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Regeneration of Imperiled Hardwoods in the Eastern United States

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I am submitting herewith a dissertation written by Joshua J. Granger entitled "Regeneration of Imperiled Hardwoods in the Eastern United States." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Natural Resources.

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We have read this dissertation and recommend its acceptance:

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(Original signatures are on file with official student records.)

Regeneration of Imperiled Hardwoods in the Eastern United States

A Dissertation Presented for the
Doctor of Philosophy
Degree
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ABSTRACT

Our ability to successfully promote forest stand health and facilitate species under the threat of extinction will hinge on our ability to identify species regeneration requirements in an ever-changing environment. In the first chapter of this dissertation, I address what is known about the nature of threatened and imperiled hardwoods in the eastern United States, and in doing so, I identify several large knowledge gaps in current potentials and methodologies for regenerating them. In my second chapter, I use recent data from the United States Forest Service, Forest Inventory and Analysis program (FIA) to quantify ash regeneration counts across FIA forest type groups containing the emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) threatened species white ash (*Fraxinus americana* L.), green ash (*Fraxinus pensylvanica* Marsh.), black ash (*Fraxinus nigra* Marsh.), blue ash (*Fraxinus quadrangulata* Michx.), Carolina ash (*Fraxinus caroliniana* Mill.), and pumpkin ash (*Fraxinus profunda* (Bush) Bush). In addition to this baseline calculation of ash regeneration potentials, all other species are quantified to determine overall species composition and levels of inter-specific competition. In the third chapter, Shannon-Wiener species diversity index values are calculated for forest communities containing each of the six ash species above. This facilitates identification of ash-dominated communities and states in need of greater conservation efforts. In the fourth chapter, I use field observations to quantify microsites supporting populations of mountain stewartia (*Stewartia ovata* (Cav.) Weatherby) across East Tennessee and examine the hypothesis that specific site requirements are limiting stewartia's distribution and abundance across its natural range. In doing so, I am able to put forth a list of site requirements that may be necessary to guarantee the future regeneration and success of mountain stewartia. In the final chapter, a 25-year data set is used to investigate the success of a novel method for regenerating northern red oak (*Quercus* *rubra* L.) in Michigan oak and pine stands. Oak regeneration is more successful in pine stands than in oak stands due to several potential factors. Overall, my dissertation seeks to highlight regeneration requirements, potentials, and methods for regenerating an important group of threatened and imperiled hardwood species.

Keywords: Conservation; Diversity; *Fraxinus* spp. (Oleaceae); *Quercus* spp; *Stewartia ovata* (Cav.) Weatherby.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The rate of biodiversity loss has increased in recent years, and biologists have long warned of earth's next sixth mass extinction (Eldrige 1998). The global transportation of pests and pathogens, alterations in disturbance regimes, depletion of natural resources, urbanization, and changes in land use all disrupt natural processes and impede our ability to preserve biodiversity. Presently, a substantial number of North American trees are at risk for extinction.

The introductions of exotic pests and pathogens alone have produced significant, large-scale alterations in forest community structure and function (Liebhold et al. 1995; Gandhi and Herms 2010). One such introduction is the devastating pathogen, American chestnut blight (*Cryphonectria parasitica* (Murrill) Barr). With no apparent resistance, an estimated 3.5 billion American chestnut (*Castanea dentata* (Marsh.) Borkh.) trees quickly disappeared from American forests between the years 1904 and 1940. Early accounts suggest that one quarter of all eastern North American trees were American chestnuts (Burnham 1988). Currently, this once abundant species has been reduced to a rare, root-sprouting, understory shrub that seldom reaches a fruiting height before being top-killed by the blight. The European bark beetle (*Scolytus multistriatus* Marsh.) served as the principal vector of Dutch elm disease (*Ceratocystis ulmi* Buism.). Starting in the early 1920s, this disease killed more than 200 million mature elm (*Ulmus* spp.) trees native to the eastern half of the United States (Gandhi and Herms 2010). Introduced in the mid 1980's, the hemlock wooly adelgid (*Adelges tsugae* Annand) has resulted in a 100% mortality of affected hemlock (*Tsuga* spp.) across much of the eastern deciduous forest (Orwig et al. 2002; Small et al. 2005). Without an ability to re-establish following the initial adelgid-induced mortality, hemlock species of the eastern United States are predicted to disappear entirely within the next two decades (Orwig et al. 2002).

Less abundant species and species restricted in geographical range represent taxa with an elevated risk for extinction. The introduction of the balsam wooly adelgid (*Adelges piceae* Ratzeburg) in the 1930s resulted in a significant decline in Fraser fir (*Abies fraseri* (Pursh) Poir) populations. Restricted to six high altitude regions in the southern Appalachians, the decline of Fraser fir has altered plant and animal communities and increased the susceptibility of neighboring trees, such as red spruce (*Picea rubens* Sarg.), to a variety of negative biotic and abiotic factors (Pauley and Clebsch 1990; Hollingsworth and Hain 1991). One of the more intriguing publicized losses in United States history was the extinction of the Franklinia tree (*Franklinia alatamaha* W. Bartram ex. Marshall). Formerly restricted to a small area along the Alatamaha River in present day Georgia, U.S., the species has been extirpated from the wild since 1773 (Plummer 1977). While the exact mechanism is unknown, over-collecting by plant enthusiasts and pathogen introductions have both been hypothesized.

Alterations in historic disturbance levels have also produced significant changes in forest composition that threatens the long-term survival of many species and communities. The lack of fire has been hypothesized to be the driver behind the increase in abundance of fire sensitive species across North American forests (Crow 1988). This may explain for example why shortleaf pines, a fire adapted species, have significantly declined in abundance throughout their ranges (Guyette and Dey 1997). Though many of the above species are not extinct, their functional roles have been lost, threatening the stability of numerous organisms that depend both directly and indirectly on these trees for their survival.

Overall, this dissertation sought to address the conservation and regeneration needs of several potentially imperiled eastern North American hardwood species: ashes (*Fraxinus* spp.), oaks (*Quercus* spp.), and mountain stewartia (*Stewartia ovata*). Like many of the species described above, each of these is threatened by one or more potential factors. Native ashes are declining significantly throughout their ranges as a result of an introduced pest, the Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire). Inadequate levels of regeneration have been documented for numerous upland oak species and may be the result of alterations in disturbance regimes. Mountain stewartia is potentially threatened by its small geographical range and by large knowledge gaps in its habitat requirements, population stability, adaptability, ecosystem function, and genotypic variability. Our ability to conserve these species and numerous others will depend largely on our ability to identify means of regenerating and conserving these species in a changing environment. The findings from this research has implications in regenerating and conserving these species, and should also facilitate additional species, and address biodiversity dependent on these tree species across the eastern United States.

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CHAPTER I

POTENTIAL FOR REGENERATING MAJOR AND MINOR ASH SPECIES (*FRAXINUS* SPP.) FOLLOWING EAB INFESTATION IN THE EASTERN UNITED STATES

This chapter was originally published by Joshua J. Granger, John M. Zobel, and David S. Buckley:

Granger, J.J., Zobel, J.M., Buckley, D.S., 2017. Potential for regenerating major and minor ash species (*Fraxinus* spp.) following EAB infestation in the eastern United States. Forest Ecol. Manag. 389, 296-305.

ABSTRACT

Incidentally introduced in 2002, the expansion of emerald ash borer (EAB) led to widespread ash mortality throughout the eastern United States. A great deal of effort has been invested in containing and controlling this invasive forest species, whereas the ability to regenerate ash from extant seedling and sapling populations following the initial EAB invasion has received less attention. Using recent data available from the U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis program (FIA), we quantified ash seedling and sapling regeneration counts across FIA forest type groups containing white, green, black, blue, pumpkin, and Carolina ash. In addition, all other seedling and sapling species in these stands were quantified to determine overall species composition of the regeneration and the potential for inter-specific competition. Ash seedlings and saplings represented the greatest proportion of regeneration across most forest type groups containing mature ash. Top competitors of ash tended to be far less economically and ecologically valuable. If retaining ash in current stands remains a management goal, and provided that an effective biological control for EAB is identified and established across infested areas, the success of extant ash seedlings and saplings into larger size classes will depend on silvicultural treatments designed for controlling inter-specific competition across stand cohorts.

Keywords: Advanced regeneration, Emerald Ash Borer, FIA, Forest Type Groups, *Fraxinus* spp. (Oleaceae).

INTRODUCTION

Originally identified in Detroit, Michigan and Windsor, Ontario in 2002, the emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) has quickly spread across the eastern United States and killed millions of ash (*Fraxinus* spp) trees (Poland and McCaullough 2006). Inadvertently introduced from Asia, few efforts have proven effective in slowing the spread of this forest pest and reducing its impact on native ash populations. Upon infestation and regardless of initial tree health, a stand can lose nearly 100% of its mature ash trees in just three to five years (Gandhi et al. 2008). Despite heavy losses of larger sapling and mature trees, ash seedlings and small saplings often survive.

As a common component of natural forest systems, the loss of ash has major economic and ecological consequences. Ash has been a major source of sawtimber in the United States representing 7.5% of annual harvests. Based on an estimate of over 8 billion forest ash trees in the United States, the value of the genus has been estimated at $282.3 billion (Poland and McCaullough 2006). Ecologically, ash provides wildlife with shelter, browse, and seeds, which are consumed by a variety of birds, small mammals, and insects (Schlesinger 1990). Several ash species tolerate frequent inundation in swamps, alluvial floodplains, and pond margins where stand diversity is limited. As a result of their prominence, several ash species are key regulators of hydrological processes and community assembly in these systems (Ellison et al. 2005; Slesak et al. 2014).

There are three major and three minor ash species commonly recognized in the eastern deciduous forests. The two most abundant and widespread ash species are white ash (*Fraxinus americana* L.) and green ash (*Fraxinus pensylvanica* Marsh.). Though similar in appearance, the two species differ greatly in site requirements. White ash is commonly located on moist uplands and dry to mesic woodlands but is rarely a major component of forest canopies. Green ash is frequently found on mesic, poorly drained bottomlands, and along riparian corridors where it is often a major canopy component (Hardin et. al 2000; Poland and McCaullough 2006). Black ash (*Fraxinus nigra* Marsh.) is the third major ash and is found in nearly pure stands within deciduous swamps in the northern Great Lakes regions and Canada (Hardin et. al 2000; Tardif and Bergerson 1999) (Figure 1.1 in Appendix). Blue ash (*Fraxinus quadrangulata* Michx.), the first of the minor ash species, is common within the Ohio and Upper Mississippi river valleys and is generally associated with dry, rocky, limestone uplands. Carolina ash (*Fraxinus caroliniana* Mill.) and pumpkin ash (*Fraxinus profunda* (Bush) Bush have more discontinuous ranges and are restricted to swamps, ponds, bottomlands, and coastal plain communities within the eastern and southeastern United States. Pumpkin ash also occurs along streams and rivers within the Ohio and Upper Mississippi river valleys (Hardin et. al 2000; Nesom 2010a; Nesom 2010b) (Figure 1.1).

Over the past two centuries, the exponential increase in the introduction of forest pests and pathogens in North America has resulted in large changes in forest structure and function in conjunction with host mortalities (Liebhold et al. 1995; Gandhi and Herms 2010). Some of the most devastating introductions include pests such as the European bark beetle (*Scolytus multistriatus* Marsh.), which has served as the principal vector of Dutch elm disease (*Ceratocystis ulmi* Buism.). This disease has been responsible for the loss of over 200 million mature elm (*Ulmus* spp.) trees native to the eastern half of the United States beginning in the early 1920s (Gandhi and Herms 2010). The Hemlock woolly adelgid (*Adelges tsugae* Annand) and Balsam woolly adelgid (*Adelges piceae* Ratzeburg) have caused widespread mortalities in Appalachian forests containing hemlock (*Tsuga* spp) and fraser fir (*Abies fraseri* (Pursh) Poir) since the mid 1980s (Orwig et al. 2002; Ellison et al. 2005; Small et al. 2005; Pauley and Clebsch 1990; Hollingsworth and Hain 1991). Further, American chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) killed approximately 3.5 billion American chestnut (*Castanea dentata* (Marsh.) Borkh.) trees in North American between the years 1920 and 1940. While these pests and pathogens have long altered the forest ecosystems of eastern North America, the recent introduction and spread of EAB presents both challenges and opportunities. In the case of all ash species native to eastern North America, susceptibility to EAB and the continued loss of mature ash trees from forest communities will challenge our ability to conserve genetic diversity and maintain ecosystem services and functions.

We examined the hypothesis that extant ash regeneration is sufficiently abundant and diverse in both seedling and sapling stages of regeneration to adequately recruit ash back into stands as ash overstories succumb to EAB. In contrast to the lack of data during earlier forest pest introductions, extensive regional and national forest inventory data provide the opportunity to closely monitor structural and composition changes that occur with the spread of EAB. Structural and compositional changes in regeneration have been studied at the state and regional scales (Kashian and Witter 2011; Klooster et. al 2013), but a broader scale perspective would be instructive for examining differential impacts of EAB across the full spectrum of forest types in the eastern United States. Using these data, we quantified existing ash seedling and sapling regeneration across forest type groups for each of the six ash species recognized in the eastern

United States. We also quantified regeneration of all other species in these stands to examine species composition and the potential for inter-specific competition. Substantial regions of the eastern United States have yet to be infested with EAB. Provided successful EAB management methods can be developed, current regeneration data will serve as valuable baseline information for understanding successional dynamics as EAB moves across the eastern United States and for restoration of the ash component in eastern forests. Results will assist timber managers and conservationists in deciding whether to restore the ash component in stands infested by EAB, or facilitate replacement of ash by other species to promote forest stand recovery and desired ecosystem services and functions. In addition, few studies have investigated the regeneration potential of extant ash populations and even fewer studies have established baseline information for any of the minor ash species (i.e., blue, pumpkin, and Carolina ash).

METHODS

Sampling Area

The initial sampling area used in this research encompassed both the northern and southern regions of the United States. This combined area included 37 states: Alabama, Arkansas, Connecticut, Delaware, Florida, Georgia, Indiana, Illinois, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, East Oklahoma, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, East Texas, Vermont, Virginia, West Virginia, and Wisconsin.

Inventory Data

For this study, we compiled and used data from the U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis program (FIA) (http://www.fia.fs.fed.us/) (USDA 2015). This federally funded program establishes and remeasures permanent inventory plots across the entire United States and its territories. In the East, each plot is comprised of four fixed-radius subplots (each approximately 1.68% of a hectare) and four fixed-radius microplots (each approximately 0.13% of a hectare) (O'Connell et al. 2015). In addition to stand level attributes, subplots facilitate measurements on individual trees ≥ 12.7 cm diameter breast height (DBH), while microplots include measurements on individual saplings (2.5 cm ≤ DBH < 12.7 cm) and counts of seedlings (< 2.5 cm DBH) by species. Every year, an independent sample of approximately 14-20% of a state's plots are measured, with an entire "cycle" of plots being inventoried every 5-7 years. Alternatively, any successive collection of plots across 5-7 years forms a complete state inventory. For this study, we compiled data for all 37 states from 2009-2013 (the most recent, common five year window before several states switched to a seven year cycle length). Data came from whole plots (i.e., plots with only one FIA condition) classified as forestland and included both live and dead trees, live saplings, and live seedlings across the entire eastern United States.

Seedling and Sapling Regeneration Inventories

To determine regeneration potential of major and minor ash species, we analyzed data for white, green, black, blue, pumpkin, and Carolina ash. In order to locate stands with sufficient ash composition (particularly the minor species), we computed large tree basal area (m^2 ha^{-1}) proportions for each species on a plot. For white, green, and black ash, a basal area of at least 25% flagged those plots as having adequate ash in the overstory for their respective species (see

Arner et al. (2001) for a similar cutoff used for other FIA procedures). For the less common blue, pumpkin, and Carolina ash, a 10% basal area cutoff was used to ensure an adequate representation of these species within the sample. Regeneration counts were collected for all ash seedlings and saplings (and their competitors) and relative proportions were calculated for all species. Regeneration potential for ash seedlings and saplings, relative to all other competitors, was then summarized and reported by FIA forest type group. Note that competitor species with a relative proportion of less than 2% were collapsed into one group labeled "Other". In addition, note that for major and minor ash species, sample sizes less than ten and five plots, respectively, by forest type group were considered insufficient and were not included in the final reporting.

RESULTS

Across the eastern United States, 12 forest type groups were found to contain ash within the target (25% or 10%) basal areas: white, red, and jack pine (W-R-J), loblolly and shortleaf pine (L-S), other conifers, (O-C), oak and pine (O-P), oak and hickory (O-H), oak, gum and cypress (O-G-C), elm, ash, and cottonwood (E-A-C), maple, beech, and birch (M-B-B), aspen and birch (A-B), other hardwoods (O-HW), other tropical hardwoods (O-TH), and other exotic hardwoods (O-EH).

A total of 553 plots were identified that corresponded to forest stands containing white ash at a basal area of 25% or greater, with 94.2% and 89.3% of plots containing white ash seedling and sapling regeneration, respectively (Table 1.1). Four principle forest type groups were identified for white ash: O-P, O-H, E-A-C, and M-B-B. Within these groups, white ash comprised the greatest proportion of seedling regeneration for O-P(21%), O-H(18%), and E-A-C(24%) and had the second highest regeneration in M-B-B(16%). Across these forest type groups, sugar maple (*Acer saccharum* Marsh.), eastern redcedar (*Juniperus virginiana* L.), redbud (*Cersis canadensis* L.), black cherry (*Prunus serotina* Ehrh.), and American beech (*Fagus grandifolia* Ehrh.) represented the highest proportions of ash competitors in the seedling cohort (Figure 1.2). For the sapling cohort, sugar maple, eastern redcedar, red maple (*Acer rubrum* L.), hophornbeam (*Ostrya virginiana* (Mill.) K.), American beech, and American elm (*Ulmus amerianca* L.) comprised the highest proportion of ash competitors (Figure 1.3). In terms of relative regeneration proportion, white ash was found to be the greatest sapling regeneration source for the E-A-C(23%) forest type group and was the second highest source in O-P(16%), O-H(9%), and M-B-B(14%) forest type groups.

A total of 508 plots containing green ash at a basal area of 25% or greater were identified, with 88.2% and 84.3% of plots containing green ash seedling and sapling regeneration, respectively (Table 1.1). Four principle forest type groups were identified for green ash, O-H, O-G-C, E-A-C, and A-B. Green ash was the greatest proportion of seedling regeneration for O-G-C(13%), E-A-C(26%), and A-B(26%) and the second greatest source in O-H(18%). Across these forest type groups, choke cherry (*Prunus virginiana* L.), sugarberry (*Celtis laevigata var. laevigata* Willd.), pawpaw (*Asimina triloba* (L.) Dunal), redbud, eastern redcedar, downy serviceberry (*Amelanchier arborea* (Michx. F.) Fernald), nuttall oak (*Quercus texana* Buckley), and elm species were the most abundant competitors within the seedling cohort (Figure 1.4). For relative sapling regeneration proportion, green ash was found to be the greatest regeneration source for O-H(17%), O-G-C(28%), and E-A-C(32%) and was the second highest source below trembling aspen for A-B(10%). For the sapling cohort, sugar maple, eastern redcedar, Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), red maple, pawpaw, American beech, sweetgum (*Liquidamber styraciflua* L.), trembling aspen (*Populus tremuloides* Michx.), and elm species comprised the highest proportion of competitors across all forest type groups (Figure 1.5).

A total of 370 plots contained black ash with at least 25% basal area, with 93.8% and 92.7% of plots containing black ash seedling and sapling regeneration, respectively (Table 1.1). Similar to white and green ash, four principle forest type groups were identified for black ash: O-H, E-A-C, M-B-B, and A-B. Black ash was the top seedling regeneration source for the E-A-C(40%) and A-B(57%) forest type groups and the second highest source in the O-H(24%) and M-B-B(14%) forest type groups. Balsam fir (*Abies balsamea* (L.) Mill.), red maple, white spruce (*Picea glauca* (Moench) Voss), American hornbeam (*Carpinus caroliniana* Walter) hophornbeam, trembling aspen, and mountain maple (*Acer spicatum* Lam.) were the most abundant competitors in the seedling cohort (Figure 1.6). Black ash was the top sapling regeneration source in the E-A-C(51%), second in O-H(13%) and A-B(12%), and fifth in M-B-B(10%). The most abundant competitors in the sapling cohort included jack pine (*Pinus banksiana* Lamb.), hophornbeam, sugar maple, red maple, and balsam fir (Figure 1.7).

For stands with 10% or more relative basal area in blue ash, a total of 25 plots were found with 96.0% and 88.0% of the plots containing blue ash seedling and sapling regeneration, respectively (Table 1.2). Two forest type groups were identified for blue ash, O-H and M-B-B. The relative proportion of blue ash seedling regeneration was highest for both of these forest type groups at 20% and 21%, respectively. Other ash species, common hackberry (*Celtis occidentalis* L.), eastern redcedar, and eastern redbud were the highest proportion of seedling competitors across forest type groups (Figure 1.8). Blue ash was the second highest sapling regeneration source in the O-H(18%) group and the fifth highest source in the M-B-B(4%) forest type group. In the sapling cohort, the most abundant competitors were eastern redcedar, black cherry, Ohio buckeye (*Aesculus glabra* Willd.), and sugar maple (Figure 1.9).

A total of 19 plots contained pumpkin ash with at least 10% basal area, with 84.2% and 73.7% of plots containing pumpkin ash seedling and sapling regeneration, respectively (Table 1.2). Only one primary forest type group was identified for pumpkin ash, O-G-C. Within this group, pumpkin ash was eighth in relative seedling regeneration, comprising 2% of the total seedling cohort. The most abundant seedling competitors were red maple, sabal palm (*Sabal palmetto* (Walter) Lodd. ex Schult. and Schult. f.), sweetbay magnolia (*Magnolia virginiana* L.), and American elm (Figure 1.10). In contrast, pumpkin ash was the top sapling regeneration source at 63%, with the most abundant competitors being sweetgum, bald cypress (*Taxodium distichum* L.), and red maple (Figure 1.11).

For Carolina ash, 13 plots met the 10% basal area or higher requirement with 84.6% and 100.0% of plots containing Carolina ash seedling and sapling regeneration, respectively (Table 1.2). Similar to pumpkin ash, the O-G-C forest type group was identified as the principal group for Carolina ash. Within this group, Carolina ash was the sixth highest regeneration source, comprising 8% of the total seedling regeneration. Within the sapling cohort, Carolina ash was also the top regeneration source with 40% of the total regeneration. The most abundant seedling competitors were red maple, sweetbay magnolia, laurel oak (*Quercus laurifolia* Michx.), sabal palm, and bald cypress (Figure 1.12), while red maple, sweetbay magnolia, and bald cypress were the most abundant sapling competitors (Figure 1.13).

DISCUSSION AND CONCLUSION

Historically, many incidental introductions of forest pests and pathogens to North America have resulted in devastating ecological and economic consequences. Local accounts and records provide some insight into the impacts of these past disturbances, but more comprehensive means of quantifying forest disturbance across an entire species ranges have not been available until now. The accumulation of annually collected FIA data has enabled ecologists, biologists, and foresters to monitor large-scale disturbances and make predictions regarding future ecosystem composition, functions, and services. Current pest management practices focus primarily on protecting highly valued tree species, identifying biological control options, and establishing local quarantines. In contrast, little effort has been allocated to monitoring regeneration potentials across forested lands impacted by pest disturbances. With current FIA data and the relatively recent introduction of EAB, the ability to collect baseline data prior to the initial EAB infestation and during the subsequent spread of this invasive species will provide silviculturists with the ability to better manage post-infestation forest resources to meet the objectives and needs of society.

In establishing an ash regeneration baseline for the eastern United States, two specific areas of interest were addressed. First, both ash seedling and sapling regeneration potential for all forest type groups containing an ash component were quantified. Second, potential sources of inter-specific competition were identified along with their relative proportions. Over the course of this study, two unique regeneration patterns emerged. Most notable was the relatively high proportions of ash seedling and sapling regeneration across forest type groups. In most cases, ash was either the most significant regeneration source, or among the most significant sources. This supported our hypothesis that the abundance of both ash seedlings and saplings would adequately facilitate recruitment of individual ash species back into forest stands devastated by EAB. If an effective biological control for EAB is identified and established across infested areas, we may reasonably assume that a portion of extant regeneration will advance and ultimately replace canopy trees lost to EAB.

A second pattern revealed that, for most forest type groups, the majority of sapling stage competition was comprised of shade intolerant species. Light requirements for ash are known to fluctuate with developmental stage. While intolerant at maturity, young ash seedlings and saplings tend to be shade tolerant and exhibit greater growth when under the effects of partial shading (Diekmann 1996). With rapid ash overstory declines due to EAB, light levels can be expected to increase and potentially facilitate the recruitment of more shade intolerant species, while reducing the competitive abilities of young ash seedlings. The majority of forest type groups contained relatively high proportions of species such as eastern redcedar, red maple, sugarberry, common hackberry, trembling aspen, eastern redbmud, American hornbeam, hophornbeam, downy serviceberry, mountain maple, and American elm. Though these species are native and provide other unique ecosystem services, they are generally selected against due to their limited potential as timber resources. For ash stands comprised of species with low economic value, artificial regeneration may be required to ensure future forest value. Still, caution should be taken in such situations to avoid the development of stand monocultures, which may have an increased vulnerability to pests and pathogens due to low diversity (Koricheva 2006).

Finally, although ash populations are proportionally abundant across most forest type groups, the spread of EAB is expected to continue geometrically across the United States (Kovacs et al. 2010). This leaves seedling and sapling cohorts as the only ash component following overstory EAB-induced mortality. Relying solely on these two sources of regeneration to restore ash populations leads to several concerns. First, although most members of the Oleaceae family, which includes the ashes, are known for developing extensive and enduring seed banks (Baskin and Baskin 1998), the viability of native ash species under natural, pre-infestation forest floor conditions appears limited to three to four years (Clark 1962). Similarly, Kashiam and Witter (2011) reported a significant decline in ash seedling densities between 2007 and 2009 following EAB-induced mortalities of mature ash trees for lower Michigan, indicating a reduction in viable seed from within the seed bank. A more recent study reported that regardless of species (white, green, or black ash), seedling regeneration quickly ceased as ash tree mortality approached 100% within study sites in Michigan and Ohio (Klooster et. al 2013). Therefore, as EAB-induced mortalities continue across the United States, retaining an ash cohort throughout forests will depend largely on the extant ash seedling and sapling populations. Second, observations suggest that native ash saplings as small as 2.5 cm DBH are as vulnerable to EAB infestation as larger, more mature ash trees (McCullough et al. 2008). Therefore, as EAB populations persist in the environment following the loss of primary host martial, there may be limited success in the recruitment of small seedlings and saplings into larger size classes without EAB control. Third, in addition to surviving EAB, ash seedlings must also continue to tolerate the effects of browsing and inter-specific competition with seedlings, saplings, and other overstory species. Though levels of browsing and competition are not expected to increase, the continued loss of ash seedlings and saplings to these factors will contribute to the loss of extant ash populations, especially as the ash seed banks decline following EAB-induced mortality of mature ashes. If retaining ash in current stands remains a management goal (and becomes biologically feasible), active control of competing saplings will be needed to facilitate the success of ash seedling and sapling size classes in stands currently being impacted by EAB. For stands not yet disturbed by EAB, efforts should focus on optimizing ash seedling and sapling populations, thus better enabling the restoration of ash following EAB infestation. In addition, silvicultural treatments should be investigated for managing even-aged ash stands. According to Dobrowolska et. al (2011), a knowledge gap exists in understanding ash stand dynamics, particularly in even-aged ash stands. Each ash species is known for its unique set of adaptations and site requirements, and as such, each species will have its own unique set of challenges for ensuring species survival and success following EAB infestation. For example, species associated with hydric environments (i.e., black, pumpkin, and Carolina ash) generally have fewer competing forest associates; however, EAB-induced overstory tree mortality may result in hydrological changes that hinder the success of extant ash seedlings and saplings. In contrast, in the case of white ash, green ash, and blue ash, competing hardwoods may present the greatest challenge in maintaining ash seedlings and saplings. With millions of ash trees disappearing each year from the effects of EAB, restoration efforts are necessary to ensure not only a continued supply of ash forest products, but also sustainability of the various forest ecosystem services and functions that ash provides.

ACKNOWLEDGMENTS

We wish to thank the U.S. Forest Service for access to the Forest Inventory and Analysis (FIA) database and the University of Tennessee, Department of Forestry, Wildlife and Fisheries for generous support throughout this project.

