmus</i>	Removal	0.03	0.03
Farm	<i>Ulmus</i>	Reference	0.07	0.04
Farm	Other	Removal	0.07	0.07
Farm	Other	Reference	0	0
Martell	<i>Acer</i>	Removal	0.20	0.07
Martell	<i>Acer</i>	Reference	2.17	0.44
Martell	<i>Celtis</i>	Removal	0.77	0.42*
Martell	<i>Celtis</i>	Reference	0.20	0.09*
Martell	<i>Fraxinus</i>	Removal	3.83	1.16
Martell	<i>Fraxinus</i>	Reference	0.23	0.13
Martell	<i>Prunus</i>	Removal	0.33	0.11
Martell	<i>Prunus</i>	Reference	0.23	0.16
Martell	<i>Ulmus</i>	Removal	0.33	0.08
Martell	<i>Ulmus</i>	Reference	0.87	0.40
Martell	Other	Removal	2.23	0.77
Martell	Other	Reference	0.47	0.13
Ross	<i>Acer</i>	Removal	0.10	0.07
Ross	<i>Acer</i>	Reference	0.40	0.14
Ross	<i>Celtis</i>	Removal	0.20	0.05*
Ross	<i>Celtis</i>	Reference	0.50	0.13*
Ross	<i>Fraxinus</i>	Removal	5.53	2.51
Ross	<i>Fraxinus</i>	Reference	7.53	1.48
Ross	<i>Prunus</i>	Removal	2.67	1.12
Ross	<i>Prunus</i>	Reference	1.30	0.30
Ross	<i>Ulmus</i>	Removal	0.40	0.25
Ross	<i>Ulmus</i>	Reference	0.1	0.04
Ross	Other	Removal	0.53	0.16
Ross	Other	Reference	0.37	0.20

In 2018 honeysuckle interacted with site to affect native saplings (stems 50-200 cm in height; $p < 0.001$). The mean density where honeysuckle had been removed at Lugar Farm (0.43 ± 0.11 stems/ m²) was higher than in the reference area, where there were no native saplings. In the removal area, $36.7 \pm 14.3\%$ of saplings were *Fraxinus*, $14.3 \pm 13.2\%$ were *Celtis occidentalis*, and $9.0 \pm 5.0\%$ were *Prunus serotina*. Notably, no *Quercus* or *Liriodendron tulipifera* saplings were present at any of the sites. *Ulmus* sapling density was higher where honeysuckle was left intact (0.72 ± 0.39 stems/ m²) than where it was removed (0.06 ± 0.06 stems/ m², $p < 0.001$). It was also higher outside the fences (0.03 ± 0.02 stems/ m²) than inside (0.01 ± 0.01 stems/ m², $p = 0.005$). *Sassafras* sapling density, on the other hand, was higher where honeysuckle was removed (0.04 ± 0.02 stems/ m²) than where it was left intact (no *Sassafras* saplings were found in these areas, $p < 0.001$).

Honeysuckle also interacted with site to affect total herbaceous-layer species richness ($p < 0.001$) in 2013. Richness was higher where honeysuckle was removed at Lugar Farm and Martell (18.30 ± 1.87 and 16.30 ± 1.41 species respectively) than where it was left intact (3.00 ± 0.68 and 15.00 ± 1.03 species respectively). However, richness was higher where honeysuckle was left intact at Ross (16.50 ± 1.43 species) than where it was removed (14.00 ± 3.21 species). The same interaction, with the same patterns, occurred in 2014 ($p < 0.001$) and 2015 ($p < 0.001$). By 2018, however, total species richness was higher where honeysuckle was removed (19.6 ± 1.93 species) than where it was left intact (10.4 ± 1.15 species) at all sites ($p < 0.001$).

Honeysuckle interacted with site to affect the proportion of plant cover ($p = 0.027$), which was lower where honeysuckle was left intact ($57.1 \pm 15.1\%$) than where it was removed ($85.5 \pm 2.4\%$) at Lugar Farm. The same trend was present at Martell, but not significant.

3.5 Discussion

3.5.1 Natural Regeneration

Natural regeneration was largely dominated by ash (*Fraxinus* spp.), making up over 20% of the relative seedling density and over 18% of the relative sapling density at each site in 2018. Similar dominance of the seedling and sapling layers by regenerating ash seedlings was observed by Goins et al. (2013). Thus, ash continues to be an important component of hardwood forests despite the effect of emerald ash borer on adult trees. The fate of these seedlings as they grow and

become less shade-tolerant, and as the invasion of emerald ash borer continues, remains to be seen. The abundance of ash species drove many of the trends seen in the response of total seedling density to honeysuckle and fencing (Figs. 1-4). Differences in the response of natural regeneration among sites may be attributed to varying honeysuckle densities, sub-canopy light levels, and deer abundance (as well as the difference in recovery time after shrub removal between Martell and the other two sites). The honeysuckle invasion created the lowest light levels at Lugar Farm, but more light became available than at other sites where honeysuckle was removed due to a windstorm that thinned the overstory. The age and density of the honeysuckle invasion at Lugar Farm was the greatest of any site, while the invasion at Martell was the youngest and least dense (Ross was intermediate in age and density) (Table 3.1; Shields et al. 2015a). Because of these large differences in light, honeysuckle removal had the greatest effect at Lugar Farm, which was most dramatic for the total sapling density in 2018. There were no saplings in the reference area at Lugar Farm, while the sapling density in the removal area was the highest of any site. Notably, there were no oak species present in the sapling layer in 2018 at any site, nor were there any tulip-poplar saplings. Both of these species have relatively high light requirements, and would be unlikely to succeed under a closed canopy. In addition, deer browse has affected the understory for decades, likely decreasing or extirpating populations of browse-sensitive species such as oak. This has been noted in other midwestern forests that have been exposed to deer browse for long periods of time (Haffey and Gorchov, 2019). It may be necessary to reintroduce such species after deer are excluded. Owings et al. (2017) underplanted oak and chestnut seedlings on our experimental sites and found that removal of Amur honeysuckle and exclusion of deer increased survival. By 2018, five years after planting, there were no survivors left in any treatment outside the fences where honeysuckle was left intact. The presence of high densities of ash seedlings should not concern managers interested in oak regeneration. Götmark et al (2005) found that ash density was negatively correlated with browsing intensity on oak. It may be that, given future stand thinning and removal of competitive vegetation, existing regeneration of ash seedlings could aid the regeneration of oaks (as long as a seed source for oaks is available and the ash are not allowed to outcompete the oaks).