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APPENDIX

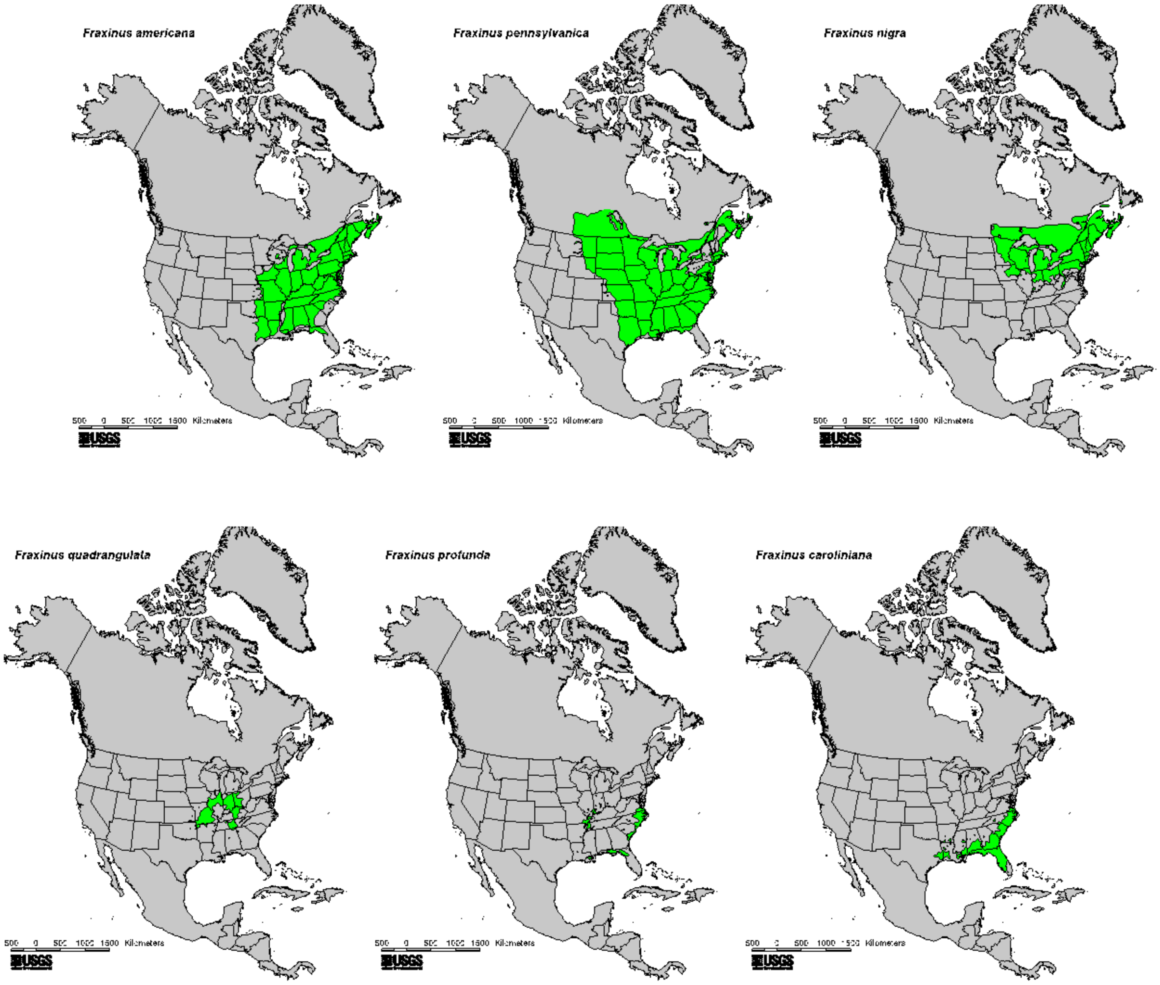

Figure 1.1. Distribution maps of white ash (*Fraxinus americana*), green ash (*Fraxinus pennsylvanica*), black ash (*Fraxinus nigra*), blue ash (*Fraxinus quadrangulata*), pumpkin ash (*Fraxinus profunda*), and Carolina ash (*Fraxinus caroliniana*). Source: USGS map based on Atlas of United States Trees by Elbert L. Little, Jr.

Table 1.1. FIA plot counts for major ash species across forest type groups in which ash comprised at least 25% of total stand basal area. Forest types were considered interpretable if they included ≥ 10 plots.

Forest Type Group	White Ash			Green Ash			Black Ash		
	Seedling	Sapling	Canopy	Seedling	Sapling	Canopy	Seedling	Sapling	Canopy
Oak and Pine	15	15	16						
Oak and Hickory	193	185	207	115	111	121	14	11	14
Oak, Gum, and Cypress				84	81	100			
Elm, Ash, and Cottonwood	23	22	27	214	203	251	239	240	259
Maple, Beech, and Birch	275	257	287				21	22	23
Aspen and Birch				17	16	17	61	60	62
Total	521	494	553	448	428	508	347	343	370

Table 1.2. FIA plot counts for minor ash species across forest type groups in which ash comprised at least 10% of total stand basal area. Forest types were considered interpretable if they included ≥ 5 plots.

Forest Type Group	Blue Ash			Pumpkin Ash			Carolina Ash		
	Seedling	Sapling	Canopy	Seedling	Sapling	Canopy	Seedling	Sapling	Canopy
Oak and Hickory	13	11	13						
Oak, Gum, and Cypress				11	10	14	7	9	9
Maple, Beech, and Birch	6	5	6						
Total	24	22	25	16	14	19	11	13	

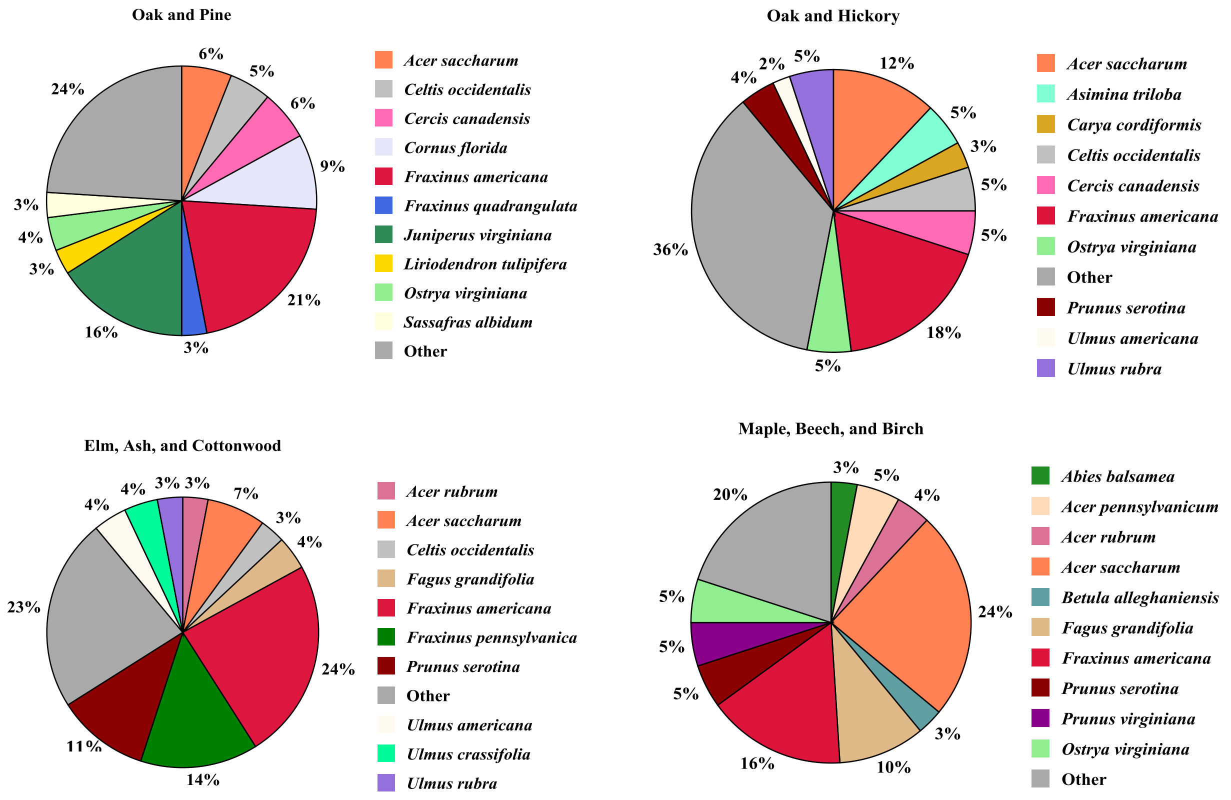

Figure 1.2. Relative proportions of *seedling* regeneration for forested areas with white ash comprising at least 25% of the total stand basal area.

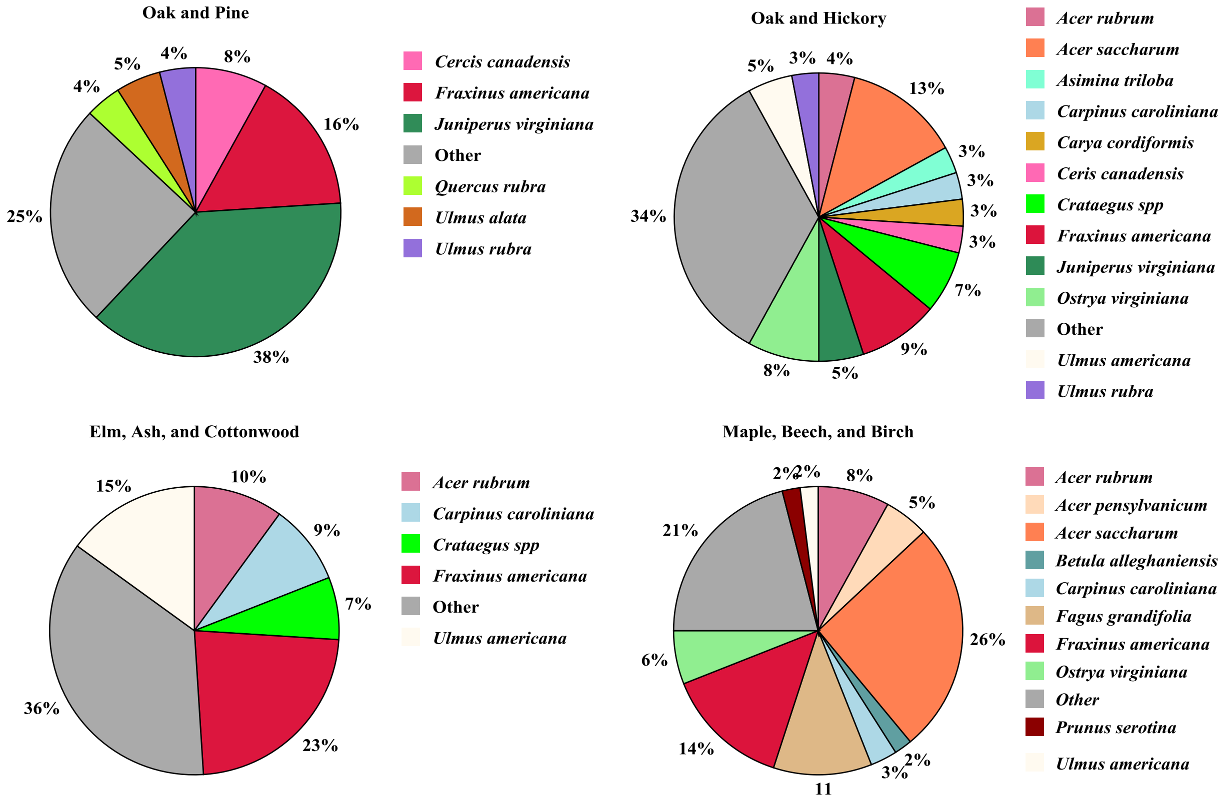

Figure 1.3. Relative proportions of *sapling* regeneration for forested areas with white ash comprising at least 25% of the total stand basal area.

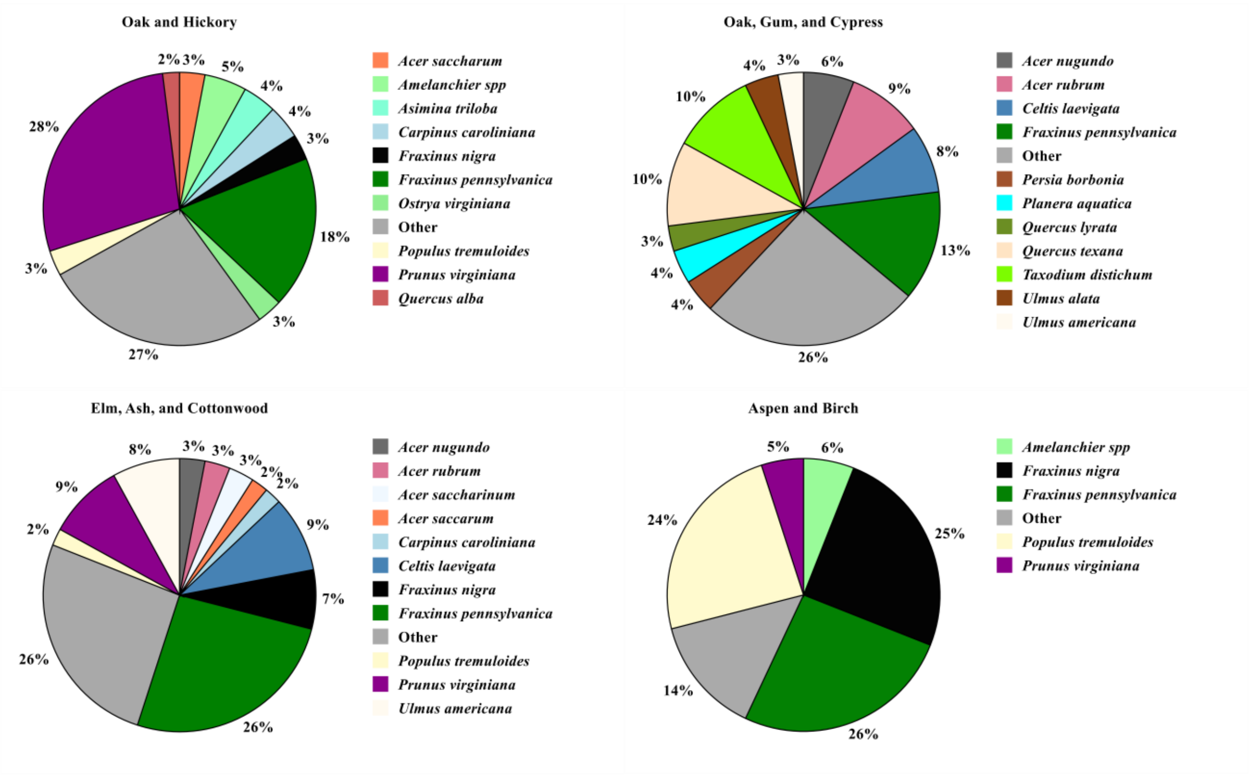

Figure 1.4. Relative proportions of *seedling* regeneration for forested areas with green ash comprising at least 25% of the total stand basal area.

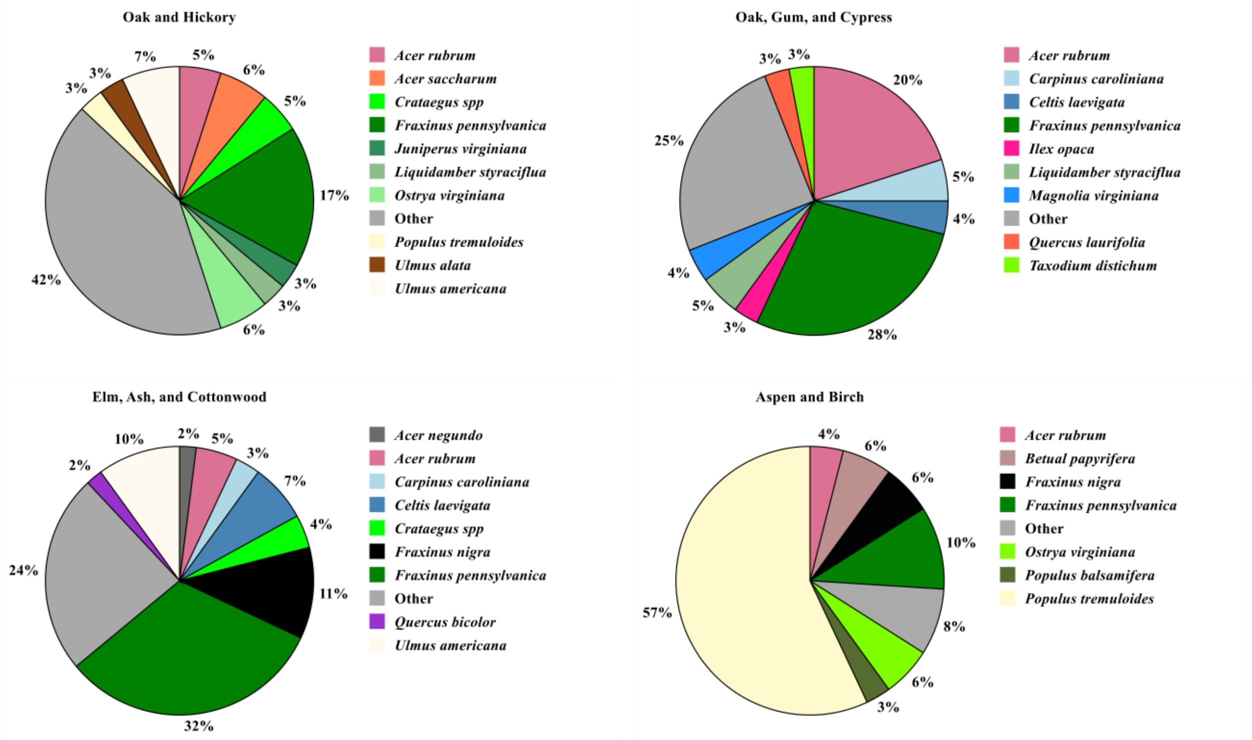

Figure 1.5. Relative proportions of *sapling* regeneration for forested areas with green ash comprising at least 25% of the total stand basal area.

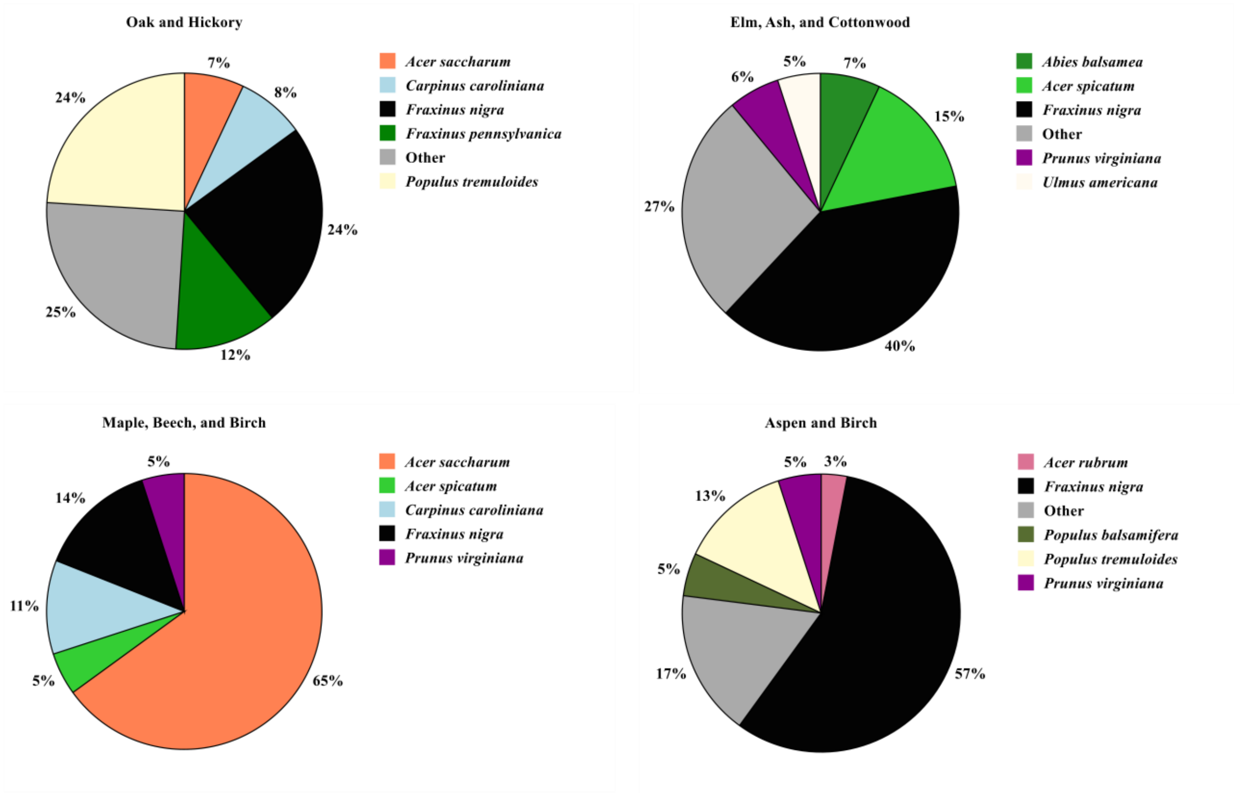

Figure 1.6. Relative proportions of *seedling* regeneration for forested areas with black ash comprising at least 25% of the total stand basal area.

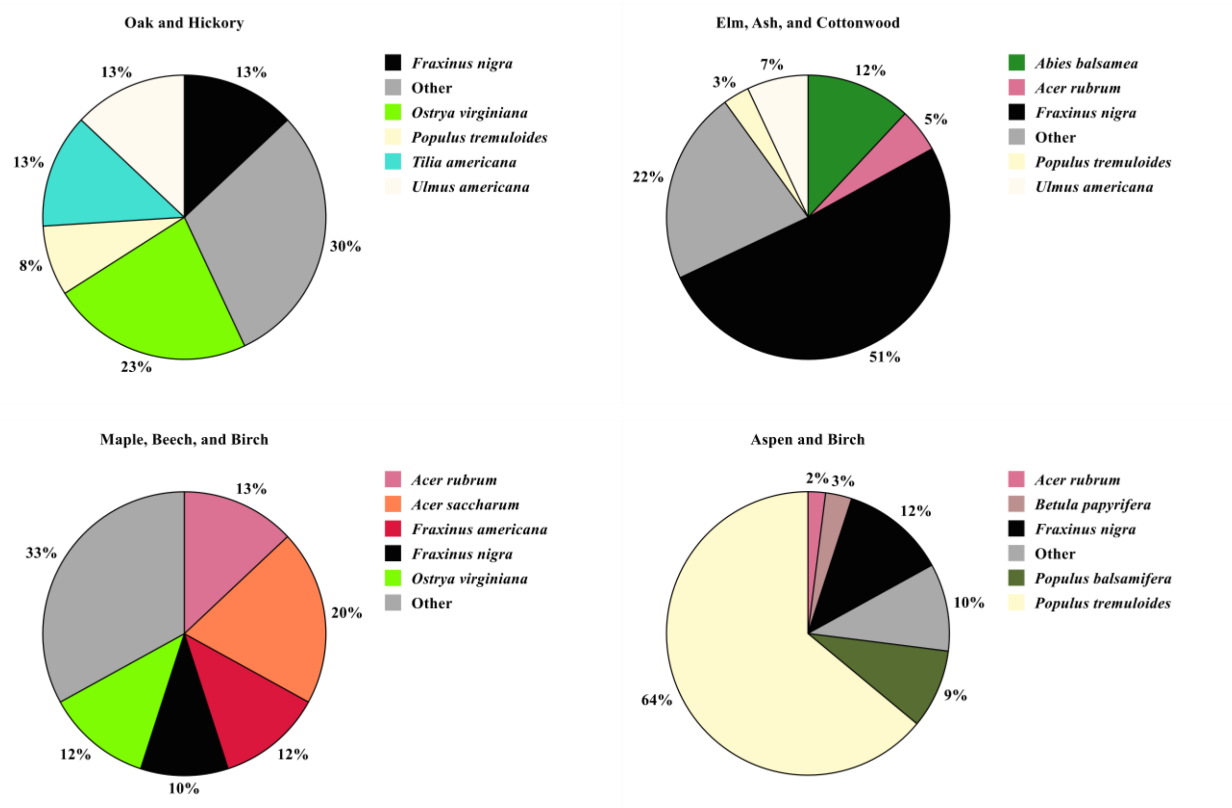

Figure 1.7. Relative proportions of *sapling* regeneration for forested areas with black ash comprising at least 25% of the total stand basal area.

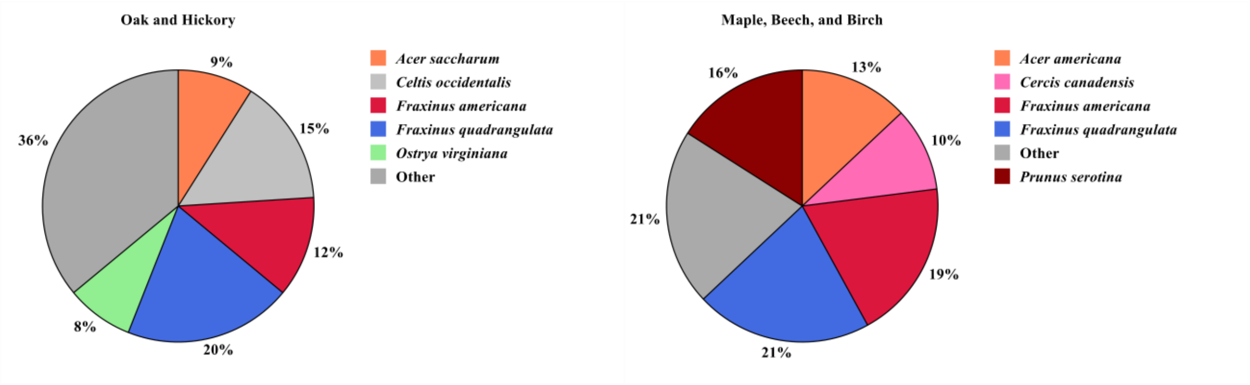

Figure 1.8. Relative proportions of *seedling* regeneration for forested areas with blue ash comprising at least 10% of the total stand basal area.

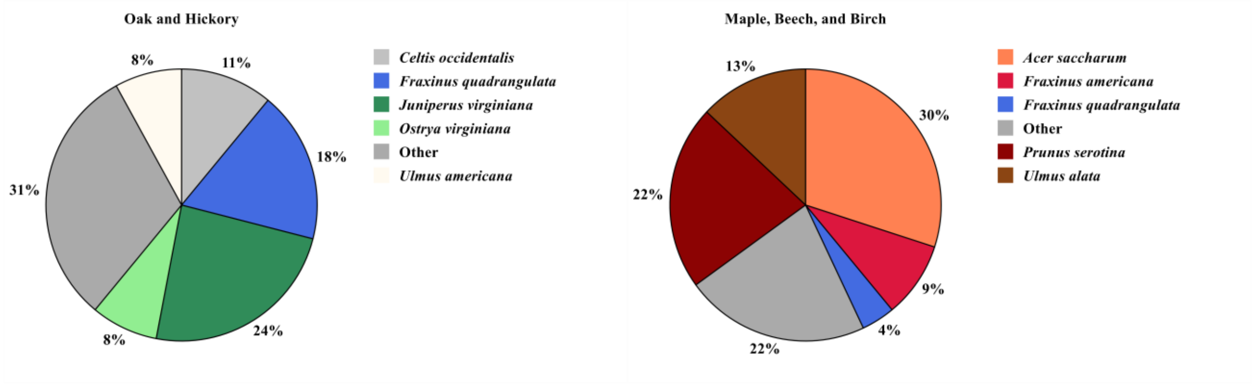

Figure 1.9. Relative proportions of *sapling* regeneration for forested areas with blue ash comprising at least 10% of the total stand basal area.

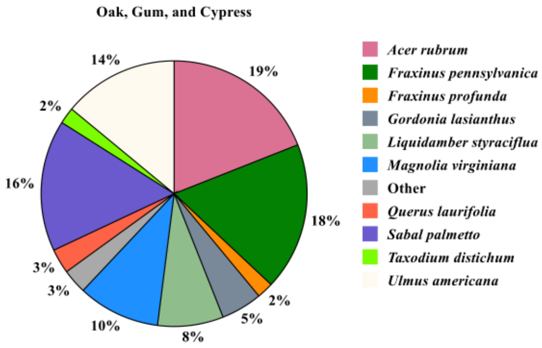

Figure 1.10. Relative proportions of *seedling* regeneration for forested areas with pumpkin ash comprising at least 10% of the total stand basal area.

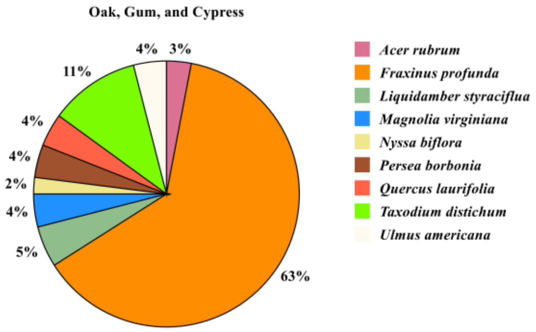

Figure 1.11. Relative proportions of *sapling* regeneration for forested areas with pumpkin ash comprising at least 10% of the total stand basal area.

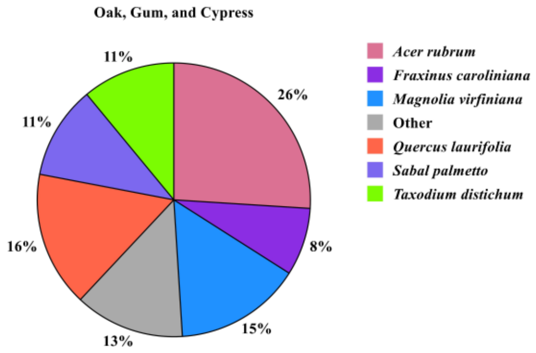

Figure 1.12. Relative proportions of *seedling* regeneration for forested areas with Carolina ash comprising at least 10% of the total stand basal area.

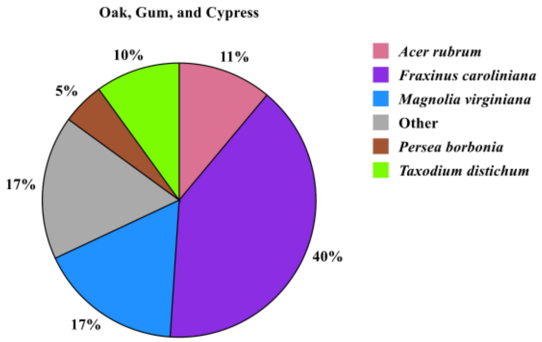

Figure 1.13. Relative proportions of *sapling* regeneration for forested areas with Carolina ash comprising at least 10% of the total stand basal area.

CHAPTER II

DIFFERENTIAL IMPACTS OF EMERALD ASH BORER (*AGRILUS PLANIPENNIS* FAIRMAIRE) ON DIFFERENT ASH-DOMINATED ECOSYSTEMS IN EASTERN NORTH AMERICA

This chapter was originally published by Joshua J. Granger, John M. Zobel, and David S. Buckley:

Granger, J.J., Zobel, J.M., Buckley, D.S., 2017. Differential impacts of emerald ash borer (*Agrilus planipennis* Fairmaire) on different ash-dominated ecosystems in eastern North America. Forest Ecol. Manag. In review.

ABSTRACT

Although the ultimate impact of disturbances depend on several ecosystem properties (e.g., species diversity, structural diversity, species composition, landform, etc.), the ability to successfully promote forest stand health and prevent diversity losses will hinge on success in focusing limited resources and efforts towards conserving key foundational species. Unfortunately, the global transportation of pests and pathogens, depletion of natural resources, and changes in land use are all human factors that hinder this conservation. Invasion by emerald ash borer (EAB; *Agrilus planipennis* Fairmaire), an exotic pest, is one such factor disrupting natural processes and inhibiting the maintenance of ash (*Fraxinus*) species across the eastern United States. All ash species native to eastern North America are susceptible to EAB, and the continued loss of mature ash trees from forest communities will challenge our ability to conserve genetic diversity and perpetuate ash ecosystem services and functions. Many ash species are considered foundational species based on their abundance, prominent roles in specific habitat types, and impacts on ecosystem properties and processes. The goal of this project was to identify those ash-dominated community types that are most at risk in terms of having altered ecosystems following EAB invasion. Using recent data available from the U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis program (FIA), we calculated

Shannon-Wiener species diversity index values for forest communities containing each of the six ash species found in the eastern United States: white ash (*Fraxinus americana* L.), green ash (*Fraxinus pensylvanica* Marsh.), black ash (*Fraxinus nigra* Marsh.), blue ash (*Fraxinus quadrangulata* Michx.), Carolina ash (*Fraxinus caroliniana* Mill.), and pumpkin ash (*Fraxinus profunda* (Bush) Bush). Forests containing each of the six ash species differed significantly in their species diversity index values, and diversity indices varied across states for individual ash species. In addition, communities containing ashes restricted in their range by exacting microsite requirements maintained lower diversity index values as compared to communities of ash species with greater geographical ranges. Finally, forest stand cohorts (i.e., seedlings, saplings, and canopy trees) had similar species diversity indices across individual ash communities. The stand-level species diversity index values quantified for individual ash species will provide managers with additional information for prioritizing EAB control measures and restoration efforts following EAB invasions. These results suggest that individual states should focus conservation efforts on the less common ash species, which occur in communities with low diversity index values

Keywords: Diversity; Emerald Ash Borer; FIA; *Fraxinus* spp. (Oleaceae); Shannon-Weiner diversity index.

INTRODUCTION

On the precipice of earth’s sixth mass extinction, the conservation of foundational species is imperative for reducing the rate of extermination and preventing ecosystem collapse. While the reasons for many past extinctions are uncertain, humans are well documented as the driving force behind the current loss of earth’s higher eukaryotic life, and over the past two centuries the rate of human-influenced extinctions have increased exponentially (Eldridge 1998). The greatest defense against species loss is the conservation of foundational species, but the ability to identify and maintain foundational species remains problematic. Common definitions for foundational species include terms such as ecosystem engineers (Jones et al. 1994), structural species (Huston 1994), keystone predators (Paine 1992), dominant species (Grime 1984), and core species (Hanski 1982). While many terms and definitions exist, Ellison et al. (2005a) recommends Dayton's definition as it is both the oldest and potentially most applicable to forested ecosystems. According to Dayton (1972), a foundational species consists of a single species that regulates and stabilizes local conditions and modulates vital ecosystem processes, which subsequently favor and support other species in the community. Several examples of North American foundational species include the following (from Ellison et al. (2005a)): American chestnut (*Castenea dentata* (Marsh.) Borkh), mangroves (*Rhizophora* spp. L.), bald cypress (*Taxodium distichum* (L.) Rich.), Fraser fir (*Abies fraseri* (Pursh) Poir), eastern hemlock (*Tsuga canadensis* (L.) Carrière), whitebark pine (*Pinus albicaulis* Englem.), and douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Though each of these species differs greatly in their historic range and niche, they are each known to have had strong impacts on the structure of biotic communities and greatly influence local processes.

In addition to difficulties in recognizing foundational species, global transportation of pests and pathogens, depletion of natural resources, and changes in land use all disrupt natural processes and hinder our ability to maintain them. Throughout North American forests, the introduction of pests and pathogens alone has produced intense large-scale alterations of forest community structure and function (Liebhold et al. 1995; Gandhi and Herms 2010). One such event in the eastern United States was the introduction of the devastating pathogen, American chestnut blight (*Cryphonectria parasitica* (Murrill) Barr). With no apparent blight resistance, the estimated 3.5 billion American chestnut (*Castanea dentata* (Marsh.) Borkh.) trees quickly succumbed to the canker-forming blight between the years 1904 and 1940 and disappeared from American forests. Early accounts estimate that one in four trees across the eastern United States was an American chestnut (Burnham 1988). Presently, this once abundant species has been reduced to a rare, root-sprouting, understory shrub that seldom reaches a fruiting height before being top-killed by the blight. Thus, while not extinct, the functional roles of American chestnut have been lost. Additionally, the introduction of the balsam wooly adelgid (*Adelges piceae* Ratzeburg) in the 1930s has resulted in declining populations of Fraser fir. Restricted to six, high altitude regions in the southern Appalachians, the decline of Fraser fir has altered plant and animal communities and increased the susceptibility of neighboring trees such as red spruce (*Picea rubens* Sarg.) to a variety of biotic and abiotic factors (Pauley and Clebsch 1990; Hollingsworth and Hain 1991). Introduced in the mid 1980's, the hemlock woolly adelgid (*Adelges tsugae* Annand) has resulted in a nearly 100% mortality of hemlock (*Tsuga* spp) across the eastern deciduous forest (Orwig et al. 2002; Small et al. 2005). Without an ability to re-establish following the initial adelgid-induced mortality, hemlock species are predicted to disappear entirely from the eastern forests within the next couple of decades (Orwig et al. 2002). The decline in hemlock has resulted in changes in both water chemistry and hydrology, which, in turn, have produced direct and indirect changes in local plant and animal assemblages (Ellison et al. 2005b; Kizlinski et al. 2002).

While these pests and pathogens have been altering forest ecosystems of North America for some time, the more recent introduction of emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) presents new challenges for conserving biodiversity across the eastern deciduous forests. Emerald ash borer was originally identified in Detroit, Michigan and Windsor, Ontario in 2002. Inadvertently introduced from Asia, EAB has quickly spread across the eastern United States killing millions of native ash (*Fraxinus* spp) trees (Poland and McCaullough 2006). Few control efforts have proven effective in preventing the spread of this forest pest or even slowing the rate of EAB-induced tree mortality. Upon infestation and regardless of a tree's initial health, the mortality rate of mature ash trees approaches 100% in three to five years (Gandhi et al. 2008).

Six ash species are recognized across the eastern deciduous forests of North America. These include white ash (*Fraxinus americana* L.), green ash (*Fraxinus pensylvanica* Marsh.), and black ash (*Fraxinus nigra* Marsh.) as the major ash species and blue ash (*Fraxinus quadrangulata* Michx.), Carolina ash (*Fraxinus caroliniana* Mill.), and pumpkin ash (*Fraxinus profunda* (Bush) Bush) as minor ash species. The most abundant and widespread of the North American ashes are the white and green ash, and though similar in appearance, the two species differ greatly in their site requirements and forest cohorts. White ash generally inhabits moist upland and dry to mesic woodland, and though common throughout its range, white ash is rarely a component of forest stand canopies. In comparison, green ash is frequently found on mesic, poorly-drained bottomlands and along riparian corridors where it is often a major canopy component (Hardin et. al 2000; Poland and McCaullough 2006). Black ash is the third major ash and is found in nearly pure stands within deciduous swamps in the northern Great Lakes regions and Canada (Hardin et. al 2000; Tardif and Bergerson 1999). Blue ash is common within the Ohio and Upper Mississippi river valleys and is generally associated with dry, rocky, limestone uplands. Carolina ash has a more discontinuous range and is restricted to swamps, ponds, bottomlands, and coastal plain communities across the eastern and southeastern United States.

Similar to Carolina ash, pumpkin ash inhabits many of the same regions, but can also be found along streams and rivers within the Ohio and Upper Mississippi river valleys (Hardin et. al 2000; Nesom 2010a; Nesom 2010b). Though each ash species is uniquely different in forest niche, they all serve as potential hosts for EAB and face being removed from eastern forests.

All ash species native to eastern North America are believed to be susceptible to EAB. Due to the foundational roles of many ash species, continued loss of mature trees from forest communities will challenge our ability to conserve genetic diversity and maintain ecosystem services and functions. Ecologically, ash provides wildlife with shelter, browse, and seeds, which are consumed by a variety of birds, small mammals, and insects (Schlesinger 1990). The importance of ash is likely to vary across different states due to differences in factors such as forest type and climate. In several states, ash species tolerate frequent inundation in swamps, alluvial floodplains, and pond margins where stand diversity is limited. Ash species are key regulators of hydrological processes and community assembly in these systems (Ellison et al. 2005b; Slesak et al. 2014).

The over-arching goal of this project was to identify those ash-dominated community types that are most at risk in terms of altered ecosystem properties and processes following EAB invasion. To do so, we calculated Shannon-Wiener species diversity index values for communities containing each of the six ash species. Four hypotheses were also tested: 1) forests containing different ash species would differ in their species diversity index values; 2) ash restricted in their range by exacting microsite requirements would have lower diversity index values as compared to communities of ash species with greater geographical ranges; 3) forest stand cohorts (i.e., seedlings, saplings, and canopy trees) would have maintained similar species diversity index values within each individual ash community; and 4) species diversity index values would differ across states for individual ash species.

METHODS

Sampling Area

The sampling area encompassed 37 states in both the northern and southern regions of the eastern United States. These states included: Alabama, Arkansas, Connecticut, Delaware, Florida, Georgia, Indiana, Illinois, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, East Oklahoma, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, East Texas, Vermont, Virginia, West Virginia, and Wisconsin.

Inventory Data

Data inventoried were compiled by the U.S. Department of Agriculture, Forest Service, Forest Inventory and Analysis program (FIA) (http://www.fia.fs.fed.us/) (USDA 2015). Permanent inventory plots have been established across the United States to permit cyclical remeasurments of an extensive list of forest attributes. This federally funded program establishes and remeasures permanent inventory plots across the entire United States and its territories. In the East, each plot is comprised of four fixed-radius subplots (each approximately 1.68% of a hectare) and four fixed-radius microplots (each approximately 0.13% of a hectare) (O'Connell et al. 2015). In addition to stand level attributes, subplots facilitate measurements on individual trees ≥ 12.7 cm diameter breast height (DBH), while microplots include measurements on individual saplings (2.5 cm ≤ DBH < 12.7 cm) and counts of seedlings (< 2.5 cm DBH) by species. An independent sample of approximately 14-20% of a state's plots are measured annually, with an entire "cycle" of plots being inventoried every 5-7 years. Alternatively, any successive collection of plots across 5-7 years forms a complete state inventory. For this study, we compiled data for all 37 states from 2009-2013 (the most recent, common five year window before several states switched to a seven year cycle length). Data came from whole plots (i.e., plots with only one FIA condition) classified as forestland and included both live and dead trees, live saplings, and live seedlings.

Tree Species Diversity Indices

To determine seedling, sapling, and canopy species diversity indices for communities dominated by major and minor ash species, we analyzed data relevant to white, green, black, blue, pumpkin, and Carolina ash. To locate stands with sufficient ash composition (particularly the minor species), we computed large tree basal area (m^2 ha^{-1}) proportions for each species on a plot. A 10% basal area cutoff was used to ensure an adequate representation of each ash species within the sample. Species diversity index values were then determined for these communities by seedling, sapling, and canopy cohorts. In addition, species diversity indices were calculated by each ash species within each of the 37 states investigated. Bootstrapped standard errors and estimated bias were determined for each species diversity index using 10,000 iterations (Manly 2007). Statistical significance between each ash species diversity index was determined using pairwise comparisons and the Bonferroni correction. The extent of each ash species (in hectares) by state and across the region were also calculated from the data.

Though several options for calculating diversity indices exist, we selected the Shannon-Wiener diversity index methodology (Spellerberg and Fedor 2003, Nagendra 2002). This methodology has been used across an array of disciplines (e.g., Corbett et all. 2013; Reiss and

Knöncke 2005; Begossi 1996; among many others) as a measure of both a species richness and abundance within communities (Spellerberg and Fedor 2003). Using this methodology for calculating a species diversity index value, indicated as (*H'*), a proportion of each species (*i*) relative to the sum of all species (*pi*) is calculated and then multiplied by the natural logarithm of (*pi*). This product is then totaled across all species and multiplied by negative one.

$$H' = -\sum_{i=1}^{R} p_i ln p_i$$

Shannon-Wiener diversity index values can then be exponentiated to represent community diversity. In this way biodiversity can be compared across communities. The evenness or equitability, denoted (E_H), can be derived by dividing (*H'*) by (H_{max}), where (H_{max}) is equal to the natural logarithm of the total number of species (*S*) in the community. The resulting value will be between 0 and 1, with the latter value representing complete equitability or evenness within the community.

$$E_H = H'/H_{Max} = H'/ln\, S$$

RESULTS

Across the eastern United States, species diversity index values for communities containing white ash, green ash, and blue ash differed significantly in their species diversity indices from all other ash communities. Diversity index values for black ash, Carolina ash, and pumpkin ash communities did not differ significantly from each other. However, the white, green, and blue ash communities were significantly different from each of the other five ash species (Table 2.1 in Appendix). Green ash communities had the highest diversity index value of 3.478, with a standard error of 0.024, and white ash communities the second highest, with diversity index 3.341 and a standard error of 0.019. Blue ash communities had the third highest

Shannon-Wiener diversity index value of 2.951, with a standard error of 0.087. Black ash, pumpkin ash, and Carolina ash community diversity index values were 2.404, 2.247, and 2.232, with standard errors 0.027, 0.110, and 0.109, respectively. In all cases, black, blue, pumpkin, and Carolina ash communities, restricted by their narrow set of habitat requirements, had lower tree diversity index values compared to communities containing white and green ash, which had greater geographical ranges.

Species diversity index values for seedlings and saplings were maintained at approximately the same levels as canopy diversity indices for individual ash communities (Tables 2.2 and 2.3). Forests containing white ash and green ash differed significantly from one another and from all other ash communities observed. White ash and green ash community diversity index values were 3.447 and 3.656, respectively, for sapling cohorts and 3.306 and 3.570, respectively, for seedling cohorts. Within the sapling cohort, black ash diversity was calculated at 2.486, blue ash at 2.653, pumpkin ash at 1.368, and Carolina ash at 1.898. Within the seedling cohort, diversity of black ash communities was calculated at 2.451, blue ash at 2.605, pumpkin ash at 1.760, and Carolina ash at 2.021.

Calculated stand diversity indices differed across states for individual ash species. A total of 34 states contained white ash stands with a basal area of at least 10%. Relatively high white ash diversity index values were observed for states including Virginia (3.257), Mississippi (3.219), Kentucky (3.216), Tennessee (3.202), and North Carolina (3.191), while other states had relatively low species diversity index values such as Oklahoma (2.402), Connecticut (2.431), Michigan (2.471), Kansas (2.491), and Massachusetts (2.497) (Table 2.4). Similarly, green ash communities were observed in 34 states. Communities in Tennessee (3.464), Alabama (3.388), Kentucky (3.279), Missouri (3.120), and Arkansas (3.101) were observed with relatively high species diversity index values, while green ash communities in North Dakota (1.514), South Dakota (1.524), Nebraska (1.599), New York (2.339), and Kansas (2.349), had relatively low diversity index values (Table 2.5). A total of 726 plots containing black ash were reported across 12 northern states (Table 2.6). The greatest abundance of black ash was observed in Minnesota and Wisconsin, with each having a black ash community diversity index value of 2.194 and 2.371, respectively. Other notable states included Michigan (2.453), Maine (1.932), and New York (2.371). Six states reported blue ash populations, but only Tennessee and Kentucky had greater than five plots (9 and 8 plots, respectively). The diversity index values for blue ash communities in these two states were similar, with Tennessee at 2.592 and Kentucky at 2.834 (Table 2.7). Florida claimed 15 of the 19 plots across five states that contained pumpkin ash communities, with a diversity index of 2.038 (Table 2.8). Similarly, 12 of the 13 plots with Carolina ash communities were also located in Florida and had a community diversity index value of 2.202 (Table 2.9).

DISCUSSION AND CONCLUSION

Ash-dominated communities are declining from EAB infestations across the eastern United States. Although impairment of these communities related to reduced diversity is a concern, few projects have investigated the diversity of eastern North American ash communities. This study was designed to elucidate which ash communities will experience the greatest impacts related to diversity loss associated with EAB invasion. Overall, the results from this study failed to reject the hypotheses that 1) forests containing different ash species will differ in their species diversity index values; 2) ash restricted in their range by exacting microsite requirements will have lower diversity index values as compared to communities of ash species with greater geographical ranges; 3) forest stand cohorts (i.e., seedlings, saplings, and canopy trees) would maintain similar species diversity index values within each individual ash communities; and 4) species diversity index values would vary across states for individual ash species.

Canopy diversity within white and green ash communities was three times greater than the diversity of black, pumpkin, and Carolina ash communities, and nearly two times greater than the diversity of blue ash communities. This greater diversity in white and green ash communities should impart greater resiliency to disturbance and overall diversity loss. Arguably, the greater the number of coexisting species, the greater the propensity for those ashes to be replaced with other species, thereby maintaining comparable ecosystem services and processes. Past studies have reported that forest stands with greater diversity and structural heterogeneity tend to be more impervious to pest disturbance than stands with homogenous structure and composition. One such study reported a reduced defoliation by the Asian chestnut gall wasp (*Dryocosmus kuriphilus*) in chestnut stands that had greater diversity in composition and structure (Guyot et al. 2015). Also, the loss of white and green ash will have significant economic consequences (i.e., loss of white and green ash forest products), whereas the innately low species diversity in blue, black, pumpkin, and Carolina ash communities may have greater ecological consequences. Several studies have hypothesized the direct and indirect implications of widespread tree mortalities caused by foreign pests. Gandhi and Herms (2010) outlined several potential impacts alien insect infestations may exert on the structure, function, and composition of native forest ecosystems. These include altered dynamics in gap formation, biogeochemical cycling, coarse woody debris, and ecological interactions among trees and terrestrial and aquatic organisms. These alterations have been known to cause cascading effects throughout biological processes, and across trophic levels.

In addition, for the bottomland ash species, changes in stand level transpiration rates resulting from EAB-induced ash mortality and experimental cutting treatments have altered hydrological processes (Slesak et. al 2014; Dubé et. al 1995). In general, sites become increasingly inundated as water tables rise. Consequently, this hinders the ability to successfully regenerate a new stand cohort and threatens niche-specific species that exist only within these ecosystems. Slesak et al. (2014) proposed the proactive approach of implementing management strategies prior to EAB infestation that will mitigate changes in hydrology, thus maintaining ecosystem functions and processes. One such approach is a silvicultural prescription where group selection cuts are combined with the artificial planting of non-ash species. Though a valid prescription, more research is needed, and quickly, to identify which ash alternatives will provide the greatest ecological and economic benefits within these stands.

The low tree diversity index values across seedling, sapling, and canopy cohorts for communities containing black, pumpkin, and Carolina ash provides evidence for the limited number of native, alternative species available for these ash species adapted to such a narrow range of microsite conditions. In a study quantifying the relative regeneration potential across forest types for each of these six ash species, ash seedlings and saplings were typically identified as being the most abundant sources of regeneration (Granger et. al 2017). If biological control measures can be identified and implemented across the landscape, alternative silvicultural treatments that facilitate the advancement of natural ash regeneration may prove to be the most cost-effective and ecologically beneficial. The option of introducing exotic hardwood species also exists, but this practice may present additional challenges requiring further investigation.

After comparing and contrasting species diversity index values across states for individual ash species, it is possible to suggest critical areas for conservation and restoration. The highest priority states are those that contain significant populations of ash species that require more exacting microsite conditions (i.e., blue, black, pumpkin, and Carolina). For example, forests containing blue ash was identified in six states, but the majority of the population was contained within Kentucky and Tennessee. Although these states receive significant economic returns from harvesting white and green ash, this financial incentive for conservation must be balanced with the long-term need for conserving the species diversity connected with blue ash communities. After prioritizing blue ash, the high diversity index values for white and green ash stands (in Tennessee and Kentucky) suggest silvicultural prescriptions can be implemented that promote regeneration of new stands comprised of economically and ecologically desirable ash alternatives (e.g., oaks, hickories, yellow-poplar, sugar maples, etc.). The restoration of white and green ash may follow later, as biological control options are identified and become more economical.

The majority of black ash stands across the north have been impacted by EAB. Therefore, efforts to preserve this species and the ecosystem services and functions it provides will largely be restorative. Black ash restoration in northern states such as Minnesota, Wisconsin, Michigan, Maine, and New York will be imperative to the success of black ash dominated communities and the plants and animals that depend on black ash for their survival.

Florida was found to contain the bulk (in terms of acreage) of both pumpkin and Carolina ash. The relatively high acreage, coupled with low diversity index values for these two species, presents an opportunity to proactively establish methods to mitigate EAB impacts within these wetland ecosystems. This represents a unique opportunity, as EAB has yet to be recorded in

Florida. In addition, the need to determine genetic diversity within populations of pumpkin and Carolina ash and conserve genetic material (e.g., seeds, seedlings, etc.) should be a focus not only in Florida, but also in neighboring states that contain isolated populations (e.g., Alabama, Illinois, Indiana, Missouri, and Texas).

White ash and green ash conservation and restoration efforts should be the focus in states that do not contain significant populations of black, pumpkin, blue, and/or Carolina ash. For example, white ash could be a conservation focus in states such as Virginia, Mississippi, North Carolina. Green ash conservation could be the focus in Alabama, Missouri, Arkansas, Nebraska, Kansas, North Dakota, South Dakota, etc. If EAB control measures cannot be identified then many states containing either large ash populations or maintaining low diversity index values may need to identify and establish alternative species.

The stand-level species diversity index values for individual ash species presented will provide a baseline for determining EAB impacts on forest ecosystems in the future. Also, these results are intended to aid conservationists in deciding where EAB control measures should be concentrated and where restoration efforts should be focused in EAB decimated forest stands. While disturbance effects are dependent on several ecosystem components (e.g., species diversity, structural diversity, species composition, landform, etc.), the ability to successfully promote forest stand health and prevent further diversity losses will hinge on our success in focusing limited resources and efforts on individual ash species and areas most impacted by EAB.

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APPENDIX

Table 2.1. Canopy diversity indices for major and minor ash species across the eastern United States. Only those stands containing at least 10% basal area in canopy trees of the specified ash species were included.

Species Name	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity $\exp(H')$	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors	
F. americana	3,847,595	1,846	146	3.341	28.247	0.670	0.019	A[1]
F. pennsylvanica	2,763,911	1,222	155	3.478	32.395	0.690	0.024	B
F. nigra	1,051,917	726	62	2.404	11.067	0.582	0.027	C
F. quadrangulata	58,975	25	44	2.951	19.125	0.780	0.087	D
F. profunda	45,308	19	32	2.247	9.459	0.648	0.110	CE
F. caroliniana	31,429	13	25	2.232	9.318	0.693	0.109	CE

[1] Shannon-Wiener index values with the same letter do not differ statistically at $\alpha = 0.05$ (Bonferroni adjusted).

Table 2.2. Sapling diversity indices for major and minor ash species across the eastern United States. Only those stands containing at least 10% basal area in canopy trees of the specified ash species were included.

Species Name	Plots Sampled	Species Present (S) In Sapling	Shannon Diversity Index (H') For Sapling	Sapling Diversity exp(H')	Shannon's Equitability (E_H) For Sapling	Boot-strap Standard Errors	
Fraxinus americana	1686	84	3.447	31.408	0.778	0.027	A[1]
Fraxinus pennsylvanica	1063	87	3.656	38.724	0.81	0.035	B
Fraxinus nigra	681	43	2.486	12.013	0.661	0.043	C
Fraxinus quadrangulata	22	23	2.653	14.203	0.846	0.160	C
Fraxinus profunda	14	11	1.368	3.928	0.571	0.236	D
Fraxinus caroliniana	13	13	1.898	6.672	0.740	0.195	CD

[1] Shannon-Wiener index values with the same letter do not differ statistically at $\alpha = 0.05$ (Bonferroni adjusted).

Table 2.3. Seedling diversity indices for major and minor ash species across the eastern United States. Only those stands containing at least 10% basal area in canopy trees of the specified ash species were included.

Species Name	Plots Sampled	Species Present (S) In Seedling	Shannon Diversity Index (H') In Seedling	Seedling Diversity exp(H')	Shannon's Equitability (E_H) For Seedling	Boot-strap Standard Errors	
Fraxinus americana	1765	100	3.306	27.286	0.718	0.029	A[1]
Fraxinus pennsylvanica	1110	119	3.570	35.530	0.747	0.042	B
Fraxinus nigra	692	47	2.451	11.604	0.637	0.047	C
Fraxinus quadrangulata	24	36	2.605	13.531	0.727	0.108	CE
Fraxinus profunda	16	17	1.760	5.813	0.621	0.388	CEF
Fraxinus caroliniana	11	11	2.021	7.546	0.843	0.167	DEF

[1] Shannon-Wiener index values with the same letter do not differ statistically at $\alpha = 0.05$ (Bonferroni adjusted).