The effects of fencing varied by site. Fencing had a positive effect on total seedling density at Lugar Farm in 2015, where deer visits were less common and honeysuckle was the densest; however, contrary to our predictions, fencing had a negative effect on total seedling density at

Martell in 2014 and 2015, mostly due to the negative effect on *Fraxinus*. Ross had no main effects of fencing in these years, possibly due to low seedling density across treatments (Figure 3.1). By 2018, the positive effect of fencing was only evident for cherry (no site interaction) and hackberry (only at Martell) seedling densities. Elm (*Ulmus*) species (including both red and American elms), on the other hand, were negatively affected by fencing in 2018. Red elms are shade-tolerant and American elms are moderately shade-tolerant, but both are less preferred by deer than black cherry and hackberry (Burns and Honkala, 1990; Strole and Anderson, 1992). Deer browse may have reduced competition from other seedlings such as black cherry and hackberry.

3.5.2 Honeysuckle x Deer Interaction

Contrary to our predictions, total seedling density (as well as *Fraxinus* seedling density by itself) was decreased by honeysuckle removal at Ross in 2013. The negative effect of honeysuckle removal at Ross was present for maple in 2014, but not for total seedling density. Light levels were much more similar between honeysuckle treatments at Ross than at other sites (Table 3.1). Ross also had the highest number of deer spotted. It may be that the competitive effects of honeysuckle were overwhelmed by the facilitative effects because of protection from herbivory. Such antagonistic interactive effects between Amur honeysuckle have been observed in Ohio by Peebles-Spencer et al. (2017), though the effect was weak. In 2015, honeysuckle removal had a negative effect on both *Acer* and *Ulmus* species (no site interaction). In 2018, the interaction between honeysuckle and fencing on elm seedlings makes the relationship clear. For elms, honeysuckle had a long-lasting positive effect, but only when deer were present. Deer visits were much higher where the honeysuckle was left intact than where it was removed (113 vs. 39 for all sites) indicating that honeysuckle is not restricting access by deer to the area; in fact, a study in Missouri showed that deer density was higher in plots invaded by honeysuckle (Allan et al., 2011). Rather, the honeysuckle may protect seedlings within the branches of each shrub, or it may reduce plant apparency. The honeysuckle reference plot may actually be increasing browse of seedlings in nearby areas where honeysuckle was removed. Nearby shelter was positively correlated with browse intensity of oak saplings in Sweden (Götmark et al., 2005), and, as previously mentioned, the most deer were captured on camera within the plot where honeysuckle was kept intact. It is important to note that the only species to receive a negative effect of honeysuckle removal are shade-tolerant, and that these effects were not present for seedlings or saplings by 2018, except for

elm seedlings outside fences. *Fraxinus* species become less shade-tolerant as they age, and we see that the negative effect of shrub removal for *Fraxinus* was not present past 2013. The 2015 interaction between fencing and honeysuckle was contrary to our predictions. Seedling density was greatest where honeysuckle was removed outside the fences, rather than where it was removed inside (where seedling density did not significantly differ from reference treatments). For total seedling density in these forests (and for the shade-tolerant *Fraxinus* seedlings), honeysuckle evidently has a greater negative effect than deer. In fact, deer exclusion causes greater harm to ash, possibly by increasing competition. This must be interpreted cautiously, however, as the tree species remaining on these sites have been subjected to browse for decades, which may have extirpated or decreased the importance of browse-sensitive species. Similarly, Haffey and Gorchov (2019) found that highly preferred species were not common enough to indicate deer browse on plots in southwestern Ohio.

3.5.3 Herb Layer Vegetation

Similar to the effect on ash seedlings, the effect of honeysuckle removal on total species richness was dependent on site. The increased light levels likely allowed more species to thrive at Lugar Farm and Martell, resulting in greater species richness. The negative effects of honeysuckle (as well as the positive effects of honeysuckle removal) on richness is supported by past research (Collier et al., 2002; Haffey and Gorchov, 2019). Contrary to our predictions, the total species richness was higher where honeysuckle was left intact at Ross. It may be that honeysuckle protected herbaceous-layer plants, as well as some seedlings, at Ross..

Freeman (2015) found no effects of fencing on total species richness or plant cover under 50 cm in the first three years after treatment. We also found no effect of fencing on total species richness. However, we did find an effect of fencing on the proportion of total plant cover in 2018. We used a different measure of total plant cover. Whereas Freeman (2015) measured the sum of the total cover of each species (which could result in over 100% plant cover in the case of overlap), we measured the total proportion of ground covered by plants. In addition, our measurements occurred five years after treatment, giving the ground vegetation time to respond to fencing. We expected to see that presence of deer would decrease total plant cover through browsing and trampling (Peebles-Spencer et al., 2017). However, at Lugar Farm, plant cover was lower inside the fences. This may be due to the interaction between honeysuckle and fencing, as well as greater

amounts of bare ground where deer are present, which may encourage the growth of annuals (Haffey and Gorchoy, 2019). Honeysuckle removal increased the total plant cover at Lugar Farm. An interaction occurred between fencing and honeysuckle (across sites), whereby the proportion of plant cover was lower inside fences where honeysuckle was left intact than in any other treatment. This points to antagonistic effects of deer against honeysuckle. Honeysuckle can form a significant portion of deer diets (Martinod and Gorchoy, 2017), so it may be that deer were helping to keep honeysuckle in check through herbivory. Haffey and Gorchoy (2019), found a similar interaction for species richness, whereby richness was lowest inside fences where honeysuckle was left intact. However, contrary to our results they found that cover (in spring) was highest where deer were excluded and honeysuckle was removed. Excluding deer without controlling invasive shrubs caused honeysuckle to have even greater negative effects for summer cover, in our case.

3.6 Conclusions

Our results from this long-term hardwood regeneration experiment confirm that deer browse management must be accompanied by control of invasive shrubs to be successful, and vice versa. In areas with dense shrub layers, removal of invasive shrubs is necessary for the success of regeneration, particularly of shade-intolerant species and especially where herbivores are excluded. Removal of invasive shrubs will also increase the cover of herbaceous-layer vegetation inside deer exclosures. Since herbaceous-layer plants contribute up to 20% of leaf litter and affect nutrient cycles (Gilliam, 2007), this has important implications for forest health. In addition, removal of invasive shrubs should be accompanied by deer exclusion or some other effective form of browse management where deer browse poses a threat, because such shrub removal exposes regenerating seedlings and herbaceous-layer vegetation cover to deer.

CHAPTER 4. A REVIEW OF RESEARCH-BASED METHODS FOR MANAGING DEER HERBIVORY OF YOUNG HARDWOODS

4.1 Abstract

Ungulate herbivory poses global challenges to forest regeneration. Deer, in combination with a multitude of other biotic and abiotic factors, threaten to shift forest composition away from oaks and other palatable hardwoods, and cause regeneration failure in some cases. Many studies have assessed methods to reduce or manage browse, but research-based assessments of these methods across experiments are lacking. To evaluate the relative effectiveness of browse management methods in controlling damage to hardwood forest regeneration, we analyzed 75 relevant studies identified using a comprehensive, systematic literature review. Fencing reduced browse across studies by $54.2 \pm 10.4\%$, shelters by $30.6 \pm 12.8\%$, logging slash by $19.0 \pm 9.5\%$, hunting by $16.7 \pm 7.6\%$, repellents by $12.4 \pm 2.4\%$, and facilitation from neighboring plants by $11.2 \pm 7.7\%$. Fertilizer applied during seedling establishment increased browse and had no effect on height growth. Tree shelters and facilitation by neighboring plants also reduced browse and increased height growth. There were no significant survival differences. We conclude that fences or other physical barriers best control for the effects of deer, but other methods such as facilitation by surrounding vegetation, logging slash, hunting, habitat management through timber harvest, and certain repellents may also be effective. Considering the discrepancies between browse effectiveness and relative costs, future research should emphasize economic analyses to provide confident prescriptions for management.

4.2 Introduction

Deer herbivory, resulting from high deer populations, poses a major obstacle to temperate hardwood forest regeneration globally (Kuijper et al., 2010; Petersson et al., 2019; Takatsuki, 2009). In some cases, deer can prevent whole stands from maturing. Deer herbivory stunts tree growth, slowing the growth of desired tree species and allowing herbaceous species to outcompete seedlings (Putman and Moore, 1998). In addition, deer often browse terminal buds (Götmark et al. 2005), reducing the quality of timber by causing lateral buds to grow into multiple leaders (Jacobs et al. 2004). In regions where markets put a premium on straight boles, this can decrease tree value,

posing an even greater challenge to forest management. Browse tends to favor some species over others, changing community composition (Akashi et al. 2015; Rooney, 2001; Strole and Anderson, 1992; Tanentzap et al., 2011). For example, high-value hardwoods such as oaks are often preferred by deer (Strole and Anderson, 1992). Deer may even shift eastern forest ecosystems to alternative stable states dominated by ferns or other competing vegetation from which they cannot recover without intervention (Stromayer and Warren, 1997).

There is much debate regarding effective carrying capacity of deer (the amount of deer that an ecosystem can support) in relation to their ecological impacts. Deer, like all wildlife, have positive and negative values that must be weighed (Conover, 2002). A total solution to the problem is not possible; even if deer could be effectively eliminated, they represent hunting and aesthetic value. In addition, small populations of deer have positive effects on plant diversity (Parker et al., 2010). Tilghman et al. (1989) controlled the density of deer within large enclosures in northwestern Pennsylvania and found that densities above 7-11 per km² resulted in failure of desirable species (e.g. sugar maple, red maple, white ash, and birch) to regenerate in clear-cuts, and similar trends were found in thinned treatments. In addition, the cover of competing vegetation, such as ferns, was higher in clear-cuts at high deer densities (Tilghman, 1989). Csigi and Holzmüller (2015) found that densities between 6 and 12 per km² resulted in reduced height of hardwood seedlings in southeast Illinois. The carrying capacity of a forest and the habitat structure also affect the deer population levels that produce “damage” (Reimoser and Gossow, 1996). Population reduction can be used to reduce damage; however, deer may be maintained at higher densities due to a desire for more deer and/or low hunter participation. In these cases, other browse management methods will be needed.

Many studies on browse management methods have been published in the scientific literature, but there is a need for practice-oriented reviews of this research that are relevant to forest management. Forest managers are desperate for cost-effective browsing control solutions, and may not be aware of the scientific research behind alternative management solutions. Beguin et al., (2016) published one such study, focused on global temperate and boreal forest regeneration. Much of the research on this topic has emphasized conifers. However, we narrowed our focus to temperate hardwood systems. Thus, our objectives in this review were to: (i) systematically evaluate and compare browse control methods to aid temperate hardwood forest regeneration; (ii) summarize the benefits of different methods along with their drawbacks and limitations.

4.3 Methods

We reviewed the scientific literature on herbivory management methods for regenerating temperate hardwood forests and summarized the relative effectiveness of the control techniques. Between December 2017 and September 2018, we performed searches to obtain abstracts in the following databases and search engines: Purdue Library, Agricola, Web of Science, and Google Scholar. The identified studies cover relevant subjects (temperate hardwood afforestation and reforestation projects), interventions (manipulation or mitigation of deer herbivory of seedlings or saplings through browse management, repellents, population control [sport hunting and culls were both considered], cultural methods, or fertilization), and outcomes (regeneration and growth of seedlings or saplings). Additional studies following our criteria were obtained from the bibliographies of selected articles.

Browse management methods were grouped into several broad categories, including fences, repellents, shelters, sleeves (similar to shelters, but made of fabric or mesh), facilitation (planting trees with shrubs, weeds, or other trees to attempt protection or defense), fertilizers, lethal population control, timber harvest (to increase forage), or slash (as a barrier). Means and standard errors of growth, survival, or browse were obtained from papers (peer-reviewed and non-peer-reviewed); some papers did not directly report measurements, but provided enough data for values to be calculated. After review, 78 publications were retained, mostly from the United States but including Canada (3), Great Britain (1), Spain (3), Germany (1), Belgium (1), and Sweden (3). Some of these studies presented results on multiple species, management methods, or sites; a total of 98 height growth entries, 61 survival results, and 62 browse entries were recorded. Hedge's G was calculated as a measure for "effect size" for the difference in height or growth, between control and treatment means. Hedge's G (Formula 1) is used for studies with small or variable sample sizes, where s_1 represents the standard deviation of the treatment group, s_c represents the standard deviation of the control group, n_1 represents the sample size of the treatment group, and n_c represents the sample size of the control group (Turner and Bernard, 2006).

$$1) \text{ Hedge's } G = \frac{\text{Treatment Mean} - \text{Control Mean}}{\sqrt{\frac{(n_1-1)s_1^2 + (n_c-1)s_c^2}{(n_1-1) + (n_c-1)}}} \times \frac{n_1 + n_c - 3}{n_1 + n_c - 2.25} \sqrt{\frac{n_1 + n_c - 2}{n_1 + n_c}}$$

Few studies reported a measure of variance for browse or survival, thus we used the absolute difference between control means and treatment means to get an "effect size" for browse and

survival (Paquette et al. 2006). Results sometimes had to be indirectly taken from plots or histograms. In these cases, a plot digitizer was used. Following Paquette et al. (2006), for studies reporting multiple treatments, values were considered independent observations if they involved different species, browse management methods, or experimental methods. Results for planted seedlings as well as natural regeneration were included, though most studies reported on planted seedlings. Stump sprouts and direct seeding were excluded.

We performed unweighted randomization tests on differences between experimental treatments and controls (calculated from published results) to test for a significant relationship between browse management method and survival and browse (Paquette et al. 2006). These randomization tests used test statistics from ANOVAs, or Kruskal Wallis tests if the assumptions of ANOVA were violated. These tests were computed in R statistical software (R Core Team, 2018) using the reshape2 and vegan packages, using 9999 permutations of the data (plus one of the original dataset) (Oksanen et al., 2018; Wickham, 2007). When significant differences were detected, pairwise differences were examined with Tukey's Honest Significant Differences test, or the Dunn test using the Dunn.test and FSA packages, if the assumptions of ANOVA were violated (Dinno, 2017; Ogle et al., 2019).