Table 2.4. White ash canopy diversity indices for the eastern United States. Only those stands containing at least 10% basal area in white ash canopy trees were included.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Alabama	38,780	17	41	2.832	16.978	0.414	0.171
Arkansas	68,614	28	47	3.183	24.131	0.513	0.086
Connecticut	36,865	13	24	2.431	11.370	0.474	0.101
Florida	4,751	2	11	2.077	7.977	0.725	0.273
Georgia	4,685	2	12	2.083	8.029	0.669	0.181
Illinois	73,837	25	46	3.108	22.387	0.487	0.084
Indiana	158,856	109	61	3.160	23.559	0.386	0.047
Iowa	37,199	15	26	2.826	16.872	0.649	0.107
Kansas	19,819	7	21	2.491	12.075	0.575	0.101
Kentucky	236,445	98	58	3.216	24.919	0.430	0.049

Table 2.4. Continued.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Louisiana	4,894	2	13	2.352	10.503	0.808	0.222
Maine	254,045	106	27	2.562	12.962	0.480	0.032
Maryland	21,817	8	33	2.858	17.424	0.528	0.191
Massachusetts	63,040	23	28	2.497	12.145	0.434	0.078
Michigan	170,034	68	40	2.471	11.835	0.296	0.103
Minnesota	1,457	1	7	1.784	5.956	0.851	0.000
Mississippi	23,795	11	41	3.219	25.001	0.610	0.151
Missouri	151,894	61	45	3.032	20.739	0.461	0.062
New Hampshire	101,617	45	33	2.519	12.422	0.376	0.052
New Jersey	77,671	28	39	2.853	17.344	0.445	0.054
New York	856,561	306	70	2.707	14.991	0.214	0.036

Table 2.4. Continued.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
North Carolina	43,174	18	43	3.191	24.313	0.565	0.097
Ohio	271,788	107	63	3.136	23.021	0.365	0.052
Oklahoma	27,264	11	21	2.402	11.049	0.526	0.107
Pennsylvania	76	189	57	2.791	16.302	0.286	0.046
Rhode Island	3,002	2	10	1.961	7.110	0.711	0.101
South Carolina	9,842	4	24	2.795	16.357	0.682	0.205
Tennessee	186,644	79	61	3.203	24.595	0.403	0.071
Texas	26,729	11	24	2.603	13.498	0.562	0.127
Vermont	207,573	88	37	2.578	13.165	0.356	0.074
Virginia	160,770	78	67	3.257	25.968	0.388	0.060
West Virginia	270,919	98	57	3.122	22.697	0.398	0.048

Table 2.4. Continued

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Wisconsin	233,135	186	43	2.516	12.377	0.288	0.052

Table 2.5. Green ash canopy diversity indices for the eastern United States. Only those stands containing at least 10% basal area in green ash canopy trees were included.

State	Estimated Area (ha)	Plots Sampled	Species Present (*S*) In Canopy	Shannon Diversity Index (*H'*) For Canopy	Canopy Diversity exp(*H'*)	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Alabama	84,178	35	57	3.388	29.619	0.520	0.082
Arkansas	178,205	72	60	3.101	22.219	0.370	0.078
Delaware	2,698	2	10	1.668	5.301	0.530	0.145
Florida	70,854	30	41	2.462	11.729	0.286	0.089
Georgia	109,452	48	59	3.061	21.358	0.362	0.086
Illinois	121,426	46	49	2.946	19.038	0.389	0.116
Indiana	39,607	26	44	3.029	20.671	0.470	0.098
Iowa	53,364	19	25	2.508	12.285	0.491	0.139
Kansas	47,762	17	25	2.349	10.472	0.419	0.099
Kentucky	138,839	58	64	3.279	26.560	0.415	0.059

Table 2.5. Continued.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity $\exp(H')$	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Louisiana	228,513	89	48	2.801	16.467	0.343	0.056
Maine	5,081	2	15	2.386	10.868	0.725	0.192
Maryland	4,775	2	10	1.779	5.924	0.592	0.428
Michigan	288,762	104	54	2.654	14.210	0.263	0.060
Minnesota	151,322	117	41	2.548	12.779	0.312	0.065
Mississippi	140,381	62	57	3.015	20.396	0.358	0.090
Missouri	55,382	22	44	3.120	22.641	0.515	0.130
Nebraska	52,999	21	18	1.599	4.946	0.275	0.151
New Jersey	2,753	1	6	1.709	5.522	0.920	0.000
New York	122,334	43	37	2.339	10.368	0.280	0.114
North Carolina	66,632	28	41	2.472	11.844	0.289	0.099

Table 2.5. Continued.

State	Estimated Area (ha)	Plots Sampled	Species Present (*S*) In Canopy	Shannon Diversity Index (*H'*) For Canopy	Canopy Diversity exp(*H'*)	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
North Dakota	88,567	36	13	1.514	4.545	0.350	0.090
Ohio	81,038	31	48	3.041	20.918	0.436	0.099
Oklahoma	59,697	24	40	2.611	13.619	0.340	0.129
Pennsylvania	12,387	4	13	2.203	9.055	0.697	0.330
South Carolina	72,111	32	47	2.761	15.821	0.337	0.084
South Dakota	27,721	10	9	1.524	4.591	0.510	0.182
Tennessee	147,115	60	73	3.464	31.950	0.438	0.062
Texas	122,144	52	57	2.834	17.005	0.298	0.108
Vermont	2,744	1	7	1.615	5.029	0.718	0.000
Virginia	54,390	26	52	2.806	16.549	0.318	0.156
West Virginia	3,508	1	11	2.139	8.492	0.772	0.000

Table 2.5. Continued.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Wisconsin	127,170	101	41	2.537	12.646	0.308	0.072

Table 2.6. Black ash canopy diversity indices for the eastern United States. Only those stands containing at least 10% basal area in black ash canopy trees were included.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Indiana	2,851	2	11	2.100	8.163	0.742	0.401
Iowa	2,990	1	7	1.810	6.107	0.872	0.000
Maine	51,514	21	21	1.937	6.939	0.330	0.134
Maryland	2,025	1	6	1.677	5.348	0.891	0.000
Michigan	179,901	82	36	2.453	11.618	0.323	0.058
Minnesota	434,338	343	35	2.194	8.967	0.256	0.041
New Hampshire	2,258	1	2	0.655	1.926	0.963	0.000
New York	44,055	17	23	2.273	9.707	0.422	0.154
Ohio	2,805	1	4	1.340	3.818	0.954	0.000
Pennsylvania	3,437	2	6	1.137	3.118	0.520	0.557

Table 2.6. Continued.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Vermont	5,205	2	8	1.590	4.903	0.613	0.170
Wisconsin	320,538	253	41	2.371	10.712	0.261	0.040

Table 2.7. Blue ash canopy diversity indices for the eastern United States. Only those stands containing at least 10% basal area in blue ash canopy trees were included.

State	Estimated Area (ha)	Plots Sampled	Species Present (*S*) In Canopy	Shannon Diversity Index (*H'*) For Canopy	Canopy Diversity exp(*H'*)	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Indiana	3,079	2	12	2.167	8.731	0.728	0.231
Kentucky	18,986	8	31	2.834	17.009	0.549	0.126
Missouri	7,943	3	15	2.382	10.828	0.722	0.216
Ohio	5,070	2	10	1.660	5.262	0.526	0.225
Tennessee	21,460	9	28	2.592	13.350	0.477	0.167
Virginia	2,437	1	13	2.289	9.867	0.759	0.000

Table 2.8. Pumpkin ash canopy diversity indices for the eastern United States. Only those stands containing at least 10% basal area in pumpkin ash canopy trees were included.

State	Estimated Area (ha)	Plots Sampled	Species Present (*S*) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Alabama	2,562	1	8	1.636	5.135	0.642	0.000
Florida	35,732	15	19	2.038	7.672	0.404	0.078
Illinois	2,440	1	4	1.127	3.086	0.772	0.000
Indiana	1,604	1	10	2.059	7.841	0.784	0.000
Missouri	2,969	1	6	1.339	3.817	0.636	0.000

Table 2.9. Carolina ash canopy diversity indices for the eastern United States. Only those stands containing at least 10% basal area in Carolina ash canopy trees were included.

State	Estimated Area (ha)	Plots Sampled	Species Present (S) In Canopy	Shannon Diversity Index (H') For Canopy	Canopy Diversity exp(H')	Shannon's Equitability (E_H) For Canopy	Boot-strap Standard Errors
Florida	28,999	12	21	2.202	9.047	0.431	0.115
Texas	2,430	1	6	1.356	3.879	0.647	0.000

CHAPTER III

MICROSITES SUPPORTING ENDEMIC POPULATIONS OF MOUNTAIN STEWARTIA (*STEWARTIA OVATA*) IN EAST TENNESSEE

This chapter was originally published by Joshua J. Granger, David S. Buckley, and John M. Zobel:

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ABSTRACT

Mountain stewartia (*Stewartia ovata* (Cav.) Weatherby) is the only member of the family *Theaceae* endemic to Tennessee. Apart from the physical description and rarity of stewartia, little is known about this woody understory species. Populations and range descriptions are founded on longstanding accounts, and microsite descriptions are limited in detail. Based on this scarcity in nature and the literature, we quantified microsites supporting populations of stewartia across East Tennessee and examined the hypothesis that specific site requirements, rather than any other factor, limit the distribution and abundance of stewartia within its natural range. Five populations of stewartia were inventoried across four counties in East Tennessee. Stewartia averaged 7.40 stems per population with a mean height of 2.46m. Soils included Jefferson-Varilla-Schelocta, Ranger-Channery-Silt Loam, Giplin-Bouldin-Petros, and Giplin-Petros. These cobbly loam soils are strongly acidic, highly permeable, well drained, and are associated with steep slopes and higher elevations. Soil analysis indicated relatively low amounts of phosphorus, potassium, calcium, and magnesium. A dense overstory comprised primarily of relatively large diameter sourwoods (*Oxydendrum arboreum*), eastern hemlocks (*Tsuga candensis*), white oaks (*Quercus alba*), eastern white pines (*Pinus strobus*), red maples (*Acer rubrum*), and mockernut hickories (*Carya tomentosa*) resulted in a low percent full PAR of 7.05%. Midstory and understory species were dominated primarily by eastern white pine, red maple, and eastern hemlock. Quantification of stand-level conditions in extant stewartia populations indicates that site conditions may be the limiting factor in the distribution and abundance of stewartia. Further investigations of stewartia habitat requirements, geographical distribution, population stability, adaptability, ecosystem function, and phenotypic variability will be key to conserving this species.

Keywords: Conservation; Microsite factors; Mountain stewartia; *Stewartia ovata* (Cav.) Weatherby; *Theaceae*.

INTRODUCTION

Summer dogwood, mountain camellia, or mountain stewartia (*Stewartia ovata* (Cav.) Weatherby) is a small tree or shrub endemic to the southeastern United States (Baldwin 1969). Rare in both abundance and occurrence, this species is more frequently encountered (based upon past herbarium records) within the mountains and Piedmont, with the highest concentration of specimens occurring in south-central Tennessee, northern Georgia, and Alabama (Kobuski 1951). A few widely scattered and minute populations are also known to exist within south central Kentucky, North Carolina, South Carolina, Mississippi, and Virginia (Figure 3.1 in Appendix). Records to date indicate that it inhabits wooded ravines between 300 and 800m on slopes along creeks and streams (Stupka 1964; Radford 1968; Swanson 1994).

Mountain stewartia is one of two native species of stewartia and one of four species representing the family *Theaceae* in North America (Price 2009). Mountain stewartia typically grows into a small tree or large shrub approximately five meters in height with a horizontally layered and rounded crown. Young wood is smooth, reddish brown and old wood (i.e., boles and larger limbs) is light brown to tan with longitudinally fissured bark. Leaves are deciduous, membranaceous, widely elliptical to ovate, 4-6cm wide and 8-12cm long, acuminate at the tip and rounded to cuneate at the base. Upper leaf surfaces are dark green and glabrous, while lower surfaces are grayish-green and slightly pubescent. Leaf margins are ciliated, slightly serrulate, with 5-7 pairs of conspicuous veins. Petioles are 3-15mm long, pubescent, and typically widen at the base (Figure 3.2). One winter bud scale is enclosed by the petiole wings, between 2-5mm in length, compressed, and densely covered in silvery hairs. Flowers appear in June-July with seeds ripening September to October (Kirkman, et. al 2007). Flowers are solitary, axillary, and held above limbs on a 5 mm long pedicel. Bracteoles are five millimeters wide and 10-12mm long, five in number, and pubescent. The five Calyx-lobes average 20mm long and five millimeters wide and are imbricate, ciliate along margin, pubescent on exterior portions, and resemble leaves. Petals are five in number, white, obovate, 2-4cm long, 2-3cm wide, and are crenulated along outer margins. Stamens are numerous, 18-20cm long, glabrous, and vary in color from white to yellow to purple. Anthers are typically orange (Figure 3.2). Ovaries are five-celled, globose, 4-5mm wide, and densely pubescent with silvery hairs. The fruit capsule is ovoid, woody, sharply pointed, five-celled, and densely pubescent. Seeds are dull brown to red in color, narrowly winged along the margins, approximately 7mm in diameter, and flattened overall (Kobuski 1951; Swanson, 1994; Kirkman, et. al 2007)

Commercially, this species is desirable for its ornamental and showy white flowers and for its orange to red autumn leaf color. However, due to propagation difficulties and specific site requirements, most horticulturalists favor oriental stewartias, which are more adaptable and hardier than their American counterparts (Kirkman, et. al 2007). Dirr (2011), a leading expert in gardening and landscaping with trees, mentioned his admiration for the mountain stewartia and its close relative, silky stewartia (*Stewartia malacodendron* L.). Unfortunately, Dirr (2011) has found that both species are challenging to grow and, to date, each of his attempts with these native stewartias have failed. An extensive search by the lead author revealed no available sources for mountain stewartia material (i.e., seeds, bare root seedlings, potted seedlings, cuttings, etc.). In several cases, greenhouses owners communicated their previous attempts at growing stewartia, but further mentioned discontinuing the species due to its difficulty in propagation and limited establishment success.

Aside from physical descriptions, little is known about mountain stewartia. Populations and ranges are based primarily on longstanding accounts, and microsite descriptions are limited in detail. A large knowledge gap in mountain stewartia habitat requirements, geographical distribution, population stability, adaptability, ecosystem function, and phenotypic variability provides a rich area for further research needed to aid conservation. Based on mountain stewartia's scarcity in nature and the literature, our main objectives were to 1) quantify microsites supporting populations of mountain stewartia in East Tennessee and 2) examine the hypothesis that specific site requirements, rather than any other factor, limit the distribution and abundance of this species across its natural range. The quantification of stand-level conditions for extant mountain stewartia populations will function as a baseline for understanding the habitat requirements of this endemic and rare forest species. Results will assist botanists, conservationists, and plant enthusiasts in pinpointing additional locations likely to support populations of mountain stewartia in the Southeast. In addition, habitat information gained in the project will allow horticulturalists and arborists to successfully improve techniques for establishing mountain stewartia in arboretums and private plantings.

METHODS

Sampling Area

Sampled stewartia populations included privately owned stands within Rhea, Roane, Monroe, and Morgan Counties, Tennessee. Each site sampled contained naturally established and mature flowering mountain stewartia. Data collection began September 17th and concluded October 31st, 2016. GPS coordinates, aspect, elevation, distance from streambed center, and percent slope were all recorded.

Vegetation Sampling

At each mountain stewartia stand, the largest specimen was designated as the central reference point for all stand measurements. A 10m-fixed radius plot was established for sampling the overstory (Figure 3.3a), with the largest stewartia at plot center. All trees greater than 10cm at diameter breast height (DBH) (1.37 m above ground) were inventoried throughout the plot. Tree measurements included DBH, height, distance, and azimuth from plot center. All mountain stewartia (regardless of size) were inventoried throughout the plot.

A 5m-fixed radius plot (Figure 3.3b) was nested within each 10m plot to sample middlestory stems (i.e., woody plants equal to or greater than one meter in heigth, but less than 10cm DBH). For each stem, root collar diameters, heights, DBH when available, and distance and azimuth from central point were measured.

Small woody stems < one meter tall and understory vegetation were sampled using five, one meter square quadrats (Figure 3.3c). Sample one was located around the central reference mountain stewartia. The four remaining quadrats were established at five meter distances from the center point in the four cardinal directions. Within each quadrat, all understory herbaceous plants and woody material were identified and percent cover was estimated.

Light Sampling

Percent canopy cover and photosynthetically active radiation (PAR) were both measured to provide an index of light available to sampled stewartia stands. Percent canopy cover was quantified at eight locations within the 10m-fixed plot using a model-C spherical densitometer held one meter above the ground (Figure 3.3d). Four points were measured at the same location as understory vegetation samples two through five. The four remaining points were offset 45^o from the previous four measurements and established 10m from plot center along the outer boundary of the plot. At each of the eight sampling points, one measurement was taken in each of the four cardinal directions, and these were averaged to provide one estimate.

A total of 12 PAR measurements were taken one meter above the ground and averaged for each stand using an AccuPAR Linear PAR/LAI ceptometer, model PAR-80 (Figure 3.3e). These measurements were taken within a one-hour window centered around solar noon at the eight locations described above for the canopy closure measurements. Four additional measurements were recorded along the outer boundary of the plot, in line with the understory sampling sites. Ambient light measurements were recorded within adjacent canopy openings, under full sun, as each stewartia stand was sampled. These measurements were used to calculate relative percent full PAR.

Soil Sampling

A 2.54cm diameter soil probe was used to extract a total of five soil samples at each inventoried stand (Figure 3.3f). One sample was taken at the base of the largest mountain stewartia (i.e., plot center used in overstory sampling). Four other samples were taken utilizing the same locations as the understory sampling described above. The organic and mineral soil horizons were measured for thickness and recorded before combining into one sample. The

Agricultural Service Laboratories in Clemson, South Carolina tested each soil sample for available phosphorus (P), exchangeable potassium (K), magnesium (Mg), calcium (Ca), hydrogen (H), soil pH, cation exchange capacity, and percent base saturation of cation elements sodium (Na), zinc (Zn), boron (B), and copper (Cu).

Statistical Analysis

Microsite descriptions were created for each stand sampled. Means and confidence intervals were determined for individual variables and significant differences between stands were checked at $\alpha = 0.05$ level of significance.

RESULTS

A total of five mountain stewartia populations were identified within Rhea, Roane, Monroe, and Morgan counties in eastern Tennessee. Stewartia stems within these populations were calculated to have a mean height of 2.46m, a mean dbh of 1.33cm, and a mean root-collar diameter of 1.97cm (Table 3.1). Populations averaged 7.40 stems per population, with a mean of 2.42m between individual plants. A heavy canopy cover resulted in a reduced mean relative PAR of 7.05%. Mean aspect, elevation, and slope were 160.80°, 328.332m, and 18.20%, respectively (Table 3.2). Populations were found at an average of 51.35m upslope of intermittent streams and approximately 16.53m from nearby roads and trails (i.e., ATV trails, logging roads, walking paths, and equestrian riding trails).

Soil maps provided by the United States Department of Agriculture confirmed a variety of soil complexes across sample sites. These soil complexes included Jefferson-Varilla-Schelocta (JvF), Ranger-Channery-Silt Loam (RgF), Giplin-Bouldin-Petros (GsF), and Giplin-Petros (GpF). Overall, these complexes are highly acidic, permeable, well-drained, cobbly loam soils that are typical of steep slopes and higher elevations across eastern Tennessee (Table 3.3). The mean percent exposed soils within these sites was estimated at 7.50%, with herbaceous and understory woody plants covering approximately 25.45% (Table 3.2). The remaining 67.05% of the site surface area was comprised of fallen leaf litter and overstory and midstory stems. The mean depth of organic matter was calculated at 3.56cm. Soil horizon A measured 4.96cm deep, and soil horizon E averaged 8.47cm in depth. Laboratory analysis of collected soil samples indicated an average percent organic matter of 6.82%. Soil pH was found to be 4.70 (Table 3.2). Soil nutrients such as P, K, Ca, and Mg were at relatively low abundances, while Zn, Mn, Cu, and B were at relatively sufficient levels (Table 3.2).

Sourwood, eastern hemlock, white oak, eastern white pine, red maple, and mockernut hickory comprised the majority of stems recorded in the overstory of stewartia plots (Table 3.4). In total, 12 of 19 species were inventoried with greater than 1.00% of stem frequency (Figure 3.4). The mean basal area of overstory trees was calculated at 35.15m^2/ha, with a mean canopy cover of 96.54% (Table 3.2). Stand diameters were recorded with an average of 23.78cm (Table 3.4). Max diameters ranged from eastern white pine at 81.50cm to sourwood at 18.50cm. Relatively large max diameters were also measured for species such as American beech (53.80cm), yellow-poplar (58.80cm), eastern hemlock (45.70cm), white oak (43.20cm), and sweetgum (41.80cm). Clear overstory stem heights, from the ground to first main lateral branch, averaged 5.97m of clean bole (Table 3.5). Max clear stem heights were greater than 10m for mockernut hickory, yellow-poplar, sourwood, shortleaf pine, eastern white pine, and white oak. Total tree heights averaged 14.76m (Table 3.6). Eastern white pine and eastern hemlock had the greatest max heights of 27.36m and 25.95m, respectively. In addition, eastern white pine comprised the greatest relative proportion of basal area within these stewartia populations at 21.08%. Hemlock had the second highest relative basal area at 13.23%, followed by white oak at

132.96%. In total, 12 species were recorded with greater than 1.00% of stand basal area (Figure 3.4).

The most frequently recorded species within midstory sample plots were eastern white pine, mountain stewartia, and red maple, with relative stem proportions at 19.09%, 16.36%, and 12.33%, respectively. In total, 16 out of 26 species were recorded with greater than 1.00% frequency (Figure 3.5). Many of the inventoried species included shrubs such as blueberry, viburnum, buffalo nut, and mountain laurel. Root-collar diameters were calculated with a mean of 2.53cm for all midstory trees sampled. Max root-collar diameters ranged from 1.84cm for maple leaf viburnum to 10.10cm for eastern hemlock. Other max root-collar diameters greater than 8.00cm were measured for American beech, black gum, eastern white pine, and white oak (Table 3.7). Total midstory tree heights averaged 2.51m, with the two most abundant species, eastern white pine and red maple, measuring at 1.66m and 2.52m, respectively. Species with a greater mean height than stewartia at (> 2.46m) included black birch at (3.16m), American beech at (3.24m), bigleaf magnolia at (3.13m), black gum at (3.89m), sourwood at (3.33m), and white oak at (3.63m) (Table 3.8).

A total of 34 species were inventoried within understory plots, including four stems of mountain stewartia. These stewartia were found to have a mean root-collar diameter of 0.29cm and a mean height of 0.23m. The species with the greatest abundance in understory plots were eastern white pine at 23.78%, red maple at 12.66%, and eastern hemlock and white oak, both at 6.29% (Figure 3.6). Mean root-collar diameters measured 0.311cm for eastern white pine, 0.24cm for red maple, 0.20cm for eastern hemlock, and 0.33cm for white oak (Table 3.9). Mean heights for these species were 0.27m for eastern white pine, 0.22m for red maple, 0.17m for eastern hemlock, and 0.26m for white oak (Table 3.10)

DISCUSSION AND CONCLUSION

The principle objective of this project was to quantify microsites supporting populations of mountain stewartia in East Tennessee and use that information to examine the hypothesis that specific site requirements, rather than some other factor, limit the distribution and abundance of this species across its natural range. The evidence acquired through our microsite measurements suggests that stewartia is indeed restricted by niche requirements and less by dispersal mechanisms. Across inventoried sites, stewartia was found consistently under closed canopy stands primarily stocked with relatively large eastern hemlocks, eastern white pines, white oaks, red maples, and hickories. The presence of large conifer snags, heavy woody debris, and large diameter eastern hemlocks and eastern white pines indicate stands with characteristics typical of old-growth, low-disturbance forests. Although soil complexes varied across plots, all soils shared similar properties (i.e., low soil pH, low nutrient availability, rockiness, quick drainage, and high permeability). The cobbly, well-drained, and highly permeable loam soils minimize water retention and maximize gas exchange within the upper soil horizons. In addition, many conifer species such as eastern white pine and eastern hemlock have densely layered canopies capable of intercepting a greater proportion of light than hardwood counterparts such as oaks, maples, hickories, and tulip poplars. This reduction in light lowers the availability of understory PAR and reduces forest floor temperatures. Lower forest floor temperatures decrease the rate of litter decomposition and allows for a greater buildup of organic matter (Crawford, Jeffree, and Rees 2003). Furthermore, the foliage of these conifer species has a lower base cation concentration compared to the foliage of hardwoods. This lower cation concentration is responsible for the acidification of upper soil horizons among many forest soil complexes (Brantberg et al. 2000). At higher acidity, nutrient cycling rates tend to slow and create soils with poor nutrient availabilities (Jenkins et al. 1999). Several authors have reported higher carbon/nitrogen ratios associated with conifer stands and mixed stands compared to stands with a greater proportion of hardwoods, due to the acidification of soils and reduced decomposition rates (Brown 1982; Whitney and Foster 1988; Augusto et al. 2003). Lastly, these sites were positioned on relatively steep slopes that accelerate the drainage of these areas following precipitation events, thus reducing the water-holding capacity of these sites.

Though dispersal mechanisms remain largely unknown, stewartia appears to inhabit a narrow range of site requirements in East Tennessee. This evidence supports the hypotheses that specific site requirements, rather than dispersal mechanisms, limit stewartia distribution and abundance. While further investigation into stewartia dispersal mechanisms is warranted, identification and sampling of sites similar to those studied in this project may lead to documentation of new stewartia populations and provide further support of the site limiting factor hypothesis.

One area of concern for the conservation of mountain stewartia populations pertains to its close association with eastern hemlock. Hemlocks are well documented as one of the most significant long-lived, shade-tolerant conifers in the eastern United States. Their dense structure and slow litter decomposition rates produce microsites that are characteristically more acidic, cool, and damp compared with other forest counterparts. The functional loss of native hemlocks through adelgid-induced mortality in eastern United States forests, over the course of the following decades, may produce adverse microsite conditions for extant stewartia populations. Orwig et al. (2002) reported that with the lack of hemlock recruitment into adeldig-infested stands, the majority of hemlocks are being replaced by hardwood species, primarily maples (*Acer* spp.), birches (*Betula* spp.), and oaks (*Quercus* spp.). Vose et al. (unpublished) found yellow-poplar (*Liriodendron tulipifera*) and *Rhododendron* spp. to be significant replacement species in southern forests. This transition from hemlock to hardwood stands will alter several forest processes. This includes changes in hydrology, soil temperatures, light regimes, soil pH, nutrient availability, and stand competition, among others.

Aside from the risks associated with the loss of eastern hemlock, it is largely unclear how stewartia competes for resources within midstory and understory canopies. The majority of these canopies in this project were comprised of red maple and eastern white pine. The large overstory crowns, formed by a lack of low lateral branching, have created stands with relatively high-vaulted canopies. This has created sufficient space for the development of midstory and understory canopies and may be a necessary component for stewartia success. The lower branching of young red maple and eastern white pine seedlings and saplings may produce a resource bottleneck as these maples and pines grow into the overstory canopy. However, further investigation into this matter is needed.

The ability to accurately age stewartia stands would provide insight into site conditions responsible for the initial establishment of these extant stewartia populations. However, extant stewartia populations in East Tennessee are mainly the result of clonal root sprouts from older established root systems and from larger diameter decaying stumps, thus making it difficult to accurately determine the initiation period of these stands. The relatively small heights and diameters of red maple compared to many of the overstory species are indicative of a younger and more recently introduced cohort in these stands. The frequency and intensity of past fire regimes have often been acknowledged for preventing fire-intolerant species (i.e., red maple and American beech) and small diameter tree samplings from establishing across the landscape (Lorimer 1984; Abrams 1992; Abrams 1998). They have also been credited for the development and maintenance of oak and pine forest types across the eastern United States. The stands inventoried in this project could accurately be classified as an oak and pine forest type, based on the relatively high proportion of oak and pine basal area within these stands. The ability of low-intensity fires to remove understory and midstory competition, coupled with mountain stewartia's ability to clonally root sprout, may be an indication of a historical disturbance relationship that in recent times has been altered or is lacking altogether.

With mountain stewartia having unique niche preferences, the species may represent an indicator species for old growth forests and areas of high biological diversity. However, the species' unknown tolerance to disturbances such as adelgid-induced mortality in eastern hemlocks, altered fire regimes, and timber harvest practices provide a rich area for future research. In addition, information is lacking on stewartia regeneration requirements, seed dispersal, wildlife and insect uses, and pollinators, which makes it difficult to assess the stability of extant stewartia populations.