Following Turner and Bernard (2006) the significance of effect on height growth was assessed by examining the 95% confidence intervals for Hedge's G. If the confidence interval did not include zero, the effect was considered significant.

4.4 Results

4.4.1 Deer Population Control and Timber Harvest

Controlling deer populations through culls or sport hunting is the most direct method of addressing damage by deer; and such control methods have been successful in some cases (Hothorn and Müller, 2010; Jenkins et al., 2015; Tanentzap et al., 2011). However, these methods of management can be hard to use, and even small populations of deer can continue to have effects after prolonged browse (Tanentzap et al., 2011; Wright et al., 2012). For example, despite the fact that sapling densities in New Zealand forests are recovering after decades of culling deer, preferred tree species are still being affected (Wright et al., 2012). Miller et al. (2010) found that localized removal of a matriarchal social unit in West Virginia was ineffective because deer subsequently

colonized from surrounding areas; instead, browse was more affected by forage availability whereby increasing natural forage due to timber harvests resulted in decreasing browse. Tanentzap et al. (2011), on the other hand, did find increases in seedling density in Ontario following reductions of deer density from >30 to 7 per km^2 . The forest still had not recovered to the conditions prevailing before the deer population reached 30 per km^2 , however, indicating that recovery can take long periods of time. Changing policy to increase deer harvest by sport hunting has been successfully used in Germany to reduce browse of hardwoods in as little time as three years (Hothorn and Müller, 2010). To be effective, hunting must be used at a sufficient pressure over multiple years with a high density of hunters killing antlerless deer in accessible areas (Simard et al. 2013). Though necessary to address the problem of deer overpopulation, methods other than hunting or sharpshooting to manage deer browse, such as physical barriers, facilitation by neighbors, or increases in forage may be required until populations are reduced on a regional level.

Reducing deer damage to seedlings can be accomplished not only by reducing the number of deer in an ecosystem, but also by increasing the amount of alternative forage available to the deer. Marquis et al. (1992) suggested that timber harvests could provide mitigation against deer herbivory by producing more than enough food in the form of regenerating trees. Reimoser and Gossow (1996) similarly suggested that using shelterwoods, rather than clear-cuts, can allow advance regeneration to survive in the presence of deer. Clearcuts that are too small can allow even a few deer to negatively influence regeneration (Reimoser and Gossow, 1996). The hypothesis that carefully planned timber harvest can reduce deer damage has been supported in several studies (Akins and Michael, 1999; Crimmins et al., 2010; Miller et al. 2009). Akins and Michael (1999) examined a range of sizes for harvest openings and suggested that they be made > 0.8 ha. Without management of deer populations in the long term, however, an increase in food abundance will have the effect of increasing carrying capacity and, thus, deer populations, exacerbating the problem. The combination of hunting and timed harvest was tested in West Virginia (Crimmins et al., 2010) and resulted in a reduction of browse to levels usually considered acceptable for regeneration. In another study, a combination of shelterwood cuts, control of competing vegetation, and deer population reduction below 5.2 deer per km^2 was required for desirable regeneration in northern hardwood forests of New York (Sage et al., 2003). More experiments are needed to determine the relative effects of population control and timber harvesting, but these

studies illustrate that a combination of methods is often the best option for successful hardwood regeneration.

4.4.2 Physical Barriers

In combination with (or in absence of) management focused on deer populations, a myriad of methods can be implemented to protect seedlings from damage. Fencing has a high cost but is one of the most effective methods of reducing deer herbivory and can eliminate browse if sufficiently tall and maintained correctly. Common options include woven wire fences, plastic mesh fences, and electrified fences. Slash piles have also been used successfully as physical barriers around patches of regeneration (Hunn, 2007), but Kota and Bartos (2010) found that, though more effective than no treatment, slash piles were no more effective than livestock fences. Another author reported that slash actually increased browse in northeastern France, possibly by increasing visibility to deer (Pellerin et al., 2010). Kota and Bartos (2010) found that “hinge barriers,” in which trees are partially cut down and left connected to the stump to form barriers around patches of regenerating seedlings, were effective against deer and elk, though not as effective as woven wire fencing. These hinge barriers also increased recruitment into higher size classes at a greater rate than fencing (possibly due to reduced evapotranspiration from shading) (Kota and Bartos, 2010).

Tree shelters were invented in Britain in the 1980s for the purposes of protection against herbivory, creation of a greenhouse effect, and assisting weed control (Tuley, 1985). They have been shown in many studies to be effective for increasing hardwood growth (Sharew and Hairston-Strang, 2005; Ward et al., 2000) and survival (Barton et al., 2015; Stange and Shea, 1998), and allowing more seedlings to reach free-to-grow status, (height [1.25-1.5 m] above which deer can no longer browse the terminal bud; Kochenderfer and Ford, 2008; Taylor et al., 2006). Many of these studies have been conducted on northern red oak (Stange and Shea, 1998; Ward et al., 2000), though a range of species have been studied in combination with different management methods. Shelter height and type affect success. Some studies have found that shelters 0.6 m high do not have beneficial effects because deer can reach terminal buds (Keeton 2008; Sweeney et al. 2007). Indeed, in one study, these shelters increased browse of silver maples, possibly by increasing visibility of seedlings (Keeton, 2008). However, a study that used direct seeding found beneficial effects of short shelters (Barton et al., 2015). The propriety of shelter height depends on height of

the seedlings planted, and Keeton et al. (2008) suggest using shelters at least 0.5 m taller than the seedlings. Despite this, shelters of the same height as seedlings may still be beneficial due to the fact that white-tailed deer can only browse the portion emerging from the shelter (Sweeney et al., 2002). Diameter and type of polymer used to make the shelters have little effect on growth (Tuley, 1985). Fabric and mesh sleeves tend to have an intermediate effect on temperature and light, and also tend to have less of an effect on height growth (Sharew and Hairston-Strang, 2005; Ward et al., 2000), though one study found that they increase diameter growth (Pinna et al., 2012). Disadvantages of shelters and other physical barriers include impeded or distorted growth as well as inhibition of light transmittance, but these can be mitigated by supporting them with stakes and/or removing shelters at the proper time (Gustafson 1983; Burger et al. 1996).

4.4.3 Repellents

Repellents are a common alternative to physical barriers; however, they are short-lived (the most effective repellents last ~3 months) (Trent et al. 2001). In 1994, federally listed deer repellents included ammonium soaps of higher fatty acids, bone tar oil, capsaicin, denatonium saccharides, putrescent egg solids, and thiram (Jacobs, 1994). We found experiments testing all of these repellents except for bone tar oil, as well as many other contact repellents (both commercially available and homemade). Among commercially available repellents, putrescent egg solids have been shown to be effective in several studies (Kimball, 2005; Palmer et al., 1983; Trent et al., 2001). Only hydrolyzed casein (in a study on western redcedar) and human hair (in a study on apple orchards) were more effective (Conover and Kania, 1988; Kimball, 2005). Repellents generally have variable effectiveness, however, depending on weather, deer density, and availability of alternative food sources. Putrescent egg solids reduced browsing of apple trees by about 50% (up to 76% for yews), while in another experiment comparing repellents to shelters, putrescent egg solids and concentrated edible animal protein failed to have a significant effect on oak survival (Kochenderfer and Ford, 2008). Repellents must be reapplied periodically to maintain their effectiveness; however, deer may become accustomed to them, especially if there is little alternative food. One study successfully overcame this by using multiple repellents, although browse was only measured during summer (MacGowan et al., 2004). Though most experiments have involved white-tailed deer, repellents should be as effective on mule deer (excepting predator urine) (El Hani and Conover, 1997). Systemic repellents have been tested (e.g., controlled release

selenium or capsaicin tablets), but success depends upon uptake of the chemical. Gustafson (1983) found that selenium was successfully taken up by several hardwood species and that it reduced deer browse of Douglas-fir seedlings by half when all seedlings were treated. There is a dearth of peer-reviewed literature documenting research on repellents and hardwoods. Much of the research on repellents has been done on conifers or is grey literature.

4.4.4 Fertilizers

Fertilization at planting may promote growth of seedlings above the browse line, especially on nutrient-limited sites (Burney and Jacobs, 2018). Some studies have shown, however, that fertilizer increases browse by increasing palatability to deer or by increasing site attractiveness (George and Powell, 1977; Tripler et al., 2002). Burney and Jacobs (2018) found that fertilization at planting only increased growth of seedlings (black cherry, bur oak, and white oak) inside fenced treatments (Burney and Jacobs, 2018). The consequences of fertilizer and browse are highly species dependent, however. For example, broadcast granular fertilizer aided the growth of American sycamore on reclaimed mine sites, but not black locust, likely because of elk preference for locust (76% of which were browsed) due to their high nitrogen concentrations (Brinks et al., 2011). Differences between species-specific herbivore response to elevated nitrogen concentrations (and, indeed species preferences in general), may be due to different consumption strategies (Tripler et al., 2002). Some species (e.g., black cherry, yellow birch, sugar maple, and white ash) are “luxury consumers” that store extra nitrogen in existing tissues until it can be used for new growth, increasing the attractiveness of the plant to herbivores (Tripler et al., 2002).

4.4.5 Alternative methods

Aside from physical barriers, repellents, and fertilizers, there are several low-cost natural methods of mitigating deer herbivory. Several studies indicate that weed control can make trees more visible to deer and thus increase browse and mortality (Stange and Shea 1998; Sweeney et al. 2007; Sweeney et al. 2002). Vegetation, despite competing with seedlings, can thus reduce browse by restricting access to seedlings. This was observed as early as 1915, when it was noted that elms could only survive in Ohio cattle pastures if they grew in the midst of rosebushes, spicebush, or other elms (Scott, 1915). Similarly, Watt (1919) indicated that oaks successfully

regenerated in England when protected by shrubs or deer exclosures.. Maltoni et al. (2019) found that the ability of *Quercus ilex* to establish after emerging from tree shelters was facilitated by neighboring pine seedlings. The ability of neighboring vegetation to mitigate browse depends on the relative palatability of the seedling and the neighboring vegetation, as well as herbivore pressure. For example, moderately unpalatable shrubs with spines protected palatable maples under moderate herbivore pressure, but not under high pressure, and shrubs increased the probability that unpalatable pines would be browsed (Baraza et al., 2006).

Consideration must also be given to the competition from neighboring vegetation; the benefit of protection must outweigh the competitive cost. In Ohio, removal of *Lonicera maackii* shoots increased biomass and stem length in caged sugar maples, but decreased biomass, root:shoot ratio, and leaf area of uncaged trees (as well as leaf area of unprotected northern red oaks), possibly due to the protection from browse afforded by *L. maackii* (Gorchov and Trisel, 2003). Owings et al. (2017) reported that the presence of *Lonicera maackii* had no effect on browsing of planted seedlings by deer, and a negative effect on survival and growth due to decreased light and water availability. Sweeney et al. (2007) found that herbicide only resulted in greater survival in sheltered treatments, emphasizing the need for protection from deer for the success of other management methods. Another study found that herbicides and mats aided the growth and survival of sheltered seedlings; however, by the final year, only sheltered seedlings had benefited (Sweeney et al. 2002).

Species selection for trees that are less palatable or browse-tolerant is also important in the presence of deer (Burney and Jacobs 2018) as deer prefer to browse some species over others, while more browse-tolerant species may be able to resist deer browse without a negative growth effect. Pinna et al. (2012) detected no effect of herbivory on sugar maple seedling height, while yellow birch showed negative effects. Many studies have demonstrated a greater preference of deer for oaks relative to co-occurring hardwood species (Sweeney et al., 2002; Strole and Anderson, 1992; Götmark et al., 2005). Browse-tolerance and preference of some species vary with context. For example, black cherry has been found to be disproportionately browsed in central Illinois (Strole and Anderson, 1992), but only moderately preferred in Indiana (Wakeland and Swihart, 2009), possibly due to differing nitrogen availability at different sites (Tripler et al., 2002).

4.4.6 Analysis of Data from Scientific Literature

Differences in browse observed between the experimental treatments and the control groups had a significant relationship with the management method used, according the Kruskal-Wallis test (there were several outliers that violated the assumption of linearity of error). Most browse control treatments had the intended effect of decreased browse. Fencing was the most effective control mechanism, reducing browse by an average (\pm SE) of $54.2 \pm 10.4\%$ (Figure 4.1). Among the fencing options, wire fencing was the most effective (an average browse reduction of $78 \pm 7.0\%$), but mesh fencing, which is less expensive, retained some effectiveness (an average browse reduction of $55.8 \pm 12.3\%$). Electric fencing reduced browse by an average of $46.3 \pm 21.3\%$. We combined solid-walled shelters and fabric or mesh sleeves into one category in this analysis because of a dearth of studies reporting on browse for these methods. Shelters were the second most effective browse management method, reducing browse by an average of $30.6 \pm 12.8\%$. Three of nine of the observations used 60-cm shelters, allowing deer to reach the buds that grew out of the shelter. When these shorter shelters were excluded, shelters remained the second most effective method for reducing browse (by an average of $47.5 \pm 14.4\%$). The best performing shelters were 150 cm tall (an average browse reduction of $68.5 \pm 22.5\%$). Shelters were followed in order of effectiveness by slash ($19.0 \pm 9.5\%$), population control ($16.7 \pm 7.6\%$), repellents ($12.4 \pm 2.4\%$), facilitation by other plants ($11.2 \pm 7.7\%$) and timber harvest ($6.3 \pm 5.0\%$). Among repellents, putrescent egg solids most consistently reduced browse ($30.7 \pm 13.8\%$). Ammonium soap salts of higher fatty acids were also as effective (Palmer et al., 1983), but were only examined in one study. Fertilizers increased browse by an average of $12.0 \pm 4.0\%$ (Figure 4.1).