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APPENDIX

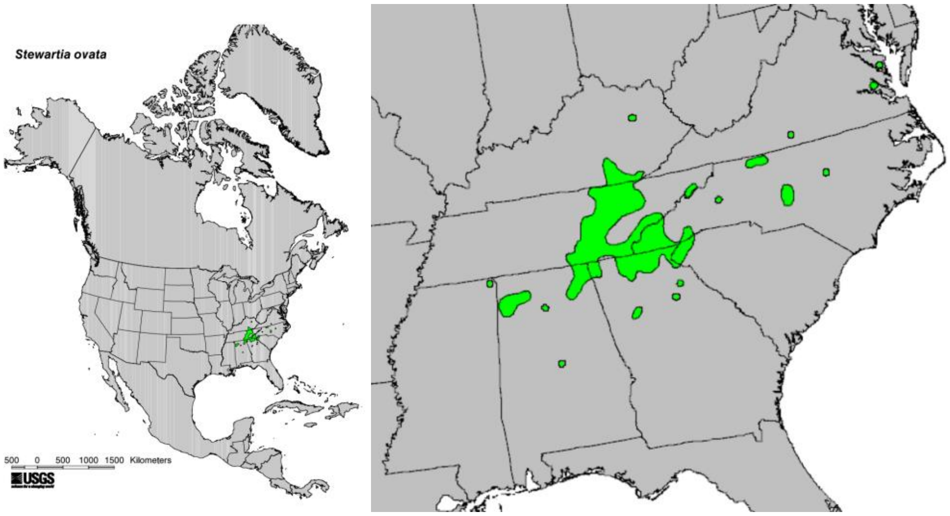

Figure 3.1. Distribution map of mountain stewartia (*Stewartia ovata* (Cav.) Weatherby).

Source: USGS map based on Atlas of United States Trees by Elbert L. Little, Jr.

Figure 3.2. Images of mountain stewartia (*Stewartia ovata* (Cav.) Weatherby) growth form, leaves, twigs, buds, flowers, fruit pods in different stages of development, and seed. Photos taken by Robert “Bert” J. Pivar and the primary author. Floral image taken by Hugh Faust.

Figure 3.2. Continued.

Figure 3.2. Continued.

Figure 3.2. Continued.

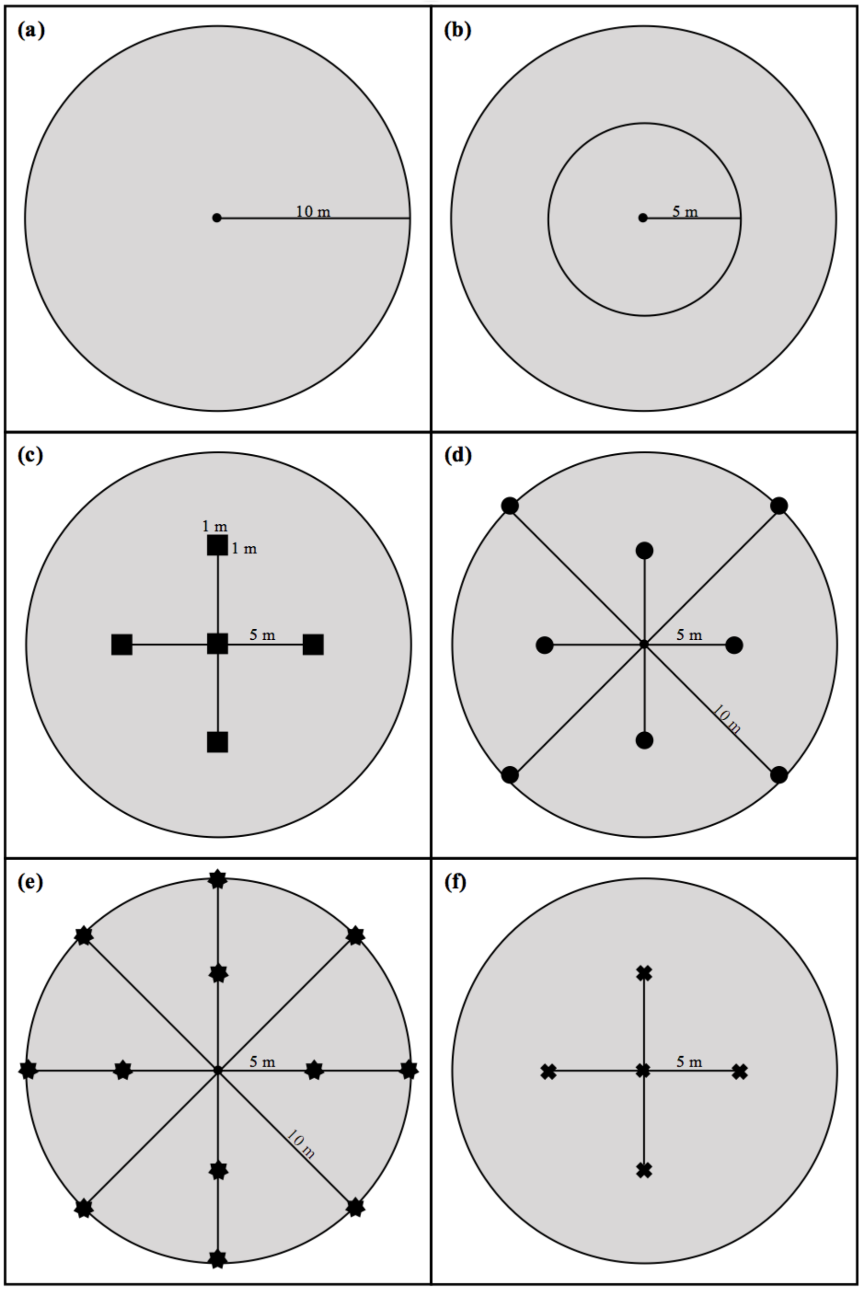

Figure 3.3. Plot layout for sampling (a) overstory trees, (b) midstory vegetation, (c) understory vegetation, (d) canopy cover, (e) percent full PAR, and (f) soils.

Table 3.1. Physical characteristics of midstory stewartia within sampled plots.

	n	Mean	Min	Max	Std. Dev.	Std. Error
Height (m)	37	2.46	0.28	9.50	1.62	0.22
Root-collar Diameter (cm)	37	1.97	0.30	6.65	1.38	0.17
DBH (cm)	37	1.33	0.00	4.13	1.04	0.14
Stems	37	1.70	1.00	4.00	1.00	0.16
Spacing (m)	37	2.42	0.00	4.95	1.54	0.19
Trees/Population	5	7.40	4.00	10.00	1.62	1.08

*Note this table includes only individual stewartia stems sampled within midstory vegetation plots and does not include immature seedlings sampled within understory plots. No stewartia were found in overstory plots.

Table 3.2. Site description variables.

	n	Mean	Min	Max	Std. Dev.	Std. Error
Basal Area (m^2/ha)	5	35.15	20.52	46.47	11.25	5.03
Canopy Cover (%)	5	96.54	94.02	98.51	1.77	0.79
Relative PAR (%)	5	7.05	2.49	11.22	3.15	1.41
Aspect (°)	5	160.80	115.00	244.00	51.41	22.99
Elevation (m)	5	328.33	272.49	288.01	49.11	21.96
Slope (%)	5	18.20	14.50	27.50	5.28	2.36
Dist. from Stream (m)	5	51.35	21.20	95.63	30.47	13.63
Dist. from Trail (m)	5	16.53	8.34	23.50	6.55	2.93
Ground Cover (%)	5	25.45	8.00	57.00	19.64	8.78
Exposed Soil (%)	5	7.50	2.00	19.00	6.80	3.04
Horizon O Depth (cm)	5	3.56	2.00	6.00	1.24	0.25
Horizon A Depth (cm)	5	4.96	2.00	9.00	2.35	0.47
Horizon E Depth (cm)	5	8.47	0.00	23.00	5.31	1.06
Ca (Kg/ha)	5	376.38	169.25	860.81	292.84	130.96

Table 3.2. Continued.

	n	Mean	Min	Max	Std. Dev.	Std. Error
P (Kg/ha)	5	8.97	4.48	16.81	4.82	2.16
K (Kg/ha)	5	104.02	75.10	150.19	34.12	15.26
Ca (Kg/ha)	5	376.38	169.25	860.81	292.84	130.96
Mg (Kg/ha)	5	69.94	34.75	149.07	45.82	20.49
Zn (Kg/ha)	5	4.15	2.35	9.19	2.85	1.27
Cu (Kg/ha)	5	1.03	0.67	1.68	0.43	0.19
B (Kg/ha)	5	0.61	0.45	0.79	0.13	0.06
Na (Kg/ha)	5	10.76	7.85	15.69	3.23	1.44
Organic Matter % (LOI)	5	6.82	3.90	9.80	2.65	1.18

Table 3.3. Soil characteristics for each sample plot inventoried. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at https://websoilsurvey.sc.egov.usda.gov/. Accessed [February/20/2017].

Plot County Soil Code	Soil Type	% Slope	Composition	Drainage	Permeability	Water Capacity	Soil Reaction	Depth to Bedrock (cm)	General Description
1 Rhea JvF	Jefferson	20-60%	45-55%	Well Drained	Moderately Rapid	Moderate	Very Strongly to Strongly Acidic	> 152.40	Friable Cobbly Loam
	Varilla	20-60%	15-25%	Excessively Drained	Moderately Rapid	Low	Very Strongly to Strongly Acidic	> 121.92	Friable Cobbly Loam
	Shelocta	20-60%	10-20%	Well Drained	Moderate	High	Very Strongly to Strongly Acidic	> 121.92	Very Friable Loam

Table 3.3. Continued.

Plot County Soil Code	Soil Type	% Slope	Composition	Drainage	Permeability	Water Capacity	Soil Reaction	Depth to Bedrock (cm)	General Description
2 Monroe RgF	Ranger	25-60%	10-35%	Well Drained	Moderate	Moderate	Very Strongly to Strongly Acidic	50.80 - 101.60	Friable Cobbly Loam
	Channery	25-60%	35-60%	Excessively Drained	Moderate	Moderate	Very Strongly to Strongly Acidic	50.80 - 101.60	Friable Cobbly Loam
	Silt loam	25-60%	10-15%	Well Drained	Moderate	Moderate	Very Strongly to Strongly Acidic	50.80 - 101.60	Very Friable Loam

Table 3.3. Continued.

Plot County Soil Code	Soil Type	% Slope	Composition	Drainage	Permeability	Water Capacity	Soil Reaction	Depth to Bedrock (cm)	General Description
3 Roane Gsf	Giplin	25-80%	27-50%	Well Drained	Moderate	Low	Very Strongly to Strongly Acidic	50.80 - 101.60	Friable Silty Loam
	Bouldin	25-80%	31-40%	Well Drained	Moderately Rapid	Low	Very Strongly to Strongly Acidic	> 203.20	Flaggy-Channery Loam
	Petros	25-80%	19-28%	Excessively Drained	Rapid	Very Low	Very Strongly to Strongly Acidic	25.40 - 50.80	Channery Silt Loam

Table 3.3. Continued.

Plot County Soil Code	Soil Type	% Slope	Composition	Drainage	Permeability	Water Capacity	Soil Reaction	Depth to Bedrock (cm)	General Description
4 Morgan GpF	Giplin	35-80%	50-70%	Well Drained	Moderate	Low	Very Strongly to Strongly Acidic	50.80 - 101.60	Friable Silty Loam
	Petros	35-80%	20-40%	Excessively Drained	Rapid	Very Low	Very Strongly to Strongly Acidic	50.80 - 101.60	Very Friable Channery Silt Loam

Table 3.3. Continued.

Plot County Soil Code	Soil Type	% Slope	Composition	Drainage	Permeability	Water Capacity	Soil Reaction	Depth to Bedrock (cm)	General Description
5 Morgan GpF	Giplin	35-80%	50-70%	Well Drained	Moderate	Low	Very Strongly to Strongly Acidic	50.80 - 101.60	Friable Silty Loam
	Petros	35-80%	20-40%	Excessively Drained	Rapid	Very Low	Very Strongly to Strongly Acidic	50.80 - 101.60	Very Friable Channery Silt Loam

Table 3.4. Diameters (DBH, cm) for overstory trees.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Acer rubrum	9	16.28	10.00	36.80	8.36	2.79
Betula lenta	2	25.90	24.10	27.70	2.55	1.80
Carya tomentosa	8	17.65	13.20	26.50	4.14	1.47
Fagus grandifolia	2	37.50	21.20	53.80	23.05	16.30
Liquidamber styraciflua	5	26.34	15.60	41.80	10.30	4.61
Liriodendron tulipifera	4	43.60	30.20	58.80	11.81	5.91
Oxydendrum arboreum	19	13.99	10.00	18.50	2.29	0.57
Pinus echinata	2	35.55	33.90	37.20	2.33	1.65
Pinus strobus	5	47.43	12.30	81.50	30.03	13.43
Quercus alba	13	24.02	10.80	43.20	12.12	3.36
Quercus velutina	2	33.50	27.20	39.80	8.91	6.30
Tsuga canadensis	13	28.23	10.50	45.70	11.24	3.12
Other*	9	18.97	12.75	27.30	5.17	1.72

Table 3.4. Continued.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Total	93	23.78	10.00	81.50	13.87	1.44

*Species with less than or equal to 1% of the total relative occurrence (basal area) were combined into the category “Other”.

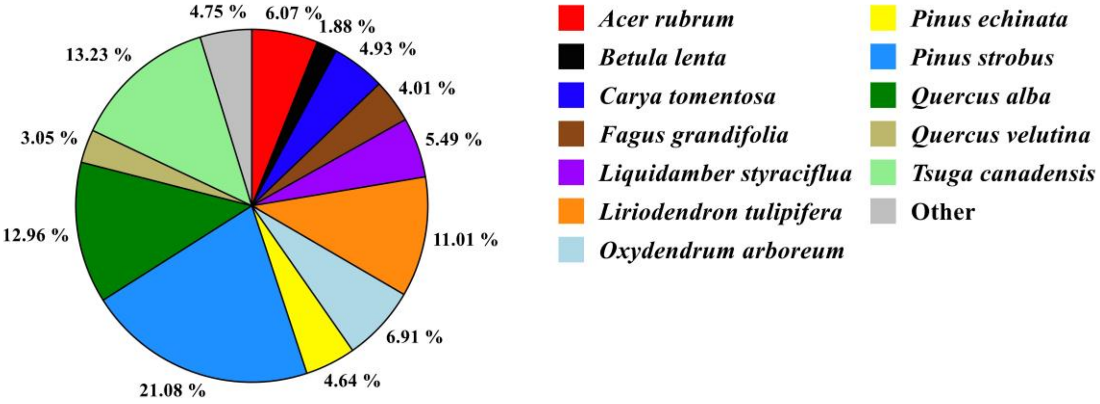

Figure 3.4. Relative proportion of basal area (m^2/ha) for each species sampled. Species with less than or equal to 1% of the total basal area were combined into the category “Other”.

Table 3.5. Overstory bole heights (m) measured from ground level to the first major lateral branch.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Acer rubrum	9	6.42	3.82	9.46	1.55	0.55
Betula lenta	2	6.54	4.83	8.25	2.42	1.71
Carya tomentosa	8	6.74	4.64	10.06	1.67	0.59
Fagus grandifolia	2	4.73	3.82	5.63	1.28	0.91
Liquidamber styraciflua	5	4.51	2.62	6.04	1.35	0.60
Liriodendron tulipifera	4	10.66	8.65	14.48	2.66	1.33
Oxydendrum arboreum	19	5.70	1.81	11.27	2.53	0.58
Pinus echinata	2	9.45	6.04	12.88	4.84	3.42
Pinus strobus	5	8.53	5.63	13.48	3.28	1.47
Quercus alba	13	7.55	5.23	11.67	1.76	0.49
Quercus velutina	2	4.53	4.02	5.03	0.71	0.70
Tsuga canadensis	13	1.89	0.60	3.02	0.84	0.24
Other*	9	6.04	2.01	13.88	4.42	1.14

Table 3.5. Continued.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Total	93	5.97	0.60	14.48	2.98	0.31

*Species with less than or equal to 1% of the total relative occurrence (basal area) were combined into the category “Other”.

Table 3.6. Total height (m) for overstory trees.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Acer rubrum	9	12.43	10.46	17.30	2.29	0.76
Betula lenta	2	17.00	15.29	18.71	2.42	1.71
Carya tomentosa	8	14.79	11.87	18.11	2.10	0.74
Fagus grandifolia	2	17.80	15.09	20.52	3.84	2.72
Liquidamber styraciflua	5	16.46	13.28	18.71	2.26	1.01
Liriodendron tulipifera	4	19.56	17.10	21.93	2.33	1.16
Oxydendrum arboreum	19	10.68	5.42	16.90	2.94	0.68
Pinus echinata	2	16.90	12.88	20.92	5.69	4.02
Pinus strobus	5	18.63	11.27	27.36	6.90	3.09
Quercus alba	13	16.40	11.27	23.34	3.85	1.07
Quercus velutina	2	21.53	18.11	24.95	4.84	3.42
Tsuga canadensis	13	16.36	8.65	25.95	6.53	1.81
Other*	9	12.61	7.04	16.50	2.76	0.92

Table 3.6. Continued.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Total	93	14.76	5.43	27.38	4.74	0.49

*Species with less than or equal to 1% of the total relative occurrence (basal area) were combined into the category “Other”.

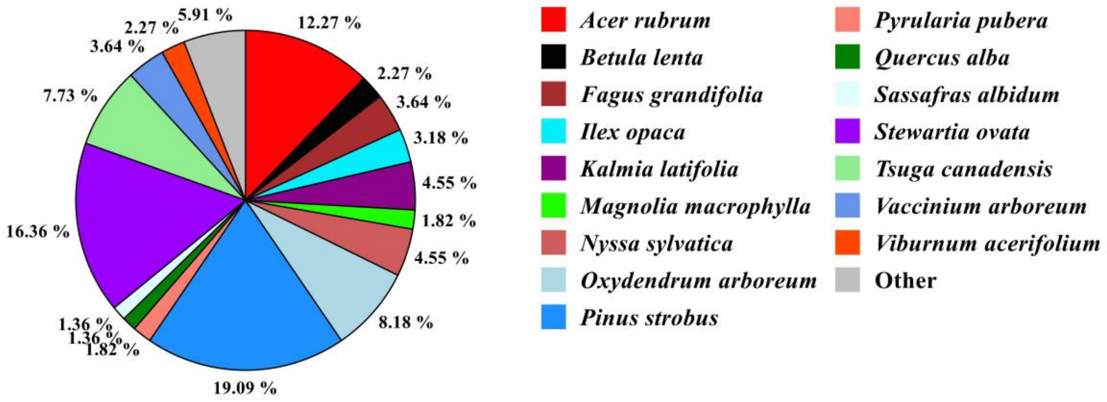

Figure 3.5. Relative proportion of stem counts for midstory species sampled. Species with less than or equal to 1% of the total stems were combined into the category "Other".

Table 3.7. Root-collar diameters (cm) for midstory species.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Acer rubrum	27	2.09	0.70	5.92	1.31	0.25
Betula lenta	5	3.24	1.93	7.94	2.64	1.18
Fagus grandifolia	8	3.89	1.03	8.62	2.93	1.03
Ilex opaca	7	2.94	1.76	4.65	0.93	0.35
Kalmia latifolia	10	2.33	1.15	6.52	1.59	0.50
Magnolia macrophylla	4	2.31	1.18	3.21	1.02	0.51
Nyssa sylvatica	10	4.61	1.74	8.04	2.52	0.80
Oxydendrum arboreum	18	3.28	1.02	5.96	1.72	0.41
Pinus strobus	42	1.80	0.26	8.65	1.30	0.20
Pyrularia pubera	4	1.94	0.88	4.35	1.63	0.82
Quercus alba	3	3.91	1.43	8.60	4.07	2.35
Sassafras albidum	3	2.00	1.66	2.34	0.34	0.20
Stewartia ovata	37	1.97	0.30	6.65	1.38	0.17
Tsuga canadensis	17	2.73	0.81	10.10	2.26	0.58

Table 3.7. Continued.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Vaccinium arboreum	8	1.50	0.84	3.20	0.81	0.29
Viburnum acerifolium	5	1.18	0.62	1.84	0.59	0.26
Other*	13	2.64	0.56	7.43	2.16	0.60
Total	221	2.53	0.26	10.10	1.81	0.12

*Species with less than or equal to 1% of the total relative occurrence (stems) were combined into the category “Other”.

Table 3.8. Total height measurements (m) for midstory species.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Acer rubrum	27	2.52	1.04	7.39	1.47	0.28
Betula lenta	5	3.62	2.29	7.28	2.06	0.92
Fagus grandifolia	8	3.24	1.41	5.54	1.69	0.60
Ilex opaca	7	2.17	1.24	3.54	0.83	0.31
Kalmia latifolia	10	1.78	1.21	2.83	0.54	0.17
Magnolia macrophylla	4	3.13	1.55	4.88	1.69	0.84
Nyssa sylvatica	10	3.89	1.75	8.35	2.10	0.66
Oxydendrum arboreum	18	3.33	1.52	6.36	1.41	0.33
Pinus strobus	42	1.66	1.03	6.40	0.97	0.15
Pyrularia pubera	4	1.93	1.03	2.82	0.88	0.44
Quercus alba	3	3.63	1.49	7.53	3.38	1.95
Sassafras albidum	3	2.60	2.04	3.40	0.71	0.41
Stewartia ovata	37	2.46	0.28	9.50	1.62	0.22
Tsuga canadensis	17	2.44	1.17	6.43	1.20	0.29

Table 3.8. Continued.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Vaccinium arboreum	8	1.68	1.10	2.68	0.59	0.21
Viburnum acerifolium	5	1.39	1.02	2.04	0.40	0.18
Other*	13	2.62	1.01	5.62	1.58	0.44
Total	221	2.51	1.01	8.35	1.46	0.10

*Species with less than or equal to 1% of the total relative occurrence (stems) were combined into the category “Other”.

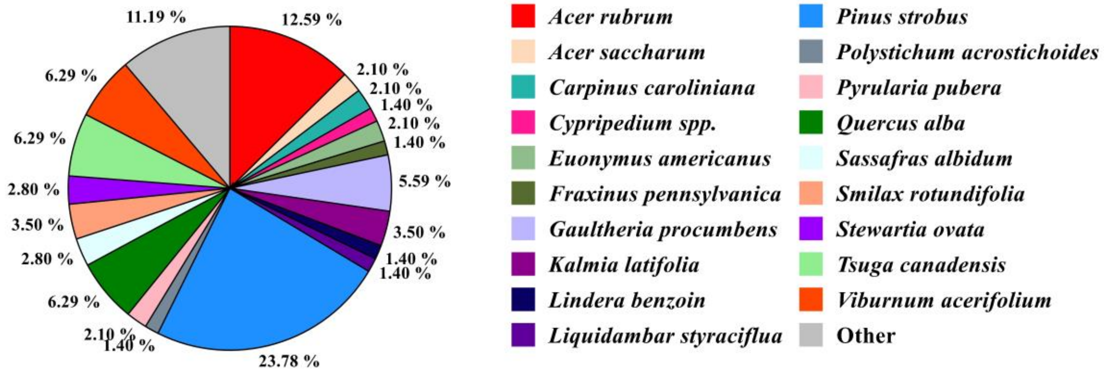

Figure 3.6. Relative proportion of stem counts for understory species sampled. Species with less than or equal to 1% of the total stems were combined into the category “Other”.

Table 3.9. Root-collar diameters (cm) for understory species.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Acer rubrum	18	0.24	0.06	0.73	0.20	0.05
Acer saccharum	3	0.23	0.20	0.26	0.03	0.02
Carpinus caroliniana	3	0.35	0.29	0.46	0.09	0.05
*Cypripedium spp.**	2	.	.	.	.	.
Euonymus americanus	3	0.25	0.22	0.30	0.05	0.03
Fraxinus pennsylvanica	2	0.30	0.27	0.33	0.04	0.03
*Gaultheria procumbens**	8	.	.	.	.	.
Kalmia latifolia	5	0.56	0.24	1.24	0.40	0.18
Lindera benzoin	2	0.43	0.38	0.48	0.07	0.05
Liquidambar styraciflua	2	0.89	0.18	1.54	0.96	0.68
Pinus strobus	34	0.31	0.02	0.82	0.22	0.04
*Polystichum acrostichoides**	2	.	.	.	.	.
Pyrularia pubera	3	0.36	0.27	0.52	0.14	0.08
Quercus alba	9	0.33	0.12	1.08	0.32	0.11

Table 3.9. Continued.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Sassafras albidum	4	0.26	0.09	0.48	0.18	0.09
Smilax rotundifolia	5	0.35	0.10	0.60	0.20	0.09
Stewartia ovata	4	0.29	0.05	0.88	0.39	0.20
Tsuga canadensis	9	0.20	0.05	0.64	0.19	0.64
Viburnum acerifolium	9	0.40	0.08	0.84	0.26	0.09
Other**	14	0.32	0.07	0.68	0.22	0.06
Total	141	0.32	0.02	1.54	0.25	0.02

*Diameters were not taken for these species.

**Species with less than or equal to 1% of the total relative occurrence (stems) were combined into the category “Other”.

Table 3.10. Height measurements (m) for understory species.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Acer rubrum	18	0.22	0.06	0.57	0.16	0.04
Acer saccharum	3	0.12	0.07	0.16	0.05	0.03
Carpinus caroliniana	3	0.28	0.19	0.35	0.08	0.05
Cypripedium spp.	2	0.11	0.03	0.19	0.11	0.08
Euonymus americanus	3	0.13	0.11	0.16	0.03	0.02
Fraxinus pennsylvanica	2	0.16	0.14	0.19	0.03	0.02
Gaultheria procumbens	8	0.03	0.02	0.03	0.01	0.00
Kalmia latifolia	5	0.44	0.18	0.94	0.31	0.14
Lindera benzoin	2	0.43	0.34	0.53	0.14	0.10
Liquidambar styraciflua	2	0.50	0.17	0.83	0.47	0.33
Pinus strobus	34	0.27	0.03	0.62	0.17	0.03
Polystichum acrostichoides	2	0.24	0.14	0.33	0.13	0.10
Pyrularia pubera	3	0.30	0.09	0.57	0.25	0.14
Quercus alba	9	0.26	0.11	0.92	0.26	0.09

Table 3.10. Continued.

Species	*n*	Mean	Min	Max	Std. Dev.	Std. Error
Sassafras albidum	4	0.33	0.17	0.52	0.15	0.07
Smilax rotundifolia	5	0.29	0.15	0.52	0.18	0.08
Stewartia ovata	4	0.23	0.06	0.61	0.26	0.13
Tsuga canadensis	9	0.17	0.07	0.37	0.11	0.04
Viburnum acerifolium	9	0.49	0.17	0.99	0.31	0.10
Other*	14	0.29	0.03	0.74	0.20	0.05
Total	141	0.26	0.02	0.99	0.21	0.02

*Species with less than or equal to 1% of the total relative occurrence (stems) were combined into the category “Other”

CHAPTER IV

NORTHERN RED OAK REGENERATION: 25-YEAR RESULTS OF CUTTING AND PRESCRIBED FIRE IN MICHIGAN OAK AND PINE STANDS

ABSTRACT

Reviews of likely causes of the oak regeneration problem published in the late 1980's and early 1990's provided the basis for multiple studies involving different methods of reducing competition between oaks and other hardwoods. In 1991, a study involving multiple overstory and understory treatments was established in natural oak stands and red pine plantations in Michigan to test hypotheses that 1) northern red oak regeneration would be more successful in pine than oak stands and 2) removal of competitors would enhance northern red oak seedling growth and survival. Late spring prescribed fires were implemented on all plots in 2002 and 2008 to investigate their effectiveness in controlling red maple saplings. Survival and growth of planted northern red oaks and natural oak and red maple regeneration have been documented periodically between 1991 and 2015. A subset of seedlings was protected against browsing with wire cages since establishment. Results suggest partial removal of competitors enhances oak seedling performance, whereas complete removal greatly increases mortality from deer browsing and frequent late spring frosts. Beneficial effects of prescribed burning in reducing red maple competition were overridden by increased browsing of post-fire oak sprouts. Although deer browsing was heavier in pine than oak stands, greater growth and survival of northern red oak stems protected from deer browsing occurred in the pine stands, with the trend strengthening in recent years. Opportunities for integrating management of oak and pine warrant further investigation.

Keywords: Acer rubrum L.; Deer browse; facilitation; fire; frost damage; *Quercus rubra* L.; oak regeneration; *Pinus* spp.; Shelterwood.

INTRODUCTION

Over the course of the last 8,000 years, oaks (*Quercus* spp.) have been a prominent component of our deciduous forests across eastern North America (Foster et al., 2002). Oaks are known for their ecological and economic importance. They are valued not only for their quality hardwood timber, but also for their structure, forage, and mast. Oaks are also an important food source for numerous species of birds, mammals, and insects due to their nutrient rich acorns (McShea et al. 2007). Oaks have been considered foundational species because of their prominence across the eastern United States and their regulatory roles, both directly and indirectly, in community assembly and ecosystem processes (Ellison et al. 2005; McShea et al. 2007). Fralish (2004) suggested that oaks be considered keystone species due to their cascading effects across trophic levels. However, in more recent years, over utilization, changes to disturbance regimes, and poor oak recruitment have been identified as key factors threatening the sustainability of future oak resources. Nowhere has oak regeneration been found to be more challenging than on the higher-quality upland sites (Crow 1988; Loftis and McGee 1993; Rogers et al. 1993). Throughout these sites, oaks are often abundant within overstories and understories as canopy trees and seedlings, but advanced oak regeneration has been lacking in these systems since the early 1900s (Abrams 1992; Brose et al. 1999a). The sustainability of forest products and the future of many forest species will hinge largely on our ability to identify and use the unique morphological, physiological, and ecological characteristics of oak to promote regeneration.