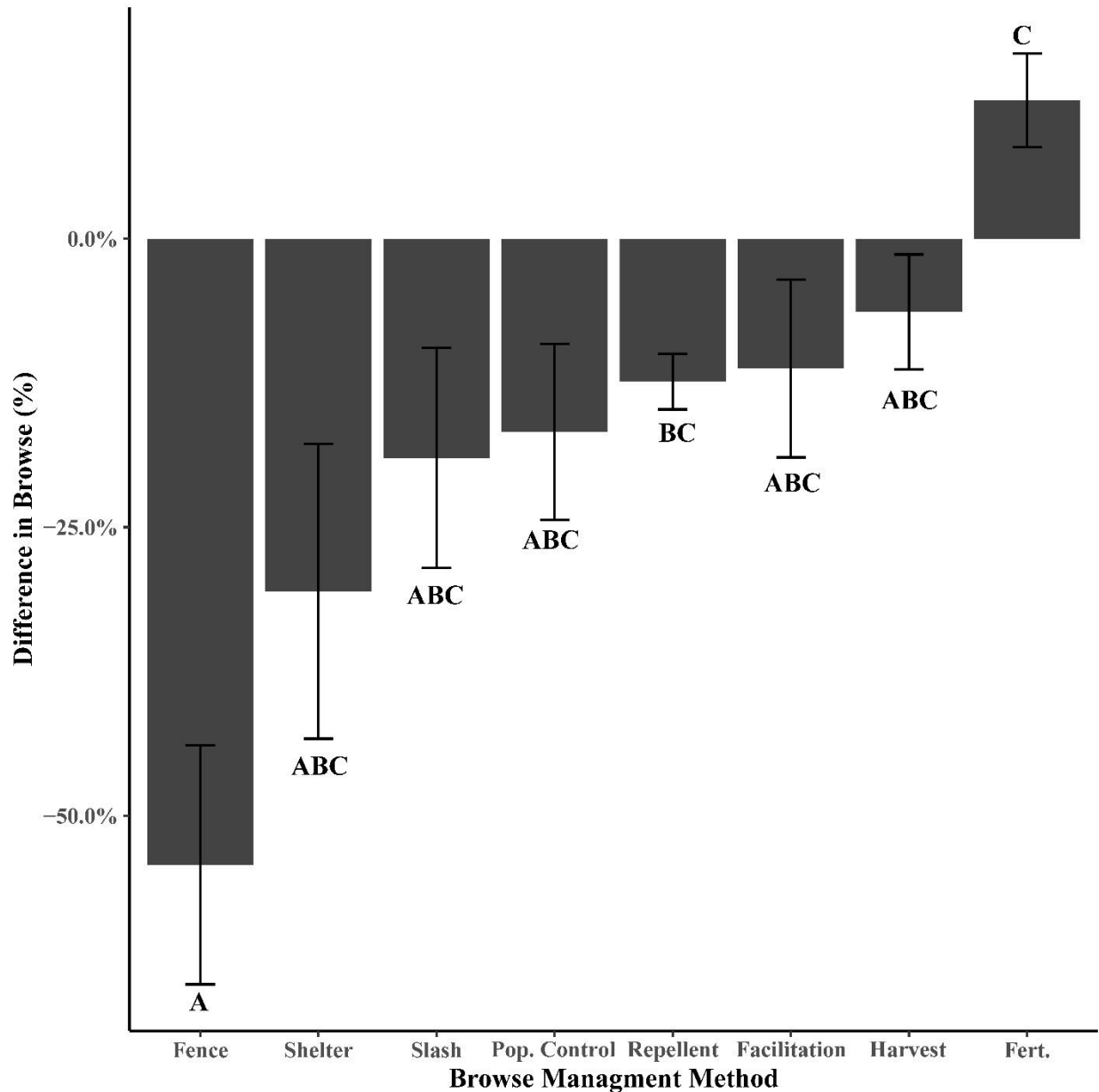


Figure 4. 1: Mean (\pm SE) difference in browse (browse of the control treatment subtracted from browse of the management treatment) among eight categories of browse management. Data is from twenty-eight studies that reported on browse. Letters represent significant difference between methods based on a post-hoc Dunn test ($\alpha = 0.05$).

Survival did not have a significant relationship with the browse management method used relative to the control, according to the Kruskal-Wallis test (there were several outliers that violated the assumption of linearity of error). The same result was obtained when using overall survival or annual survival. Survival tended to increase most, however, with fences ($13.5 \pm 10.4\%$), followed by shelters ($10.6 \pm 2.6\%$), facilitation ($6.7 \pm 6.3\%$), repellents ($5.3 \pm 3.2\%$) and sleeves ($2.2 \pm$

1.3%) (Figure 4.2). The standard error of fences included zero. In two fencing studies that reported negative effects of fencing on survival, factors other than deer browse were suggested as causal mechanisms. These factors were drought and digging by squirrels (Taggart and Long, 2015) and higher transpiration rates due to greater leaf area in the absence of herbivory (Burney and Jacobs, 2018). After removing these two studies, fencing was the most effective method for increasing survival (average of $16.4 \pm 9.3\%$). Mortality from deer browse often results from cumulative stress rather than an immediate response (Russell et al., 2001), which may explain the large variation in effectiveness of management methods. While browse indirectly contributes to mortality by making trees less competitive, some trees can survive years of browse in stunted form.

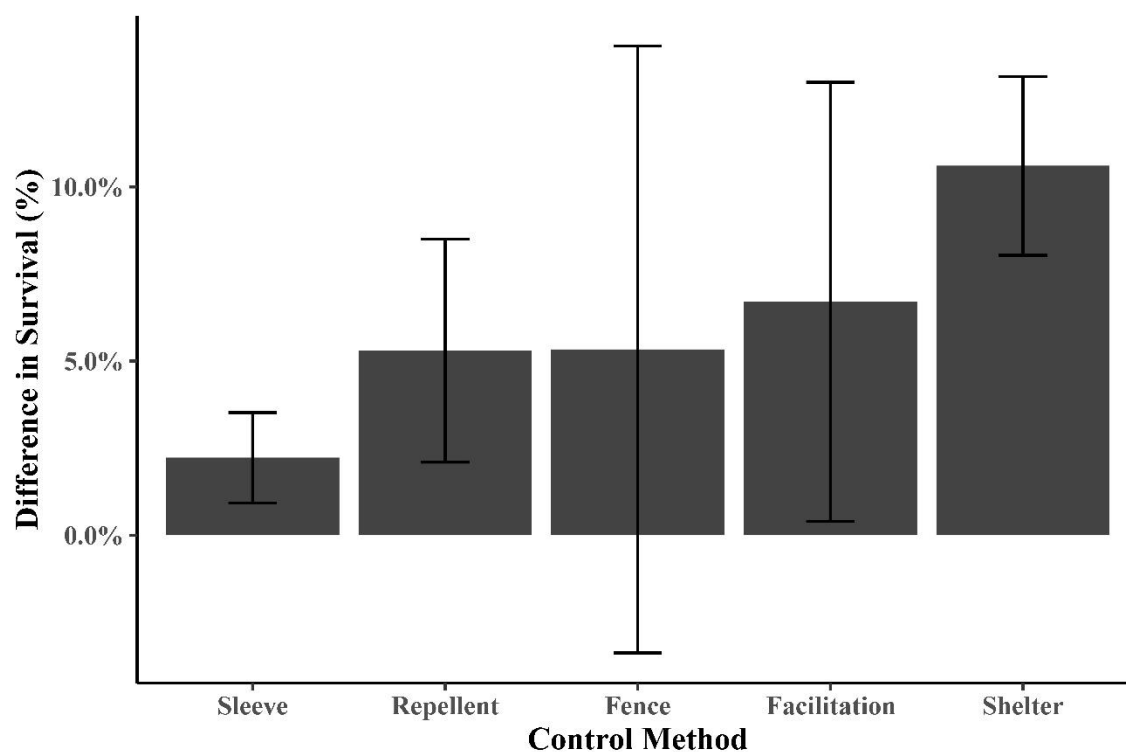


Figure 4. 2: Mean (\pm SE) difference in survival (survival of the control treatment subtracted from survival of the management treatment) among six categories of browse management. Data is from twenty-six studies that reported on survival.

All methods, except for fertilizer, had a significant, positive effect size on height or height growth (Figure 4.3). Fences had the greatest effect size (0.80 ± 0.20), followed by shelters (0.74 ± 0.08), repellents (0.57 ± 0.42), and facilitation by neighboring plants (0.22 ± 0.18 ; Figure 4.3). The 95% confidence interval for fertilizers included zero, indicating no significant effect 0.09 ± 0.40 ;

Figure 4.3). Few studies with repellents reported on growth and associated variance (i.e., only one, which examined two repellent types, could be used for this analysis).

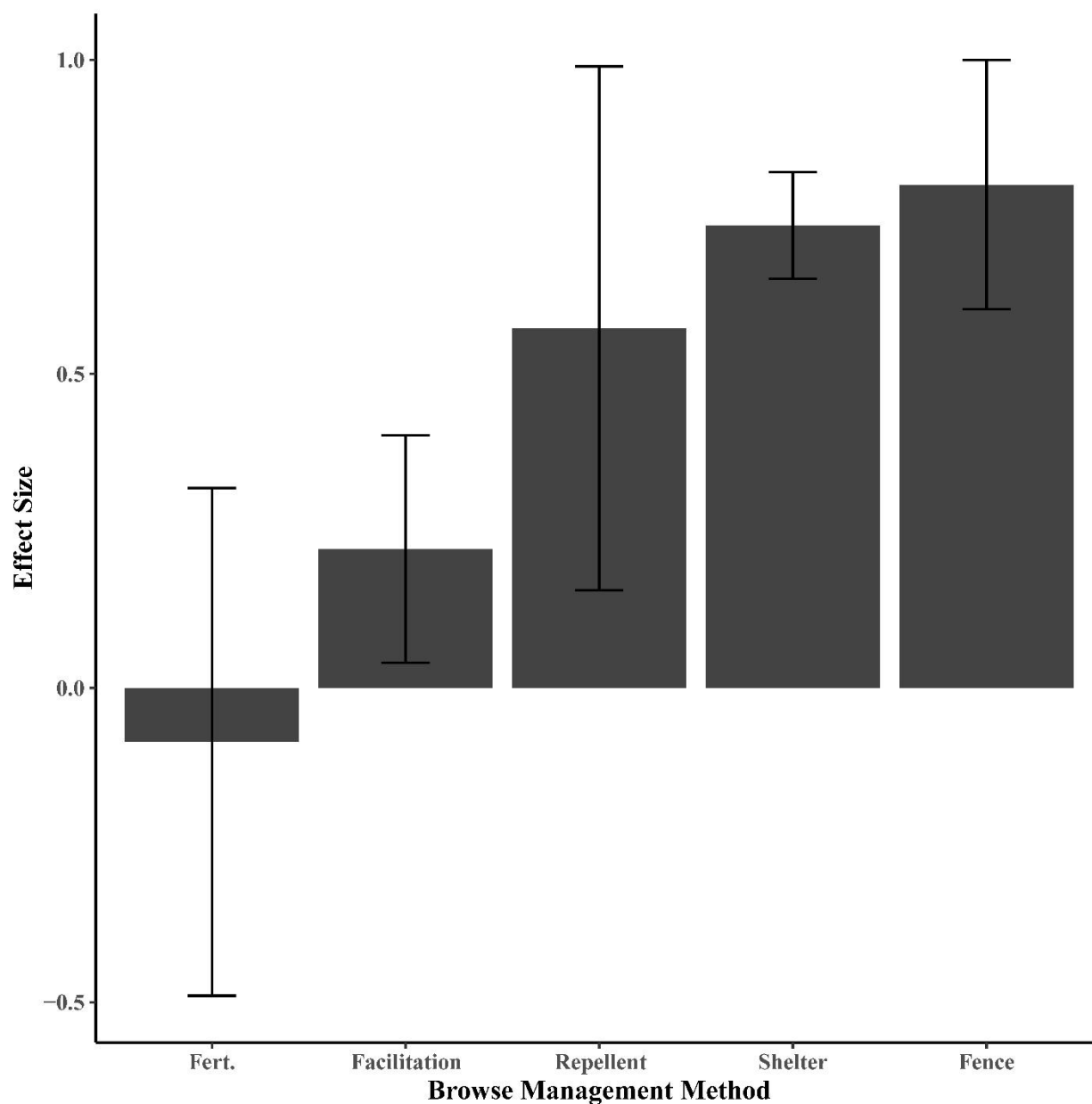


Figure 4. 3: Mean (\pm 95% CI) height growth effect size (Hedge's G) among seven categories of browse management. Data is from fourteen studies that reported on height growth (5 fencing studies, 6 shelter studies, 3, facilitation studies, 2 fertilizer studies, and 1 repellent study [with two repellent types]).

4.5 Conclusions

Based on our systematic literature review, fencing is clearly the most effective method for browse control in temperate hardwood forests. Solid-walled tree shelters are also relatively effective, but only if the shelter height sufficiently protects seedlings until they reach free-to-grow height (between 120-150 cm). While use of logging slash, habitat management through timber harvest, facilitation by other vegetation, and lethal population control to reduce browse of hardwood species show promise, more research is needed to more clearly substantiate their likelihood of success under varying forestry systems. Fertilization at establishment showed little potential for reducing browse damage and/or increasing growth in areas subject to high levels of herbivory, and in such cases fertilizer benefits are only likely to be realized if ungulate browse is controlled.