Unlike many oak competitors, upland oaks have evolved numerous morphological and physiological adaptations to withstand a variety of site conditions. These adaptations have enabled upland oaks to persist through large-scale disturbances such as extreme fire events and droughts. Paleoecological studies have shown that both droughts and fires were more prevalent during the early Holocene epoch when warm and dry conditions resulted in greater fire frequency (Abrams 1992). The unique adaptations of upland oaks to fire and drought coupled with the higher frequency of these disturbance factors during the Holocene epoch may explain why oak populations were most abundant during that period. It may also provide evidence for how successful upland oak regeneration can be achieved today.

To resist the damaging effects of fire, oaks have developed the ability to initiate new shoots from dormant buds along the root-collar and stems. By re-sprouting, oaks are more apt to recover from injuries acquired during fire events, wildlife browsing, and other extreme weather-related disturbances compared to many of their top deciduous and coniferous competitors. Brown (1960) and Swan (1970) both noted fewer sprouts of oak competitors than oaks following prescribed burns. In Brown's study, upland oaks accounted for 94% of the total basal area post-fire compared with 53% within unburned control plots. Swan's study found that 43% of hardwood competitors re-sprouted post-fire compared to 87% of oaks. Oak seedlings and saplings also share this ability to re-sprout from dormant buds following top kill. Johnson (1974) reported 38% of first year northern red oak seedlings were able to re-sprout post-fire and Lorimer (1985) reported that 78% of four-year old saplings resprouted. The ability to reinitiate new stems following top kill provides oaks with an advantage over numerous fire-intolerant species.

In addition, the trunks and stems of upland oaks are adapted to resist fire. This is primarily the result of thick bark. Their increased bark thickness and insulation have enabled oaks to historically occupy regions that would otherwise be uninhabitable for woody plants. One such region is the tall grass prairies of central North America. Under historical conditions, thick bark enabled many upland oak species to resist low-level fires that were once frequent prior to European settlement (Gleason 1913; McPherson 1997;Anderson et al. 1999). It is also the primary reason why the most commonly encountered species within extant North American savannas are upland oak species such as bur, chinquapin, post, black, blackjack, white, and northern pin oak (Abrams 1992). Overall, the white oak group maintains the thickest bark of any of the central hardwoods, followed by red oaks, then by all other hardwoods (Sutherland and Smith 2000). Many current competitors of upland oaks are thin barked, fire-sensitive species such as American beech (*Fagus grandifolia* Ehrh.), maple species (*Acer* spp.), hickory species (*Carya* spp.), flowering dogwood (*Cornus florida* L.), and black cherry (*Prunus serotina* Ehrh.). With the persistence of altered fire regimes, many of these competitors continue to increase in abundance across the landscape.

Finally, seedbeds created by fire have been viewed as more favorable for acorn germination. For example, the number of beetle and weevil species known to prey upon acorns was significantly reduced throughout burned sites compared to unburned sites (Galford et al. 1988). Several sources have suggested that blue jays prefer to cache acorns in open areas with limited understory vegetation and thin litter layers (Bossema 1979; Darley-Hill and Johnson 1981; Healy 1988), which commonly occur on burned sites.

In recent years, these fire adaptations have been cited as evidence for the hypothesis that fire was historically a requirement for perpetuating eastern North American upland oaks. Fire suppression over the past century is thought to have hindered oak regeneration by increasing the abundance of fire intolerant species and decreasing understory light availability (Abrams 1992). Several dendrochronological studies have revealed past fire intervals to be 4-20 years prior to European settlement and that extensive fires were frequent, during and just prior to the establishment of extant overstory oaks (Dey and Guyette 2000; Shumway et al. 2001; Abrams 2005; McEwan et al. 2007). In contrast, the lack of widespread fire in recent decades has resulted in many mixed-oak forests in the eastern United States entering the understory reinitiation stage of development and containing dense understories of fire-intolerant red maple and other shade-tolerant species (Abrams 1998; Albrecht and McCarthy 2006; Arthur et al. 1998). These undisturbed stands have developed stratified layers of shade-tolerant species beneath the overstory canopy that can limit understory light levels to 1-3% of above canopy photosynthetically active radiation (PAR) (Lorimer et al. 1994; Miller et al. 2004; Aldrich et al. 2005). These dense canopies and low light levels have been considered the primary obstacle limiting both growth and survival of upland oak seedlings and sprouts (Lorimer et al. 1994).

In addition to the numerous fire adaptations, oaks have evolved characteristics to withstand low soil nutrient levels and drought. Morphologically, oaks are more deeply rooted as compared to many of their competitors across North American forests (Kozlowski 1971; Spurr and Barnes 1980; Gale and Grigal 1987). For example, the rooting depth of white oak (*Quercus alba* L.) has been measured around 4.5m, whereas black walnut (*Juglans nirga* L.) has a rooting depth of 3.3m and sugar maple (*Acer saccharum* Marsh.) and eastern red cedar (*Juniperus virginiana* L.) had root systems less than 1.0m in depth (Hinckley et al. 1981). The seedlings of oaks also tend to exhibit a similar rooting habit, with bur oak (*Quercus macrocarpa* Michx.) seedlings having a greater root elongation compared to black walnut, shagbark hickory (*Carya ovate* (Mill.) K. Koch), basswood (*Tilia americana* L.), and sugar maple (Holch 1931; Biswell 1935; Sprackling and Read 1979). Northern red oak (*Quercus rubra* L.) saplings produced deeper root systems on mesic sites compared to red maple (*Acer rubrum* L.) within the same stands (Lyford 1980). Kozlowski (1971) reported that northern pin oak (*Quercus ellipsoidalis*

E.J. Hill) and bur oak were more deeply rooted than jack pine (*Pinus banksiana* Lamb.) within Wisconsin sand plains, with root systems greater than 2.5m in depth. The deep root systems of oaks may confer an advantage during periods of limited water availability.

The anatomy of oak stems, especially the xylem, equips upland oaks with an enhanced ability to deal with water shortage. In general, oaks are ring-porous and contain early-wood vessels that are relatively large in diameter. This minimizes hydraulic resistance and enables oaks to achieve rapid rates of water movement. The velocity within the xylem of northern pin, northern red, and bur oak has been measured between 27.5 to 60 m h^{-1}, while diffuse porous hardwoods were measured between 1.0 to 6.2 m h^{-1} and conifers between 1.0 and 2.1 m h^{-1} (Zimmerman and Brown 1977; Kramer and Kozlowski 1979). These large diameter vessels have a greater tendency for cavitation compared to small diameter xylem elements (Tyree and Dixon 1986). However, upland oaks create smaller diameter late-wood which provides an avenue to move water as larger vessels are lost to cavitation. This enables oaks to move greater quantities of water when water is abundant and then sustain water movement when the supply is limited (Abrams 1990).

Upland oaks can be characterized as having xeromorphic leaves, relative low water-potential thresholds needed for stomatal closure, and a greater ability to adjust osmotically compared to their deciduous and coniferous competitors. Abrams and Kubiske (1990) reported a greater stomatal density, smaller guard cells, and thicker leaves for bur, white, northern pin, black (*Quercus velutina* Lam.), and northern red oak compared to the 21 other hardwood competitors measured within central Wisconsin. They also found that these characteristics were maintained for both sun and shade leaves. These adaptations are consistent with xeric-adapted species. In addition, compared to other trees, oaks exhibit a greater photosynthetic rate with a relatively low rate of gas exchange as drought stress increases. Greater water use efficiency was also observed for black, bur, white, and northern red oak compared to sugar maple (Wuenscher and Kozlowski 1971). Greater photosynthetic rates were measured in chestnut (*Quercus Montana* Willd.), white, northern red, black, and bear oak (*Quercus ilicifolia* Wangenh.) saplings compared with mesic flowering dogwood, American chestnut (*Castanea dentata* (Marsh.) Borkh.), and sugar maple (Bahari et al. 1985; Abrams et al. 1990).

Upland oaks also have a greater ability to survive nutrient-poor locations compared to other upland species (Reich and Hinkley 1980). Kolb et al. (1989) reported northern red oak to have a greater resistance to reduced levels of light, nutrients, and moisture compared to yellow-poplar (*Liriodendron tulipifera* L.). In contrast, as nutrient levels increased, yellow-poplar out-competed northern red oak in capturing and capitalizing on the more abundant resources. The pygmy forest studied by Reich and Hinkley (1980) was characteristically xeric and contained low levels of calcium and magnesium and high levels of aluminum. In this particular forest, only upland oak species were able to exist, while other hardwoods were unable to colonize the area. This provides evidence for the ability of upland oaks to thrive in areas with limited nutrient resources, while other competing species require greater levels of nutrients.

Early work by Crow (1980) pointed to five general conditions that must be met to successfully regenerate upland oaks: 1) competing vegetation must be controlled, 2) overstory densities must be reduced to release more resources to the understory, 3) regeneration sources must be established (i.e., natural or planted seedlings), 4) seedlings must be given time to become advanced regeneration, and 5) following successful establishment of advanced regeneration, overstory trees need to be removed to release the new cohort of oaks. Arthur et al. (2012) described the role of fire for perpetuating oak through each of these general steps. For this reason, upland oaks can be thought of as requiring a high level of disturbance compared to other hardwoods. Fire and drought are often credited with the success of oak regeneration in the past, but present silvicultural techniques can be utilized to mimic these past disturbances. Loftis (1990) proposed the use of a shelterwood technique for facilitating natural northern red oak regeneration throughout the southern Appalachians. Throughout that region, yellow-poplar is the major competitor of upland oaks. However, by mimicking past disturbances (i.e., insect outbreaks, ice storms, wind events, droughts, and fire), openings are generated that increase PAR within the understory and promote the development of advanced oak regeneration (Loftis, 1990; Johnson et al., 2002). Canopies are later removed once adequate advanced regeneration is achieved (Loftis, 1990). However, when this method is applied to stands situated on intermediate and mesic sites, excessive woody competition often develops following partial harvests. Extensive measures are often necessary to control understory and midstory oak competition in the new stand (Brose, 2008). The applications of herbicide treatments, mechanical treatments, and prescribed burning have all been used to control understory oak competitors. The combination of prescribed fire and shelterwood cutting treatments has been proposed as a cost-effective and efficient means of reducing oak competitors and advancing regeneration (Brose and Van Lear 1998; Brose et al. 1999a). This methodology (i.e., shelterwood-burn technique) has been reported as successful in controlling yellow-poplar and other hardwood oak competitors (Brose et al. 1999a, 1999b, 2001).

Upland oaks are well equipped to survive environments with higher frequencies of disturbance compared to other deciduous and coniferous species. They have developed morphological and physiological adaptations such as deep root systems, rot-resistant wood, strong sprouting ability, thick bark, xeromorphic leaves, low water-potential thresholds for stomatal closure, and an ability to adjust osmotically, which have all historically provided upland oaks with an advantage over other upland deciduous and coniferous trees during periods of drought and fire disturbance. However, shifts in historic disturbance regimes have led to increases in competing mesophytic-species (i.e., red maple, sugar maple, and yellow-poplar) throughout the eastern United States (Crow 1988; Abrams 1992, 1998, 2005; Lorimer 1993; Iverson et al. 2008). These species are able to capture limited resources (e.g., moisture, nutrients, space, light, etc.) and outcompete upland oaks (Abrams and Nowacki, 1992; Abrams, 1998).

More studies and more long-term projects are necessary to elucidate methodologies for regenerating oak. The number of replicated long-term (i.e., projects ≥ 5 years) oak regeneration projects is limited. In 1990, Buckley et al. (1998) initiated an oak regeneration study in northern Lower Michigan. Overstory manipulations were used to test the survival and growth of both artificially planted and natural oak regeneration. Regional pollen fossil records indicated a long-term co-occurrence of upland oaks and pines, with changes in oak species dominance relative to pines throughout the past 10,000 years (Webb 1974; Jacobson 1979). In addition, observations within the region noted oak seedlings and saplings within mature pine stands, while young pines were noticed in mature oak stands, suggesting a potential for cyclical replacement of pines by oaks and oaks by pines (Crow 1988; Sarnecki 1990; Johnson 1992). It was hypothesized that oak regeneration would be enhanced in pine stands relative to mixed hardwood stands, although the exact mechanisms were unknown. Sarnecki (1990) documented abundant oak regeneration beneath red pine canopies at relatively low levels of canopy cover, suggesting that pines may provide favorable light conditions for oak regeneration, while excluding other hardwood competitors. Pine canopies may create favorable microsite conditions in several ways. The densely layered canopies of many pine species are capable of reducing forest floor temperatures by intercepting a greater proportion of light compared to many hardwood counterparts such as oaks, maples, hickories, and yellow-poplars. A reduced forest floor temperature decreases the decomposition rate of litter and allows for a greater buildup of organic materials (Crawford et al. 2003). Furthermore, conifer litter has a lower base cation concentration compared to hardwood litter. A lower cation concentration results in a great acidification of upper soil horizons over time (Brantberg et al. 2000). At lower pH values, the rate of nutrient cycling slows and nutrient availability is reduced (Jenkins et al. 1999). Several authors have also reported higher carbon/nitrogen ratios associated with conifer stands and mixed stands compared to stands with a greater proportion of hardwoods, due to the acidification of soils and reduced decomposition rates (Brown 1982; Whitney and Foster 1988; Augusto et al. 2003). In addition, Buckley et al. (1998) tested the hypothesis that partial removal of understory and overstory canopies would increase the success of oak regeneration on moderately productive sites. Due to logistical limitations, the use of prescribed fire could not be originally implemented in this project. However, by 2000, increased emphasis on prescribed fire and the advancement of red maple competition in some treatments led to an additional research project involving prescribed fire conducted by Hartman et al. (2005). This follow-up study tested a modification of a shelterwood-burn methodology forwarded by Brose et al. (2001). Hartman et al. (2005) hypothesized that a shelterwood-burn combination would reduce the abundance of red maple and other oak competitors. Although red maple was temporarily set back, the densities of red maple and oak stems in various size classes in 2006 differed little from their pre-burn levels in 2002. In 2008, a second prescribed burn was implemented in all treatments to evaluate the effects of multiple fires on oak regeneration and competition control. The research presented here will summarize the combined treatment effects that have occurred over the past 25 years. To our knowledge, no one has evaluated this approach in Michigan and no long-term shelterwood-burn projects such as this exist where oak regeneration and red maple suppression are the primary focus within two canopy types.

The principal aim of this project was to examine the effects of canopy manipulation treatments, understory manipulation treatments, and two prescribed fires on both artificial and natural oak regeneration, 25 years post-implementation, in Michigan natural northern red oak and planted red pine stands. Specific objectives were to 1) test the hypothesis that northern red oak regeneration would be more successful in pine than oak stands, 2) evaluate overstory canopy treatment effects on long-term oak regeneration, 3) evaluate understory treatment effects on long-term oak regeneration, 4) test the hypothesis that woody understory competitors would be reduced with prescribed fire, and 5) evaluate oak regeneration pre- and post-fire treatments.

METHODS

Sampling Area

Study sites were established on state forests in southern Roscommon County (84˚41’ W, 44˚14’ N, elevation 300m) and southern Crawford County (84˚45’W, 44˚31’ N, elevation 400m) in Michigan, USA. Both counties are within the Grayling Outwash Plain of the Highplains District of the northern Lower Peninsula (Albert 1995). Soils are characteristic of sandy, mixed, frigid, Alfic Haplorthods developed in pitted outwash. The physical and chemical properties of soils were comparable among sites and slopes $\leq 5\%$ (Kim et al. 1996). Stands utilized in the study were either second-growth natural oak, or unthinned planted red pine stands. Sites were designated as moderately productive. Site index for northern red oak according to curves for the Lake States region was 17-18m at a base age of 50 years (Carmean et al. 1989; Kim et al.1996).

Site index for red pine was about 17.2m at age 50, based on curves for red pin in Minnesota (Gevorkiantz 1957). Tree ring counts on stumps, following canopy treatment in 1991, indicated the oak stands were 88-100 years old and the pine stands were between 59-75 years old (Buckley et al. 1998). Planted red pine stands were selected for the study because natural stands of sufficient size and density for the experimental design could not be located in the region (Buckley et al. 1998).

Experimental Design

Natural oak stands and red pine plantations were each divided into three replicate blocks measuring 1.74ha. Each of these six blocks was subdivided into four 66 x 66m plots measuring 0.44ha each. One of four canopy cover treatments (clearcut (0%), 25% residual canopy (25%), 75% residual canopy (75%), or uncut control (100%)) was randomly assigned to each plot (Figure 1). A minimum 20m wide buffer zone was established between each treated area and adjacent access roads. Stands receiving canopy cover reduction treatments were cut from fall 1990 to early spring 1991. Partial canopy cover reduction treatments were performed by initially removing subcanopy trees ≥2.54cm dbh from below, then removing additional canopy trees as needed to meet the required treatment objective. In all treatments, red maple and suppressed red pine in subordinate canopy positions were removed first. In clearcut treatments, all woody plants ≥ 2.54cm dbh were removed. To accurately achieve a 25%-cover plot treatment, an additional removal of woody stems was required in the winter of 1991-1992. Rubber-tired forwarders were used during completion of all canopy cover reduction treatments. Additionally, medium duty trucks were employed when necessary to remove firewood from the treatment sites after it was cut and split. To minimize soil compaction and disturbances to understory vegetation, logging equipment was restricted to the 20m wide buffer zones. All other woody debris was cleared from planting areas by hand.

Four 15 x 15m understory treatment subplots (0.02ha each) were arranged in a square pattern at the center of each canopy treatment plot (Figure 4.1 in Appendix). By centering these understory treatment subplots within the canopy treatment plots, a resulting 18m buffer was formed to reduce edge effects from adjacent canopy treatment plots. The four understory treatments were randomly assigned to each canopy treatment. These treatments included Shrub Layer Removal (S) (herbs, shrubs, and saplings > 25cm tall up to stems of saplings 2.54cm dbh), Herb Layer Removal (H) (herbs, shrubs, and seedlings < 25cm tall), Litter Removal down to humus layer (L), and Control (C). The removal treatments for herb and shrub layers were accomplished by hand over the entire 15 x 15m plot in order to minimize additional disturbance. Understory treatments were completed in 1991, just prior to planting. Additionally, these treatments were maintained periodically from 1992 to 2001. No maintenance of understory treatments was performed from 2001 to 2015.

Northern red oak acorns and nursery seedlings were planted for comparison of treatment effects across individuals of different ages and sizes. As outlined by Buckley et al. (1998), all acorns were collected in October of 1990 at the University of Michigan Biological Station (UMBS), Cheboygan County, Michigan, USA. To more accurately obtain a representative sample of genetic diversity among northern red oaks, acorns were gathered from 20-30 dominant trees throughout a range of sites. Damaged acorns were detected through water floatation and discarded, while sound acorns were treated with captan and cold stratified over winter in a 7°C cold room. Nursery seedlings (2-0) were acquired from Wyman State Tree Nursery in Manistique, Michigan, USA. Unusually small and large acorns and seedlings were culled and remaining acorns and seedlings were mixed to achieve an equal representation of sizes among treatment plots.

The planting of acorns and nursery seedlings was performed in late April of 1991. Plantings were spaced 2m apart on a 10 x 10m grid for each 15 x 15m understory treatment plot (Figure 4.1). Of the total 36 planting sites in each understory treatment plot, 20 were randomly selected and planted with acorns and the remaining 12 were planted with nursery seedlings. In total, 5760 acorns and 1152 nursery seedlings were originally planted. In order to guarantee a seedling at each acorn planting location, three acorns were planted at each location, 3cm below the mineral soil surface. Following emergence, seedlings at each of these locations were randomly thinned down to one seedling per location. To prevent damage from wildlife, temporary hardware-cloth (1.27cm^2 mesh) cages 20 x 20cm on a side were installed over all direct-seeded locations. Cylindrical cages were constructed from chicken-wire measuring 0.45m in diameter x 1.83m in height for all nursery seedlings. In the summer of 1991, temporary hardware-cloth cages were removed and a random sample of both direct seeded seedlings and nursery seedlings were selected for permanent caging. In April 2008, these original cages were showing signs of deterioration and were subsequently replaced with new cages constructed in the same fashion as described above and secured around seedlings with steel rods.

Fire Parameters

Pre-burn assessments suggested that fire treatments could not be implemented under identical conditions across all sites due to varying amounts of precipitation and excluded wind directions. However, when fire treatments were applied, the average wind speeds and relative humidity were nearly uniform for all sites. The goal of both prescribed fires in 2002 and 2008, Fire 1 and Fire 2, hereafter, was to attain strip-head fires with approximately 0.9m flame lengths so as to top-kill all planted oak seedlings, along with all their competitors on all six blocks.

The first fire in the oak stands occurred on May 15, 2002. The nearest weather station recorded 0.15cm of precipitation two days prior to burning. On-site dry bulb temperature was 18°C, with an average relative humidity at 34%. Weather station wind speed was recorded at 16km/h, but mid-flame wind speed averaged only 1.6km/h. The combination of southwesterly winds and a north-facing slope hindered effective wind speed across oak stands.

Oak stands were burned a second time on May 16, 2008. The nearest weather station recorded a 0.13cm precipitation event the day of the burn. Weather station temperatures averaged 19°C, with an average relative humidity at 35%. Westerly winds were measured at 11.2km/h.

Pine stands were burned for the first time on May 21, 2002. The nearest weather station to pine stands 1 and 2 recorded 0.23cm precipitation eight days prior to burning. On-site dry bulb temperature averaged 12°C, with an average relative humidity at 42%. Mid-flame wind speed was from the north-northwest and averaged 2.1km/h. Pine stand 3 received 0.13cm of precipitation five days prior to burning. On-site dry bulb temperature averaged 11°C, with an average relative humidity at 37%. Mid-flame wind speeds for pine stand 3 occurred from the west and averaged 2.6km/h.

All pine stands were burned a second time on May 13, 2008. The nearest weather station to pine stands 1 and 2 received 2.5cm of precipitation five days prior to burning. Weather station temperature averaged 18°C, with an average relative humidity at 41%. Wind speed was recorded at 11.2km/h from the south. On-site dry bulb temperature averaged 19˚C, with average relative humidity at 45%. On-site winds were recorded from the south-southeast at 6.4km/h.

Measurements

Temperature indicating paints (Temqilaq Paints, B.J. Wolfe Enterprises Inc.) were used to quantify relative differences in fire temperature. Eight separate paints calibrated to liquefy at 79°, 149°, 204°, 260°, 316°, 371°, 593°, and 816°C were painted onto ceramic tiles mounted on steel rods face down 0.6 m above the soil surface in the center of each understory treatment plot.

Total heights to the nearest 0.5cm were recorded for the tallest stem of each direct-seeded and nursery seedling in 1991, 1992, 1996, 2000, 2001, 2002, 2003, 2006, 2009, and 2015. Mortality and deer, insect, frost, and other forms of damage were recoded. Due to the inability to accurately determine the proportion of a seedling lost to browsing, the severity of browsing damage per individual was not quantified. Seedlings were inventoried as dead when no trace of root or shoot could be located, or when live buds or other tissues could not be found along shoots, root collars, or roots. Basal area was estimated with a 10-factor prism. Percent canopy cover was measured with a Lemmon spherical densitometer. Four densiometer measurements were taken in each of the four cardinal directions at understory treatment plot-centers (Figure 4.2). An average percent canopy cover was obtained by averaging all measurements within each understory treatment.

Natural regeneration was measured in late-July/early-August of 2001, 2003, 2006, 2009, and May of 2015. All ramets and genets of woody stems were recorded by species into three size-classes: (Small) stems < 25cm height, (Medium) stems ≥ 25cm tall and < 2.54cm diameter, and (Large) ≥ 2.54cm diameter and <10cm diameter. A 1m^2 quadrat was used to quantify small size-class stems, a 2m diameter circular plot was used to measure all medium size-class stems, and a 4m diameter circular plot was used to measure all large size-class stems (Figure 4.2). A total of four sampling locations were placed within each 15m^2 subplot, centered at planting locations 8, 11, 26, and 29 (Figure 4.2). Smaller sampling plots were nested within larger plots. All species of oak regeneration were pooled into a single category for analysis.

Statistical Analysis

Data were analyzed using analysis of variance (ANOVA) models and *F* tests appropriate for split-plot experimental designs. All F tests were reported at $\alpha = 0.05$ significance level. Tukey's Honestly Significant Difference (HSD) at $\alpha = 0.05$ was used for all pair-wise comparisons of fire temperature, canopy composition, and canopy cover treatment means. Separate analyses using reduced models were conducted within canopy composition types when the overall ANOVA indicated statistical canopy composition by canopy cover interactions. Data were arranged by several categories (species, mean heights, caged vs. uncaged) and analyzed separately, but statistical differences were analyzed and reported across canopy composition and canopy cover treatment. The ANOVA model used to examine effects of oak and pine canopy composition, canopy cover, and understory treatments was the following:

$$Y_{i(j)kl} = \mu + \beta_j + \tau_{i(j)} + \gamma_k + \lambda_l + \beta\gamma_{jk} + \beta\lambda_{jl} + \gamma\tau_{i(j)k} + \lambda\tau_{i(j)l} + \gamma\lambda_{kl} + \beta\gamma\lambda_{jkl} + \varepsilon_{i(j)kl}$$

where:

μ = *Overall Mean*

β_j = Canopy Composition

$\tau_{i(j)}$ = Block (Canopy Composition)

γ_k = Canopy Cover Treatment

λ_l = Understory Treatment

$\beta\gamma_{jk}$ = Canopy Composition x Canopy Cover Treatment

$\beta\lambda_{jl}$ = Canopy Composition x Understory Treatment

$\gamma\tau_{i(j)k}$ = Canopy Cover Treatment x Block (Canopy Composition)

$\lambda\tau_{i(j)l}$ = Understory Treatment x Block (Canopy Composition)

$\gamma\lambda_{kl}$ = Canopy Cover Treatment x Understory Treatment

$\beta\gamma\lambda_{jkl}$ = Canopy Composition x Canopy Cover Treatment x Understory Treatment

$\varepsilon_{i(j)kl}$ = Error term consisting of the interaction $\tau\gamma\lambda_{i(j)kl}$

$i = 1, 2, 3$

$j = 1, 2$

$k = 1, 2, 3, 4$

$l = 1, 2, 3, 4$

Since prescribed fires contained only one treatment level, the fire treatment factor was not included in the overall ANOVA model. The effects of the fire treatment were measured by comparing conditions before and after each burn. One-tailed t-tests were used to assess paired differences between pre- and post-burn planted oak sprout heights and natural regeneration stem densities associated with each fire. All analyses were performed in NCSS 2015.

RESULTS

Canopy Cover and Basal Area

By 2015, percent canopy cover in all treatments had shifted significantly since the original implementation of canopy treatments in 1990-1991. Mean percent canopy cover was statistically greater in oak stands at 67.7% than in pine stands 47.2%. Within oak stands, the 0% or clearcut treatments had increased to 56.5%, and the 25% canopy treatments and 75% treatments were 65.1% and 67.7%, respectively (Table 4.1). The 100% control treatments averaged 73.7% canopy cover. As intended during treatment implementation, oak stand basal areas increased across canopy cover treatments (Table 4.1).

Within pine stands, mean canopy cover levels in 2015 had risen in both the 0% and 25% canopy cover treatments to 9.7% and 44.5%, respectively. In the 75% and 100% canopy cover treatments, mean canopy cover was 66.9% and 67.7%, respectively. Only the 75% canopy and 100% canopy treatment means were not statistically different from one another (Table 4.1). As planned, red pine stand basal areas increased across canopy cover treatments (Table 4.1).

Fire Characteristics

Mean maximum temperature recorded for the second fire across all treatments (108°C) was statistically higher than measured in the first prescribed fire (81°C) across all treatments (p = <0.0001). Mean temperatures for both burns were statistically higher for pine stands than oak stands (Figure 4.3). The mean temperature of the second fire in pine stands was 51°C higher than the first fire (significant with p= <0.0001). Within oak stands, mean temperatures for the second fire were not statistically different from mean temperatures in the first fire (p = 0.5894).

Within oak stands, 25% and 75% canopy cover treatments maintained greater mean temperatures across both fires (Figure 4.3). There were no statistical difference between canopy cover treatments for the first fire, but 0% and 25% canopy treatments differed for the second fire (Figure 4.3). Mean temperatures for 0% canopy cover treatments in pine stands were statistically lower than all other canopy cover treatments for both fires (Figure 4.3).