CHAPTER 5. CONCLUSIONS

5.1 Overview of this research

Together the projects in this thesis add to the body of research seeking to characterize and address the problem of deer herbivory for hardwood regeneration. Due to overpopulation and resource-poor habitat structure, deer threaten the future of oak and other browse-sensitive species in hardwood forests (Aronson and Handel, 2011; Csigi and Holzmüller, 2015; Frelich et al., 2002; Götmark et al., 2005; Jacobs et al., 2004; Kuijper et al., 2010; Petersson et al., 2019; Putman and Moore, 1998; Royo et al., 2010; Stromayer and Warren, 1997; Takatsuki, 2009). Many methods are available to address the problem (Beguin et al., 2016). Though deer population control and predator reintroduction will help to solve the issue, these are not available options everywhere, and it is unlikely that forests will return to their historic state (Stanturf et al., 2014; Tanentzap et al., 2011). Instead, appropriate tools must be used to ensure desirable, diverse, and ecologically stable regeneration of future forests and the sustainability of native plant communities.

The purpose of this research was to examine the effectiveness of available methods for managing browse of hardwood seedlings and to discover how these interact with each other and other silvicultural methods. The first study examined how fencing interacts with controlled-release fertilization (CRF), seed source (genetically select and non-select), and site type (afforested and reforested sites) to enhance the regeneration of planted northern red oak (*Quercus rubra* L.), white oak (*Quercus alba*), black cherry (*Prunus serotina*), and black walnut (*Juglans nigra*, Chapter 2). The experiment also studied whether CRF was a viable method to increase survival and growth in the presence of deer herbivory. The second study investigated how fencing and invasive shrub removal affected natural regeneration, species richness, and herbaceous-layer plant cover under closed-canopy forests (Chapter 3). The third study synthesized the existing literature on browse management options for hardwood regeneration to evaluate their relative effectiveness (Chapter 4).

5.2 Synthesis of Results

5.2.1 Chapter 2: Silviculture at establishment of hardwood plantations is relatively ineffective in the presence of deer browsing

In this 9-year hardwood plantation study, fencing proved to be the greatest determinant of seedling growth, survival, and quality. Fertilizer enhanced the early growth of white oak and black cherry, though for black cherry this occurred only inside fences. Select seed sources grew better and showed greater quality (especially for black walnut, for which the genetic improvement program was more advanced). However, the growth potential of select seedlings was limited by deer browse in absence of fences. Trees at afforested sites had greater growth, but were browsed more than those at reforested sites if left non-fenced.

5.2.2 Chapter 3: Response of natural regeneration to fencing and invasive shrub removal

This study tested fencing, as well as the removal of the invasive shrub (*Lonicera maackii*) and their interactions within natural forests. The focus was on natural regeneration rather than planted seedlings. Honeysuckle removal had more pervasive and consistent effects on seedlings and the plant community than fencing, though this may have been due to the loss of browse-sensitive species over many years. Honeysuckle removal had a negative effect on shade-tolerant elm and maple seedlings and a variable effect on ash depending on site. Honeysuckle removal may have made seedlings more visible and accessible to deer, or the greater light availability favored less shade-tolerant species. Deer fencing had a positive effect on cherry and hackberry seedling density, and a negative effect on elm seedling density. Honeysuckle and deer fencing did interact in some instances, most of which were antagonistic. Fencing without honeysuckle removal resulted in decreased abundance of elm seedlings. The only saplings to be negatively affected by honeysuckle removal were elms; but in the densest invasions, leaving honeysuckle intact resulted in a complete lack of recruitment into the sapling layer.

5.2.3 Chapter 4: Research-based methods for managing deer herbivory of temperate hardwood regeneration

This study evaluated the available research on browse management methods and compared their relative effectiveness. Fences, tree shelters, repellents, facilitation by neighboring plants, population control, timber harvest, and slash all had positive effects on height growth of regenerating seedlings under deer browse pressure. Fences were more effective at reducing browse than repellents, while fertilizers increased browse. Fertilizer had no effects on height growth. There were no significant effects on survival among browse management methods.

5.3 Management Implications

My work summarized nine years of data showing that prevention of deer browse through exclusion is necessary to protect investments in other silvicultural treatments where deer browse is a limiting factor (Chapter 2). Controlled-release fertilizer, though beneficial for some species, is not a solution to deer browse. Vegetation and browse control should be paired in areas where invasive shrubs and deer herbivory pose serious challenges (Chapter 3). Honeysuckle may protect the most shade-tolerant of seedlings, but may shade out these species if allowed to grow too densely. If deer browse is controlled, honeysuckle should be removed as well and vice versa. Deer browse will especially be needed if browse-sensitive species such as oaks are planted (Owings et al., 2017), which may be necessary after decades of understory exposure to deer (Chapter 3). Chapter 4 added to the evidence in Chapter 2 to indicate that fertilizer should not be considered a browse management method (in isolation). Repellents, while variable in effectiveness, are less effective than fencing. Managers must take economic considerations into account, but fencing is mainly a one-time cost that can be reused with semiannual maintenance, while repellents must be continually purchased and applied. Shelters are also effective management methods, if their sizes match the context, as are slash, lethal population control, appropriately planned timber harvests (clearcuts of the correct size, encouraging sufficient food to satiate deer in the short-term), and facilitation by neighboring plants. More research is needed on these latter methods.

5.4 Future directions

Future research must examine the long-term effects of fencing, select seed source, site type, and invasive shrubs on hardwood stands in the first thinning or stem exclusion stages. It is possible that the effects of seed source may increase, or decrease, with age. The study in Chapter 2 was limited by the low number of site type replicates and the lack of select seed sources for white oak. Future studies that focus on the differences between afforested and reforested sites should include more sites. Select seed sources for white oak, while not available at the outset of this study, are now available and should be studied. More work is being done to examine the interaction of invasive shrubs with deer, and should delineate the factors that can change interactions from antagonistic to synergistic.

The study presented in Chapter 3 was limited by the low number of sites (two sites had to be abandoned after 2015). Future studies may focus on the composition and density of invasive species as they regrow and recolonize after the initial removal. How often should invasive shrub removals be implemented to maintain a healthy understory?

More research must be done on the many repellent options available to deer. Specifically, repellents based on putrescent egg solids show promise and should be further examined. More research is also needed on the effectiveness of deer population control, timber harvest, timber slash, and facilitation. Studies examining the effectiveness of browse management at different deer abundances are needed, but for these studies to be done, a consistent and reliable method for assessing deer populations must be created and implemented. Analyses must also be done to compare relative cost-effectiveness, in addition to efficacy of different methods in managing browse. These studies will have to take costs of labor and materials into account, as well as regional differences.

Forest managers must implement this research on the ground and policy should reflect the application of scientific findings to a socially complex wildlife-forestry interface. Communication between researchers, practitioners and stakeholders from different fields, as well as education of the public, is essential in these efforts.

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