Planted Oak Responses Between 1991 and 2015

After 25 years, direct planted and nursery stock seedlings have suffered significant mortality across treatments. Oak and pine stand types differed in overall losses, with oak stands having fewer surviving seedlings than pine stands in 2009 ($p < 0.0001$). Hereafter, the measurement period of 2009 will be used as an end point for all oak stand variables pertaining to planted oak as a result of caging treatments being compromised for two oak block replicates between 2009 and 2015. Within oak stands in 2009 and pine stands in 2015, understory treatments and planting stock types had no effects and no significant interaction effects on long-term seedling survival or growth, (p = 0.3776 and 0.8101), respectively. These factors were subsequently dropped from the full model. Overall, pine stands combined with canopy cover treatments of 25%, 75%, and 100% maintained greater survival in planted seedlings for both 2009 and 2015 measurement periods (Figure 4.4). Mortality within oak stands was similar across canopy cover treatments through time (Figure 4.5). In pine stands, the 0% canopy cover treatment experienced greater losses early on than all other canopy cover treatments. Percent mortality within the 25%, 75%, and 100% canopy cover treatments was similar and statistically lower than the 0% treatment over time (Figure 4.5).

Height growth during the first growing season in 1991 did not differ between treatments, with planted oaks having a mean starting height of 7.69cm (Figure 4.6). By 2001, mean heights of planted and caged oaks differed statistically by stand type, with planted and caged oaks having a mean heights of 45.32cm (oak) and 82.13cm (pine) (Figure 4.6). In 2002, post burn heights were reduced across both stand types. Stand types maintained a similar pattern in mean heights with sprout heights in oak stands at 17.72cm and sprout heights in pine stands at 24.74cm (p = 0.0858). By 2006, mean heights had increased more in pine stands than in oak stands, with mean sprout heights of 57.49cm and 19.35cm, respectively. The second prescribed burn in 2008 had less effect on post burn mean heights. Height growth for all caged oaks differed in 2009 between oak and pine stand types (p = 0.0053) (Figure 4.6). In oak stands, planted and caged oaks had a mean height of 9.21cm, while planted and caged oaks in pine stand averaged 42.02cm. By 2015, planted and caged oaks within pine stand types had regained pre-burn heights with a mean of 101.33cm (Figure 4.6).

Canopy cover treatments had significant effects on mean height growth for planted and caged oaks in both oak and pine stands. Within oak stands, pre-burn heights of caged oaks in 2000 and 2001 were greater for 0% and 25% than for 75% and 100% canopy cover treatments ($p = 0.0163$) (Figure 4.7). However, no differences between canopy cover treatments occurred within oak stands since that time. Similar trends were noted within pine stand types with 0% and 25% canopy cover treatments having greater mean heights of caged seedlings in the pre-burn years of 2000 and 2001 than the 75% and 100% treatments. However, in 2009 and 2015, caged sprouts in the 25% and 75% canopy cover treatments had greater mean heights than those in either the 0% or 100% canopy cover treatments (Figure 4.8). Many height growth patterns in uncaged seedlings were similar to those in caged seedlings, although all mean heights remained below 30cm between 1991 and 2015.

Deer Browsing

Pine stands experienced greater levels of browsing by deer over the years than oak stands ($p < 0.0001$). The mean percentage of planted oaks browsed by deer was significantly greater in 0% and 25% canopy covers treatments over the years in both oak and pine stand types ($p < 0.0001$) (Figure 4.9). The percentage of seedlings browsed in the 75% canopy cover treatment within pine stands was statistically similar to that in the 0% and 25% canopy cover treatments. The 75% and 100% canopy cover treatments within oak stands and the 100% canopy cover treatment in pine stands all had lower percentages of deer damaged oaks across all measurement years. With respect to specific years, the percentage of seedlings browsed by deer was greater in 2000 (43.0%) than 2015 (27.6%) ($p < 0.0001$). All other years experienced lower and similar levels of damage as a result of browsing by deer. Furthermore, mean heights for caged oaks were greater than mean heights for uncaged planted oaks across years (Figures 4.7, 4.8, and 4.10). In

2009, height growth for caged as opposed to uncaged planted oaks differed across stand types with greater growth occurring in caged seedlings within pine stands.

Frost Damage

Late spring frost events damaged significant proportions of planted oaks over the past 25 years (Figure 4.11). Heavy levels of frost damage were quantified in five years (1992, 1996, 2000, 2001, and 2015) out of the total of ten measurement years. Stand type had no significant effect on percentages of seedlings with frost damage ($p = 0.1935$). With respect to canopy cover, the 75% and 100% treatments consistently received less frost damage than the 0% and 25% treatments ($p < 0.0001$).

Natural Oak Regeneration Responses Between 2001 and 2015

Across oak stands, oak regeneration comprised a lower relative proportion of the total regeneration in 2015 (16.17%) after two prescribed burns than in 2001 (35.92%) before burning. In 2001, natural oak regeneration was most abundant in pine stands and comprised 39.56% of the relative proportion of all regeneration in pine stands across treatments (Figure 4.12). However by 2015, the relative proportion of oak regeneration had declined to 27.84%, with red maple surpassing this proportion by 20.80%. Eastern white pine comprised the largest proportion of regeneration within the other category for both oak and pine stand types and across years.

The abundance of natural oak regeneration in all size classes was greater in oak stands than pine stands (Figure 4.13). Small size class (< 25 cm height) oak stem densities in oak stands decreased in 2015 from the original 2001 levels within 0% and 75% canopy cover treatments (Table 4.2). The regeneration of small size class, natural oak stems within the 25% and 100% canopy cover treatments remained unchanged between 2001 and 2015 (Table 4.2). No statistical difference was found between canopy cover treatments for 2015 ($p = 0.1968$). In pine stands, no detectable difference in small size class, natural oak regeneration occurred for the 0% canopy cover treatment. However, statistically significant declines in the abundance of small size class oak regeneration were quantified within the 25%, 75%, and 100% canopy cover treatments between 2001 and 2015 (Table 4.2). By 2015, canopy cover treatments within pine stands did not differ in the abundance of natural oak regeneration ($p = 0.1647$).

Natural oak regeneration within the medium size class (stems > 25 cm height and less than 2.54 cm dbh) was more abundant across all canopy cover treatments in all years for oak stands than pine stands (Figure 4.12). Stem densities in the 25% and 100% canopy cover treatments were statistically lower in 2015 than in 2001 (Table 4.2). In contrast, no statistical changes occurred in the 0% and 75% canopy cover treatments between 2001 and 2015. In 2015, there were no statistical differences in canopy cover treatments ($p = 0.2092$). Within pine stands, no statistical difference in the abundance of medium natural oak regeneration occurred between 2001 and 2015 (Table 4.2). In 2015 alone, the 75% treatment had statistically more abundant medium size class oak regeneration than the 0% canopy cover treatment ($p = 0.0417$) (Figure 4.13).

As with the prior regeneration size classes, large natural oak regeneration (stems > 2.54-10cm dbh) was greater in oak stands than in pine plantations ($p < 0.0001$) (Table 4.1, Figure 4.13). No statistical changes in the abundance of large oak regeneration with time were found for any canopy cover treatment across either stand type (Table 4.2).

Red Maple Regeneration Responses Between 2001 and 2015.

The relative proportion of maple regeneration in 2001 was higher in oak stands than in pine stands, comprising 51.09% and 27.12%, respectively (Figure 4.12). Over time, red maple regeneration increased in relative proportion for both stand types. In oak stands, red maple increased to 80.87% in 2015. Across pine stands, red maple increased to 48.64%.

The density of red maple stems across all regeneration size classes was greater in oak stands than in red pine plantations ($p < 0.0001$) (Table 4.3, Figure 4.14). Small size class (< 25 cm height) red maple regeneration densities in oak stands increased significantly over the course of this project within the 0% and 100% canopy cover treatments (Table 4.3). No significant reductions in small size class red maple stems were measured for 25% and 75% canopy cover treatments for oak stands. Within 2015, the 0% canopy cover treatment had the greatest abundance of small red maple stems in the oak stands ($p < 0.0001$) (Figure 4.14). No other differences between canopy cover treatments were observed within oak stands. In pine stands, small red maple stem densities were greater in 2015 compared to 2001 in 100% canopy cover treatments (Table 4.3). In addition, 0%, 25%, and 75% canopy cover treatments were quantified with lower levels of small red maple stem abundance in the 2015 measurement period than in 2001 ($p < 0.0001$). No statistical differences were measured for small red maple stem densities between the 0%, 25%, and 75% canopy cover treatments between 2001 and 2015.

Similarly, medium size class red maple regeneration densities were significantly higher in oak stands than in red pine stands ($p < 0.0001$) (Figure 4.14). Within oak stands, the 75% canopy cover treatment had greater medium red maple stem densities in 2015 compared to 2001 (Table 4.3). All other canopy cover treatments within oak stands were measured with statistically similar levels of medium red maple stem densities. Within 2015, the 25%, 75%, and 100% canopy cover treatments in oak stands had a greater abundance of medium red maple stems than in the 0% size class. In pine stands, declines in the number of medium red maple stems per hectare were measured for the 25% canopy cover treatment (Table 4.3, Figure 4.14). All other

2015 medium red maple stem densities were found to be statistically similar to 2001 levels in the 0%, 75% and 100% canopy cover treatments. Within 2015, canopy cover treatments did not differ in medium size class red maple abundance ($p = 0.8019$).

Large size class red maple regeneration was more abundant in oak stands than pine stands ($p < 0.0001$) (Figure 4.14). Within oak stands, decreases in large red maple abundance were measured in 2015 for the 0%, 25%, and 75% canopy cover treatments (Figure 4.3). The abundance of large red maple stems in 2015 within the 100% canopy cover treatment did not differ significantly from the 2001 level. Unlike the medium size class, the 0% canopy cover treatment had significantly greater abundance in large size class red maple regeneration ($p = 0.0001$), with 25% canopy cover treatments being statistically similar (Figure 4.14). In pine stands, a complete lack of large red maple regeneration was measured for 0%, 75%, and 100% canopy cover in both 2001 and 2015 (Figure 4.14). A nonsignificant change in the abundance of large size class red maple stems was seen for the 25% canopy cover treatment (Table 4.3). The occurrence of red maple stems in this treatment was the result of stump sprouts persisting from two large red maple stems originally removed during the 1990-1991 canopy reduction cuts.

DISCUSSION AND CONCLUSION

Throughout the 25-year duration of this study, canopy cover treatments, understory treatments, and two prescribed fires had variable effects on artificial and natural oak regeneration in Michigan oak and pine stands. Greater mortality in planted oak within oak stands than in pine stands supports the hypothesis that oak regeneration may be facilitated to a greater degree in pine stands. This hypothesis was further supported by greater natural oak regeneration in pine stands (Figure 4.12) and reduced mortality of planted oaks observed in pine stands at 25%, 75%, and

100% canopy cover treatments relative to the 0% or clearcut canopy cover treatment. In addition to survival, greater mean heights were observed for planted oak in pine than oak stands. Aside from the early establishment years (i.e., 1990-1992) and burn years (i.e., 2002 and 2008), average heights were statistically greater in pine stands than in oak stands.

Overstory canopy treatments produced varying but long-term effects on mean oak heights. In oak stands, the two treatments with the least amount of cover, the 0% and 25% treatments, produced the greatest mean height. This is consistent with the conclusions of Brose (2008), who suggested that oak stands should be thinned to 50% or less canopy cover in order to stimulate height growth in oak regeneration. Conversely in pine stands, the two treatments with moderate cover (25% and 75% canopy cover) produced greater mean heights consistently across years, excluding the establishment and burn years. By 2015, the mean canopy cover across both of these canopy cover treatments was approximately 65%, which exceeds Brose's (2008) recommendation. The lack of red maple midstory and other understory competitors in pine stands likely provided planted oaks with increased light levels, which would have been unavailable in the more dense understories of the mixed oak stands. Differences in crown architecture could have also contributed to greater light levels in pine stands. Buckley et al. (1999) documented greater understory light levels in pine stands than in oak stands (at a given basal area) on these study sites in 1992.

Aside from competing for limited resources (space, light, moisture, and nutrients), the observed impacts of deer browsing and late-spring frosts provide further evidence of additional factors limiting oak regeneration success. Though local deer densities were not determined across treatments or individual years, greater percentages of planted oaks browsed by deer were recorded in pine stands than in oak stands. Although this could result from larger deer populations within pine stands, Buckley et al. (1998) formulated an alternative explanation based on oak seedlings having greater apparency within pine stands than in the understories of oak stands. In addition, Buckley et al. (1998) suggested that the greater abundance of oak and maple stump sprouts in oak stands with canopy cover reduction treatments may have provided deer with an alternative food source that was lacking in pine stands. Studies have reported preferential feeding behaviors in white-tailed deer (*Odocoileus virginianus*), whereby seedlings and saplings of one species are fed upon more frequently than another (Hough 1965; Anderson and Loucks 1979). The ability to alter species abundance and forest community composition across trophic levels has labeled white-tailed deer as a keystone herbivore (Waller and Alverson 1997). Furthermore, a study in Illinois found that deer preferred white oak (*Quercus alba*) and shagbark hickory (*Carya ovata*), even though they are less abundant than other tree species (Strole and Anderson 1992). Deer have also been observed feeding more heavily on different species throughout the year, such as oak leaves and twigs during the summer months and other species such as red maple during the winter (Bramble and Goddard 1953). In their study, Bramble and Goddard (1953) determined summer browsing of oak leaves and twigs to be more detrimental to oaks than the winter browsing of twigs was to red maple. Boerner and Brinkman (1996) have concluded that effects of deer browsing are more important factors in determining tree seedling mortality than environmental conditions. It is evident in this study that deer are severely browsing planted oak seedlings across treatments. Regardless of treatment type, mean heights for uncaged oak are all substantially less than the mean heights of caged oak. If the findings from the previously mentioned studies hold true and deer hinder red maple less than oak seedlings and saplings, this may further explain the differential increase in natural red maple regeneration over natural oak regeneration observed in this study. Although the impact of browsing is considered more of an aggravating factor underlying the oak regeneration problem in regions with lower deer populations, the differences in heights of caged and uncaged seedlings over the past 25 years suggests that browsing is an overriding factor in the study area.

Frost as a limiting factor in the regeneration of North American oak species has seldom been considered in the literature. Late-spring frosts that damaged a significant percentage of planted oaks were documented in half of the ten years when the study areas were remeasured. Although stand type had no effect in protecting or sheltering planted oaks from late-spring frost, heavier canopy cover treatments had lower proportions of frost damage than lighter canopy cover treatments. One European study found that frost damage during stem elongation periods, for five-year-old seedlings, was more damaging to overall height growth than damages acquired during later stages of development when elongation had concluded (Char and Colin 1999). Another European study measured reduced height growth in European beech (*Fagus sylvatica*) following frost damage in open gaps and clearcuts (Lüpke 1998). In addition, working in Pennsylvania, Nichols (1968) found frost and insects to be the two most significant factors leading to northern red oak crown dieback. Furthermore, García-Mozo et al. (2013) showed that temperatures near 0°C during initial stages of catkin development resulted in complete halting of microsporogenesis and catkin elongation. This resulted in a loss in pollen production and a failure in that year’s acorn crop. These negative factors associated with frost may be limiting the reproductive success of overstory canopy trees while simultaneously reducing the ability of young oak seedlings to reach a competitive height advantage necessary for outcompeting other hardwood species.

Understory treatments had no statistical effect on mean heights or survival of planted oaks, indicating that understory competition had less of an impact on oak regeneration than overstory competition across time. In the early stages of this project, Buckley et al. (1998) reported an understory by canopy cover treatment interaction, in which the removal of herb and shrub layers within the 0% canopy cover treatment negatively impacted the growth and survival of planted oaks. It was suggested that these understory saplings provided planted oaks a temporary shelter from frost and deer damage when overstories were absent. This interaction was relatively short-term and did not continue across time. The lack of significant effects of understory treatments across time does not coincide with the results reported by Lorimer et al. (1994) who found greater survival and growth in planted oaks with understory vegetation removals than in controls. An inability to consistently maintain understory treatments over the 25-year duration of this project may have reduced the overall effects of understory treatments.

The role of fire in regenerating oak has ecological merit and has been a long-standing focus in the literature (Crow 1988; Abrams and Nowacki 1992; Abrams 1992; Brose and Van Lear 1998; Brose et al. 1999a; Brose et al. 1999b; Abrams 2005; Iverson et al. 2008). However, results for this long-term study do not support this fire hypothesis. For burning techniques to successfully promote oak regeneration, two conditions must be met: 1) oaks must have higher survival rates than competing species and 2) surviving oaks must out-perform competing species (i.e., they must have greater growth rates) (Dey and Hartman 2005). Percent mortality of planted oaks following the first fire increased in both oak and pine stands. However, following the second fire, fewer losses were observed in pine stands, and oak stands continued to suffer higher mortality rates. Mean height growth of sprouts was greater in pine stands than oak stands. However, both prescribed burns forced planted oak seedlings to resprout each time following fire top-kill. Because the pine stands had very little red maple regeneration at initiation, no measureable benefit was observed in the burning of pine stands. This treatment ultimately reduced the mean heights of planted oak regeneration and kept planted oaks within the reach of browsing deer longer, which was consistently more widespread in pine stands than in oak stands throughout this study. Furthermore, burning in oak stands temporarily set red maple back, but proved ineffective in reducing the abundance of red maple sprouts. Coupled with the increased mortality of planted oak within oak stands, the use of fire should be carefully considered in similar systems. The use of more frequent, low-intensity fires long-term over several decades may be more effective in controlling red maple, but will also have direct impacts on regenerating oaks.

The prescribed burns were largely ineffective in stimulating natural oak regeneration. In all but one canopy cover treatment, natural oak regeneration either remained unchanged, or significantly declined. The only increase in stems per hectare occurred in the medium size class of oak regeneration within the 100% canopy cover treatment in oak stands. Reasons for this increase remain unclear, but fire may have prompted more stump sprouts from larger diameter oaks, or the heavier and more intact overstory may have resulted in less abundant red maple in the understory.

The increased abundance of woody competition across treatments, especially red maple stems, failed to support the hypothesis that woody competitors in the understory would be reduced with the first and second prescribed fires. The two fires differed, with the first prescribed burn being cooler than the second. However, the first fire reduced medium and large size class red maples more than the second. In the initial fire, medium size class red maple densities were reduced by an average of 50% across all canopy cover treatments, whereas the second fire reduced the same size class densities by 35%. Unfortunately, these reductions in medium size class red maple regeneration were not sustained. By 2015, stem counts had returned to 2001 pre-burn levels within the 0%, 25%, and 100% canopy cover treatments. The 75% canopy cover treatment had an increase of more than 7,500 red maple stems per hectare.

Similarly, large size class red maple stems were reduced in the first fire (70%) and the second fire (40%). Reductions in large size class red maple stems following both fires were greater within the 0% and 25% canopy cover treatments. The majority of large size class red maple stems across canopy cover treatments were stump sprouts, which originated from stumps left behind when trees were removed during the 1991 canopy cover reduction cuts. According to Blankenship and Arthur (2006), this form of regeneration is capable of rapid and sustained height growth post-disturbance. Between 2001 and 2015, reduction in large stem counts were observed in the 0%, 25%, and 75% canopy cover treatments. Reasons for this reduction are less clear, as many stems have been suspected of transitioning into dominant and co-dominant canopy positions, while others have succumbed to the effects of fire-induced stressors such as pathogens, pests, and diseases.

The significant increase from 2001 to 2015 in small size class red maple stems across canopy cover treatments provides strong evidence for red maple’s propensity to root sprout from top-killed stems and seed in from adjacent forest (Gilbert et al. 2003). Reducing the abundance of red maple stems would require additional burning, which would further reduce the competitive ability of the planted and natural oaks across stands.

The relatively low quantity of red maple stems present in pine stands prior to the implementation of fire limited the ability to interpret significant declines in red maple stems per hectare post-fire (for all canopy cover treatments). However, aside from fire, pine stands were able to maintain a lower abundance of red maple regeneration than in any other treatment throughout the course of this study (Buckley et al. 1998; Hartman et al. 2005). Hartman et al.

(2005) suggested that a lack of overstory red maples within pine stands prior to the initial reduction cuts in 1991 was an indication of maple's reduced ability to survive on these sites. Poor survival may have occurred as far back as the 1930s, when these red pine plantations were becoming established. Abrams (1998) reported red maple samaras to be one of the lightest samaras produced by any North American maple species. This characteristic, which aids in wind dispersal, may hinder red maple's ability to establish across pine stands. The low energy reserves contained in the light-weight red maple seeds may limit the ability of red maple radicles to penetrate mineral soil beneath pine litter.

This investigation in Michigan oak and pine stands over the past 25-years provides important management implications. First, if advanced oak regeneration is not naturally available, then it will likely have to be achieved through planting. Second, the benefits from using pine stands to facilitate oak regeneration include fewer oak competitors and greater height growth and survival in planted oaks. This may provide opportunities for establishing both mixed oak-pine plantings or pure oak stands, depending on the level of pine canopy removal once planted oaks are adequately established. Third, an overstory canopy reduction treatment is needed to reduce overstories to 25%-75% canopy cover. These canopy cover treatments produced the greatest mean heights and percent survival of planted oaks, while simultaneously providing greater levels of frost protection and a lower incidence of browsing. Shelterwood removal could have potentially enhanced the development of planted oaks. In this study, the greater height growth response to an overstory removal would have likely been obtained ten years after establishment in 2000. Fourth, if deer densities are too high, protective measures such as caging or reductions in deer numbers should be considered. Finally, the use of prescribed burning for reducing hardwood competitors is not recommended under the circumstances of this study, which included heavy deer browsing. Fire consistently reduced the competitive nature of planted oaks and failed to reduce hardwood competition such as red maple across treatments. However, in this study, fire may not have been applied in a scenario where it would be helpful. Hartman et al. (2005) concluded prescribed burning was not necessary in pine stands, which in this case were relatively free of midstory competitors compared to the oak stands. In addition, planted oak seedlings may not have been large enough to benefit from burning.

Results for this research suggest additional testing of potential positive interactions between oaks and pines would be beneficial. Specifically, future investigations into mycorrhizal associations, increased availability of limited resources (i.e., nutrients, moisture, space, and light), protection against winter stressors such as frost, snow, and ice loads, allelopathy, dispersal vectors, microsite conditions, disease and insect prevention, and fire regimes would be instructive. In addition to investigating potential positive interactions between oak and pine, negative interactions between pines and competitors of oak should also be investigated. Though mechanisms underlying positive interactions between oak and pine may be difficult to identify, additional long-term underplanting studies established throughout eastern forests would be helpful. These plantings would facilitate the development of underplanting methodologies and practices that could lead to more diverse oak-pine mixtures.

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APPENDIX

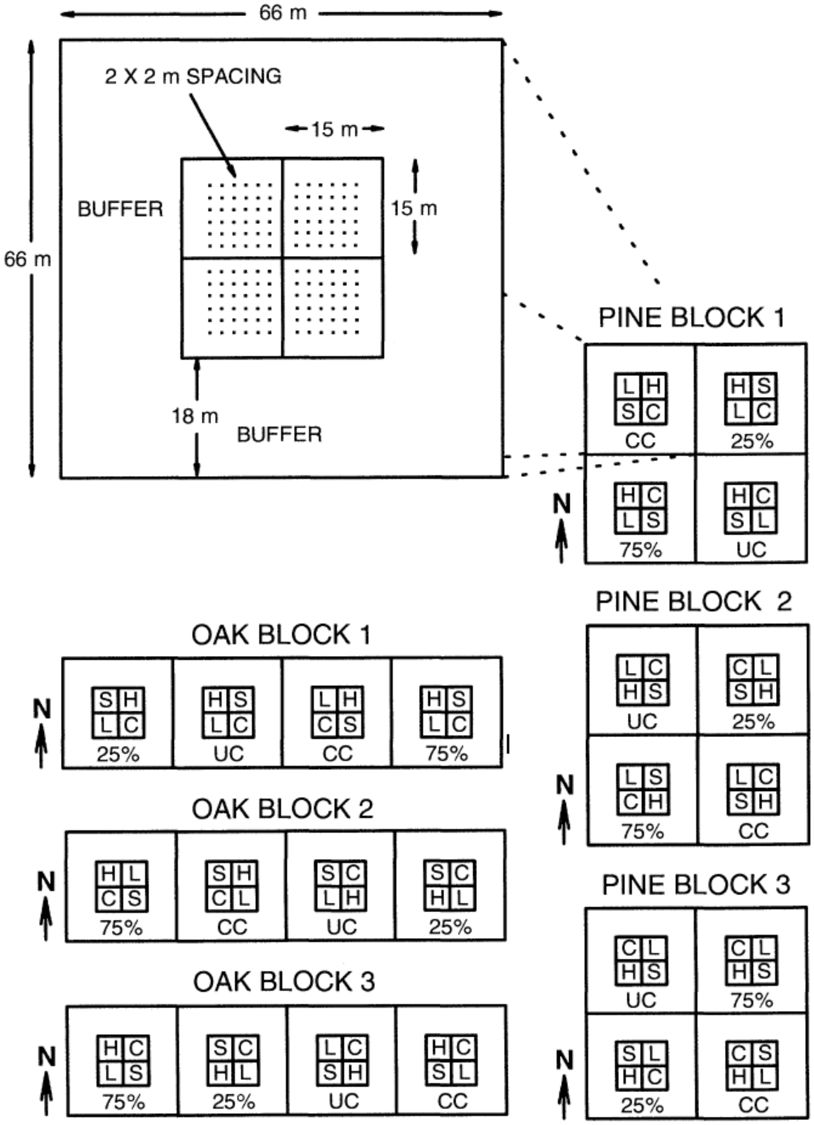


Figure 4.1. Experimental design as reproduced from Buckley et al. (1998), northern Lower Michigan, USA: planting locations, buffer zones, understory treatment plots, and canopy cover treatment plots (to scale) within replicate oak and pine blocks. True spatial relationships between replicate blocks have been altered for the purpose of efficient presentation although shape and orientation of blocks are correct. For canopy cover treatments, CC = clearcut or 0% canopy cover, 25% = 25% canopy cover, 75% = 75% canopy cover, UC = uncut control or 100% canopy cover. For understory treatments, C = control, L = litter removal, H = herb removal, and S = shrub removal.

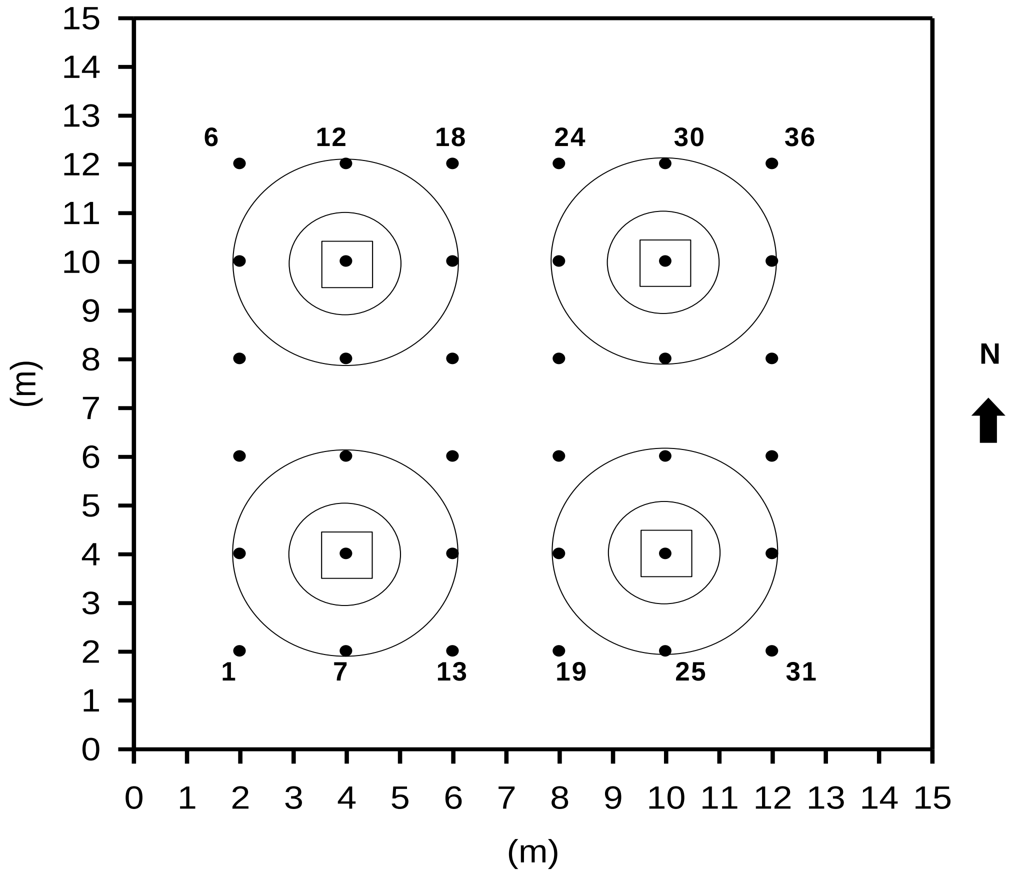


Figure 4.2. Sampling plots within each 15 x 15m subplot. Plot centers were located at planting locations 8, 11, 26, and 29 in the planting grid. Image reproduced from DeBord's thesis in 2008.

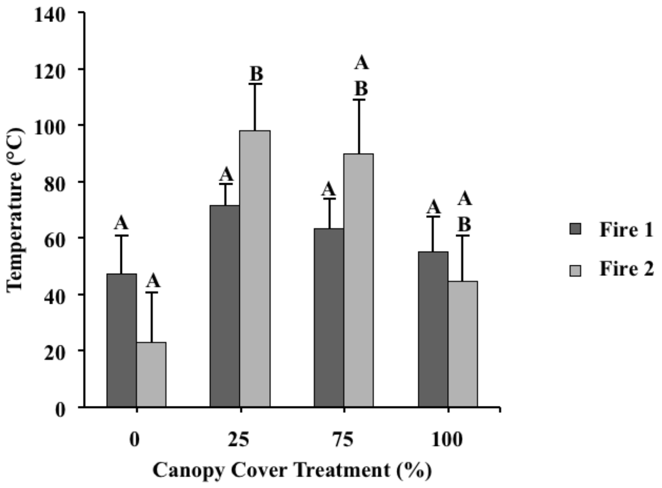
Table 4.1. Basal area and percent canopy cover by canopy treatment within oak and pine stands for 1992 and 2015. Canopy treatment codes are as described in Figure 4.1. Standard errors are in parenthesis.

	Oak Stands		Pine Stands	
	1992	2015	1992	2015
Canopy Cover Treatment (%)	Basal Area (m^2 * ha^{-1})*			
0%	0	10.9 (2.3)	0	1.2 (0.5)
25%	6.1 (2.8)	9.2 (0.8)	8.6 (0.3)	15.7 (1.2)
75%	15.4 (0.8)	20.5 (0.71)	34.3 (2.1)	39.4 (1.6)
100%	34.0 (0.7)	35.8 (1.2)	42.8 (1.4)	44.8 (2.0)
	Canopy Cover (%)$^+$			
0%	0	56.5 (7.4)	0	9.7 (4.2)
25%	28 (0.7)	65.1 (3.4)	27 (1.2)	44.5 (2.4)
75%	70 (0.6)	67.7 (1.5)	69 (4.0)	66.9 (0.98)
100%	86 (1.5)	73.7 (0.68)	78 (4.2)	67.6 (2.0)

Note: Overstory basal area was measured using a 10 factor prism.

* *n* = 4. + *n* = 16.

Oak Stands:



Pine Stands:

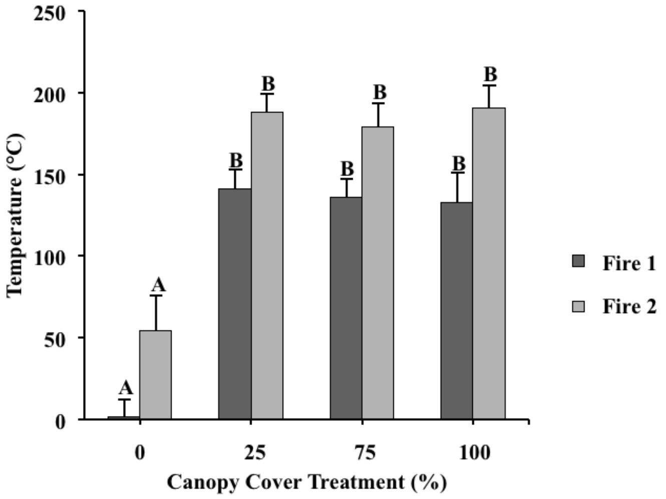


Figure 4.3. Mean fire temperatures (°C) by fire and canopy cover treatment within oak and pine stand types. Means with the same letter do not differ statistically based on Tukey's HSD (α = 0.05). Upper case letters indicate statistical differences across canopy cover treatments in fire temperatures during the first fire applied in 2002. Lower case letters indicate statistical differences in fire temperatures during the second fire implemented in 2008. Error bars represent one standard error of the mean.

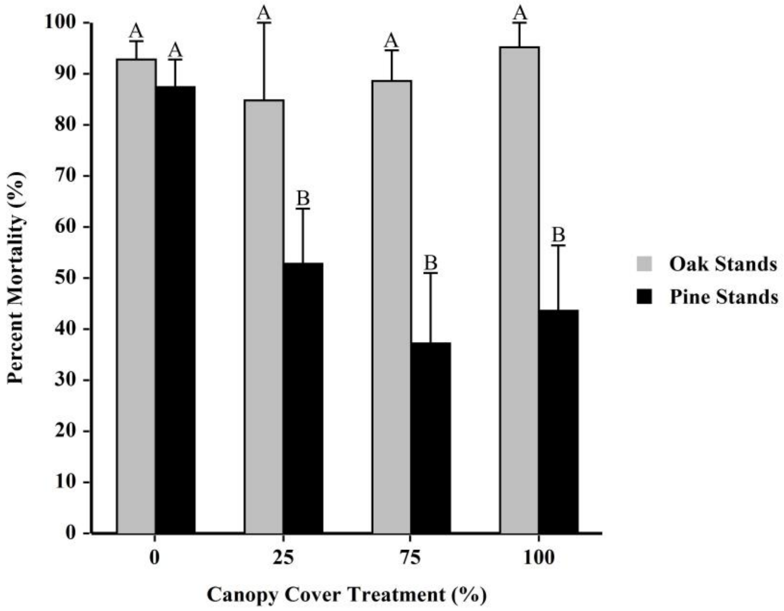
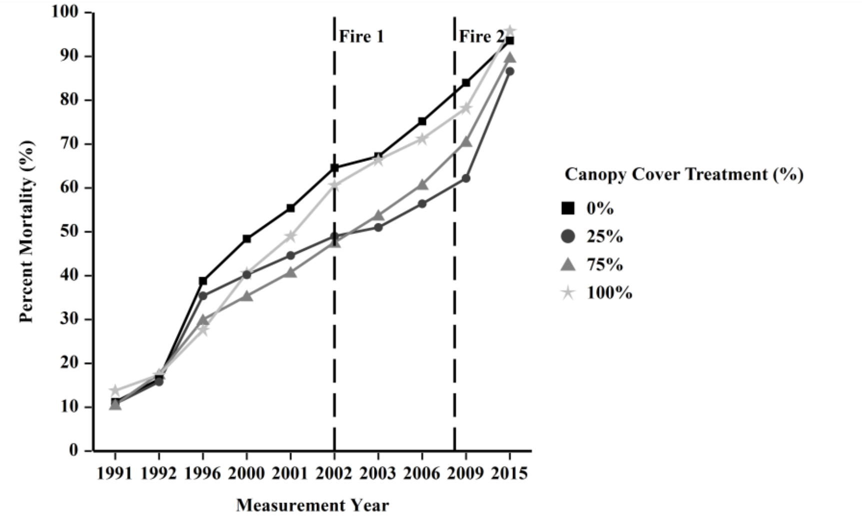


Figure 4.4. Percent mortality for planted oaks within oak and pine stands by canopy cover treatments. Means with the same letter are not statistically different among treatments based on Tukey's HSD (α = 0.05). Letters correspond to differences among canopy cover treatments within a given stand type. Error bars represent one standard error of the mean.

Oak Stands:*



Pine Stands:

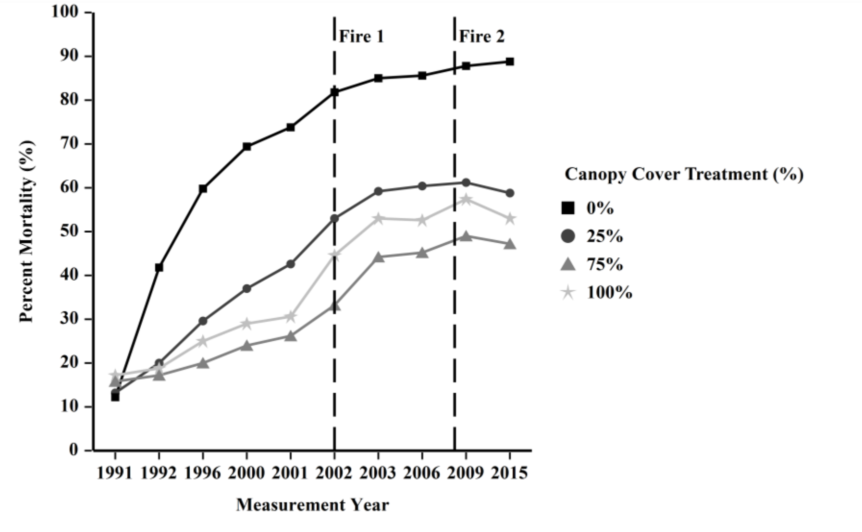


Figure 4.5. Percent mortality for planted oaks by measurement year and canopy cover treatments. Means are calculated across all other treatment levels. *Two replications within the caging treatment were compromised between the 2009 and 2015 measurement periods in the oak stands. Therefore, percent mortality for oaks in 2015 should be interpreted with caution.

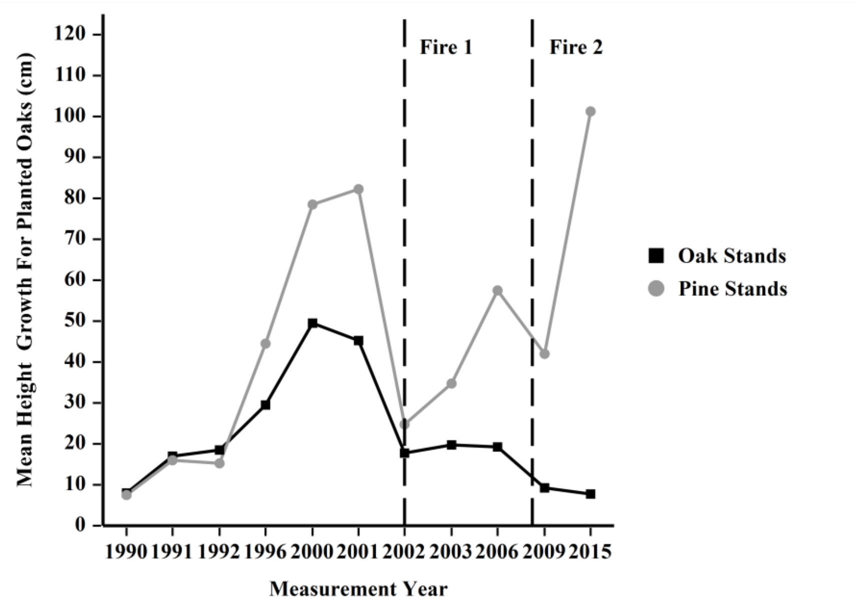
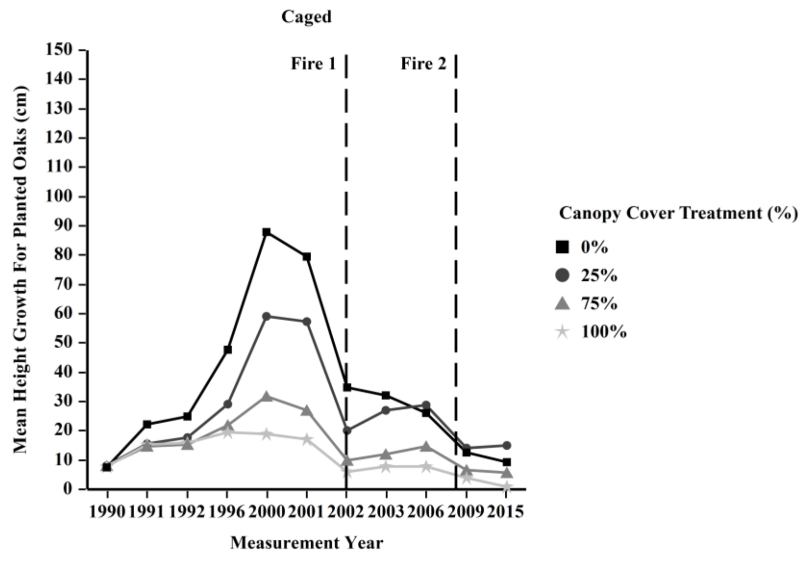


Figure 4.6. Mean height growth for planted oaks by measurement year and stand type. Means calculated across all other treatment levels are for caged seedlings only. *Two replications within the caging treatment were compromised between 2009 and the 2015 measurement period. Therefore, mean height growth for oaks in 2015 should be interpreted with caution.

Oak Stands:*



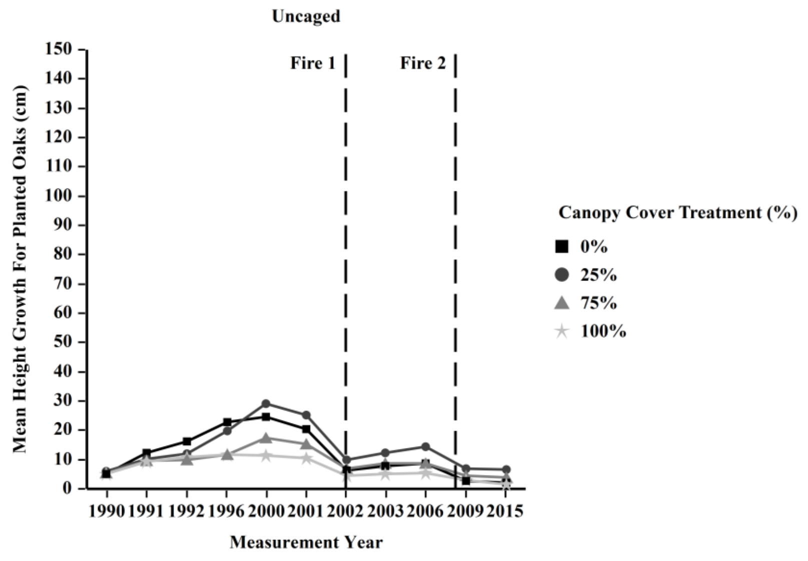


Figure 4.7. Height growth responses for planted oak within canopy cover treatments and years. Means are calculated across all other treatment levels. *Two replications within the caging treatment were compromised between 2009 and the 2015 measurement period. Therefore, mean height growths for caged oaks in 2015 should be interpreted with caution.

Pine Stands:

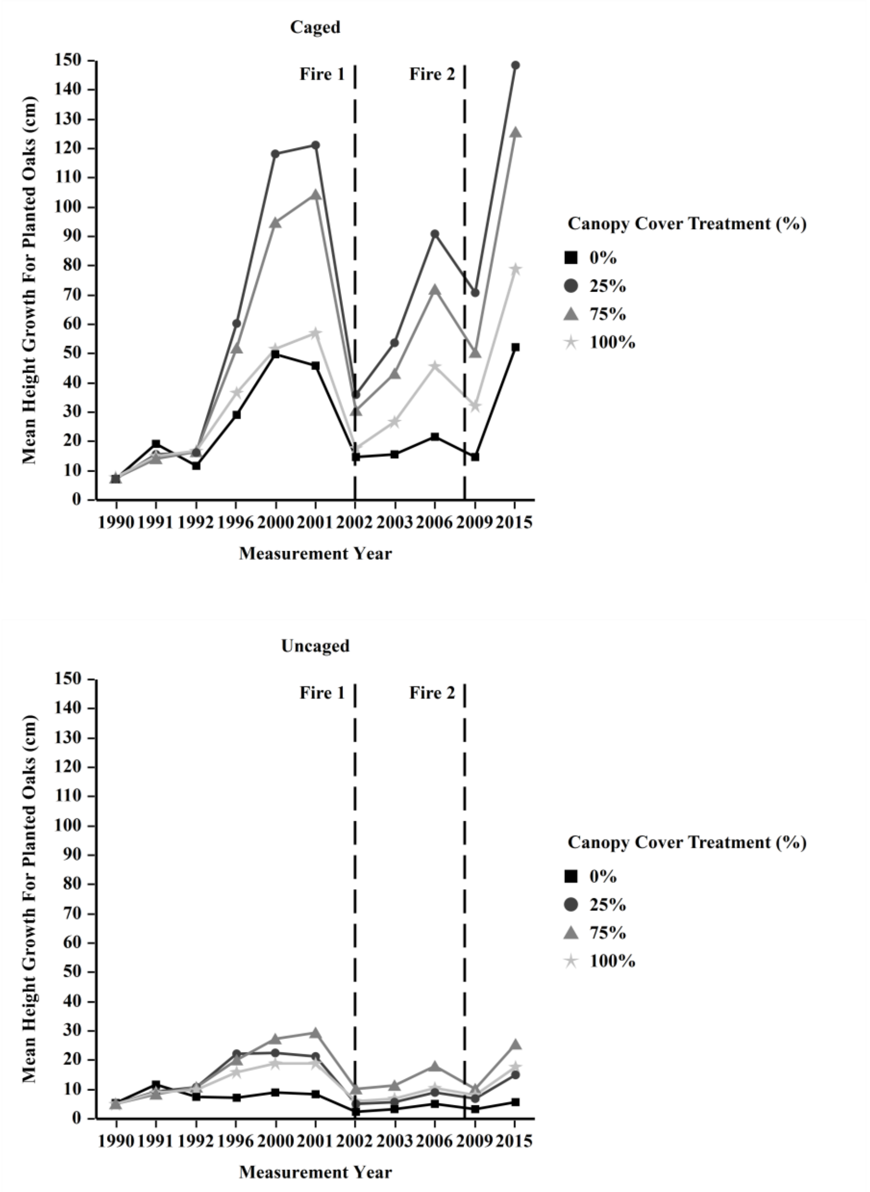


Figure 4.8. Height growth responses for planted oak within canopy cover treatments and years. Means are calculated across all other treatment levels. *Two replications within the caging treatment were compromised between 2009 and the 2015 measurement period. Therefore, mean height growths for caged oaks in 2015 should be interpreted with caution.

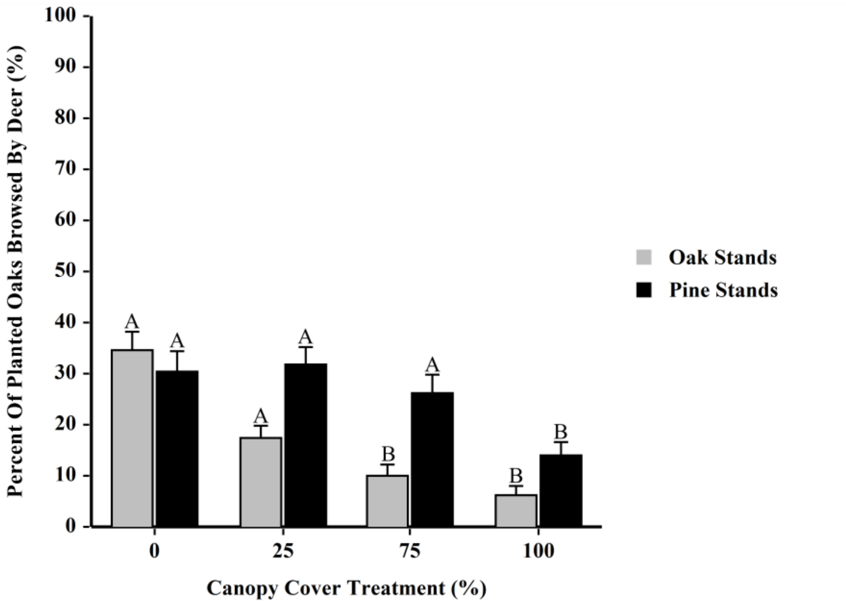
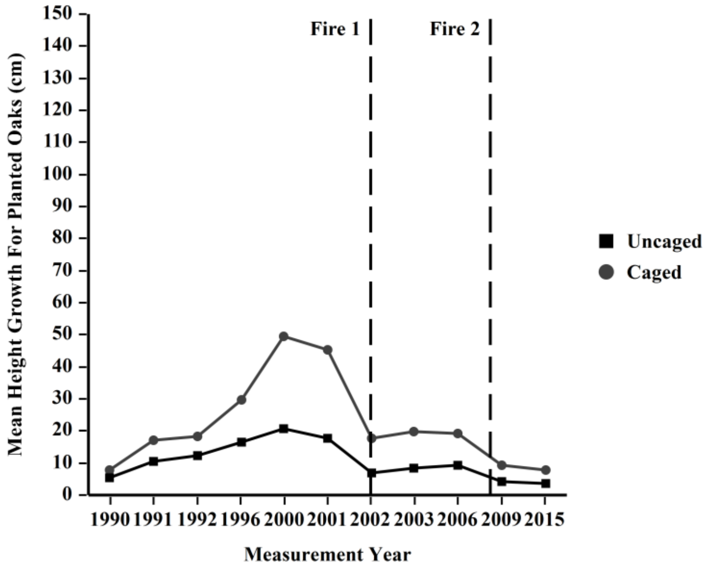


Figure 4.9. Mean percentage of planted oaks browed by deer across years, stand types and canopy cover treatments. Within stand types, means with the same letter are not statistically different among treatments based on Tukey's HSD ($\alpha = 0.05$). Letters correspond to differences among stand types and canopy cover treatments. Error bars represent one standard error of the mean.

Oak Stands:*



Pine Stands:

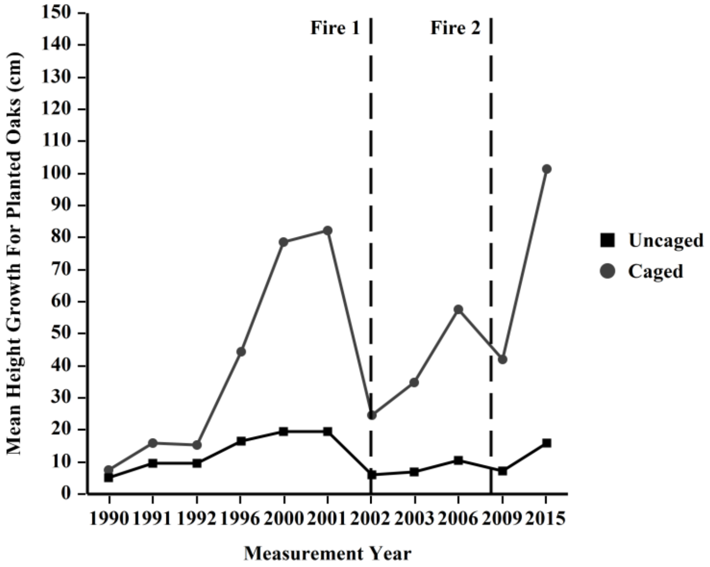


Figure 4.10. Mean height growth for caged and uncaged planted oaks for each measurement year. Means are calculated across all other treatment levels. *Two replications within the caging treatment were compromised between 2009 and 2015. Therefore, mean height growths for oaks in 2015 should be interpreted with caution.

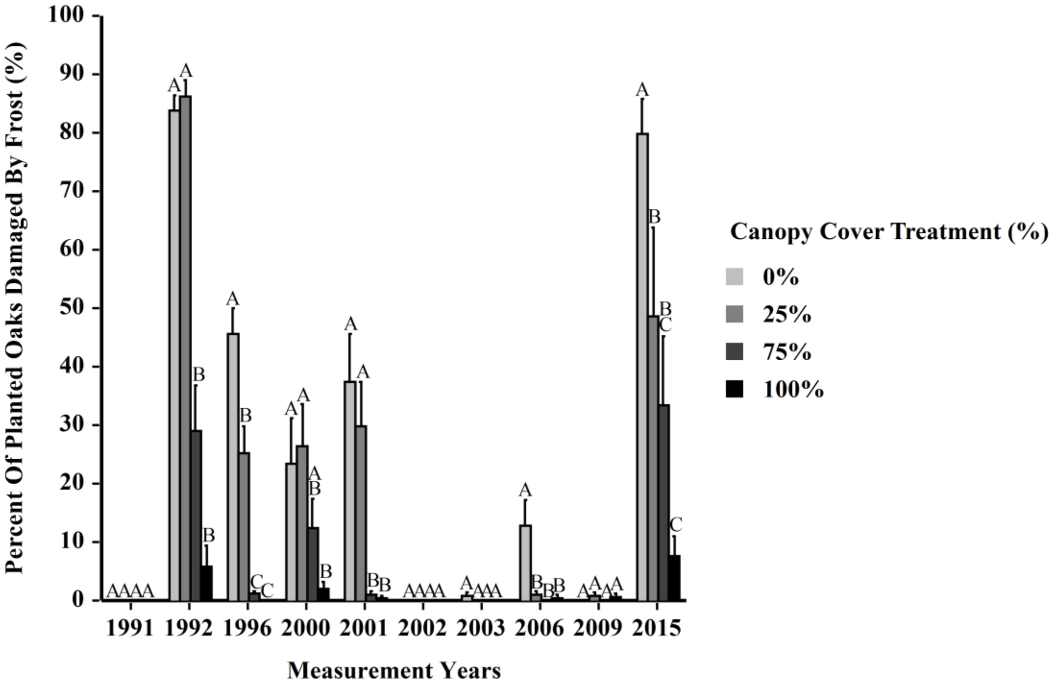


Figure 4.11. Percentage of planted oaks damaged by frost within canopy cover treatments.

Within years, means with the same letter are not statistically different among treatments based on Tukey's HSD ($\alpha = 0.05$). Error bars represent one standard error of the mean.

Oak Stands: **Pine Stands:**

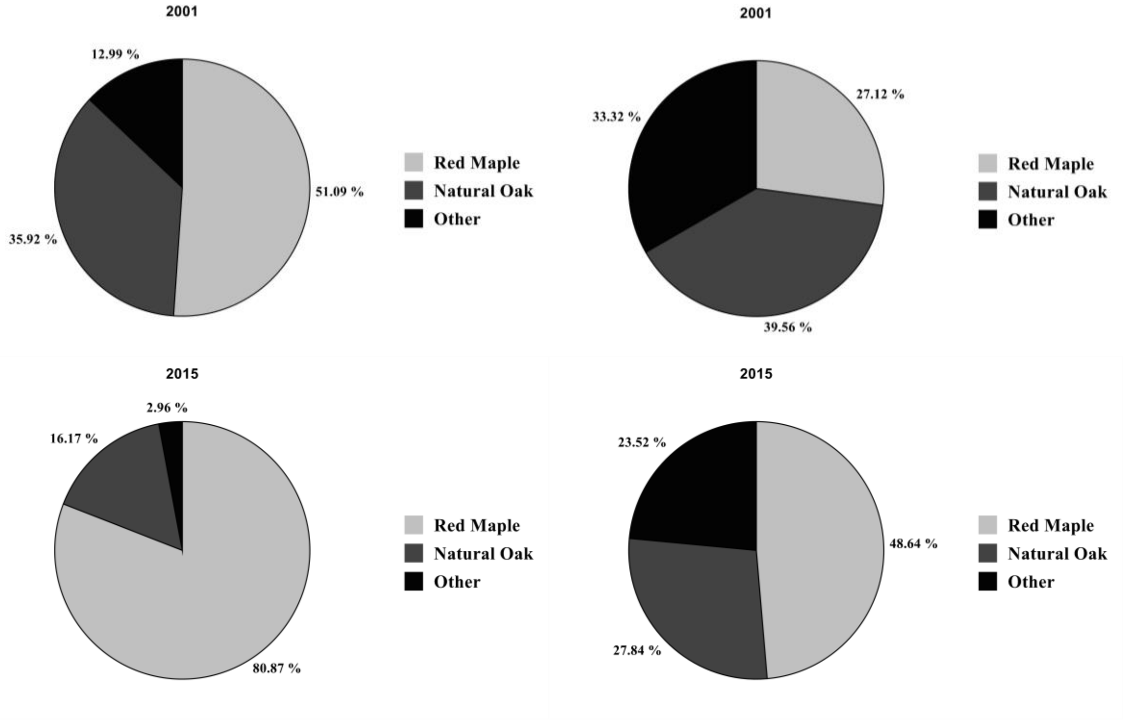


Figure 4.12. Relative proportions of regeneration calculated across all other treatment levels within oak and pine stand types for 2001 and 2015.

Figure 4.13. Small, medium, and large natural oak regeneration within oak and pine stands by year and canopy cover treatment. Canopy cover treatment codes are as described in Figure 4.1. Within a year, means with the same letter are not statistically different among canopy treatments based on Tukey's HSD ($\alpha = 0.05$). Error bars represent one standard error of the mean.

Natural oak regeneration in oak stands: **Natural oak regeneration in pine stands:**

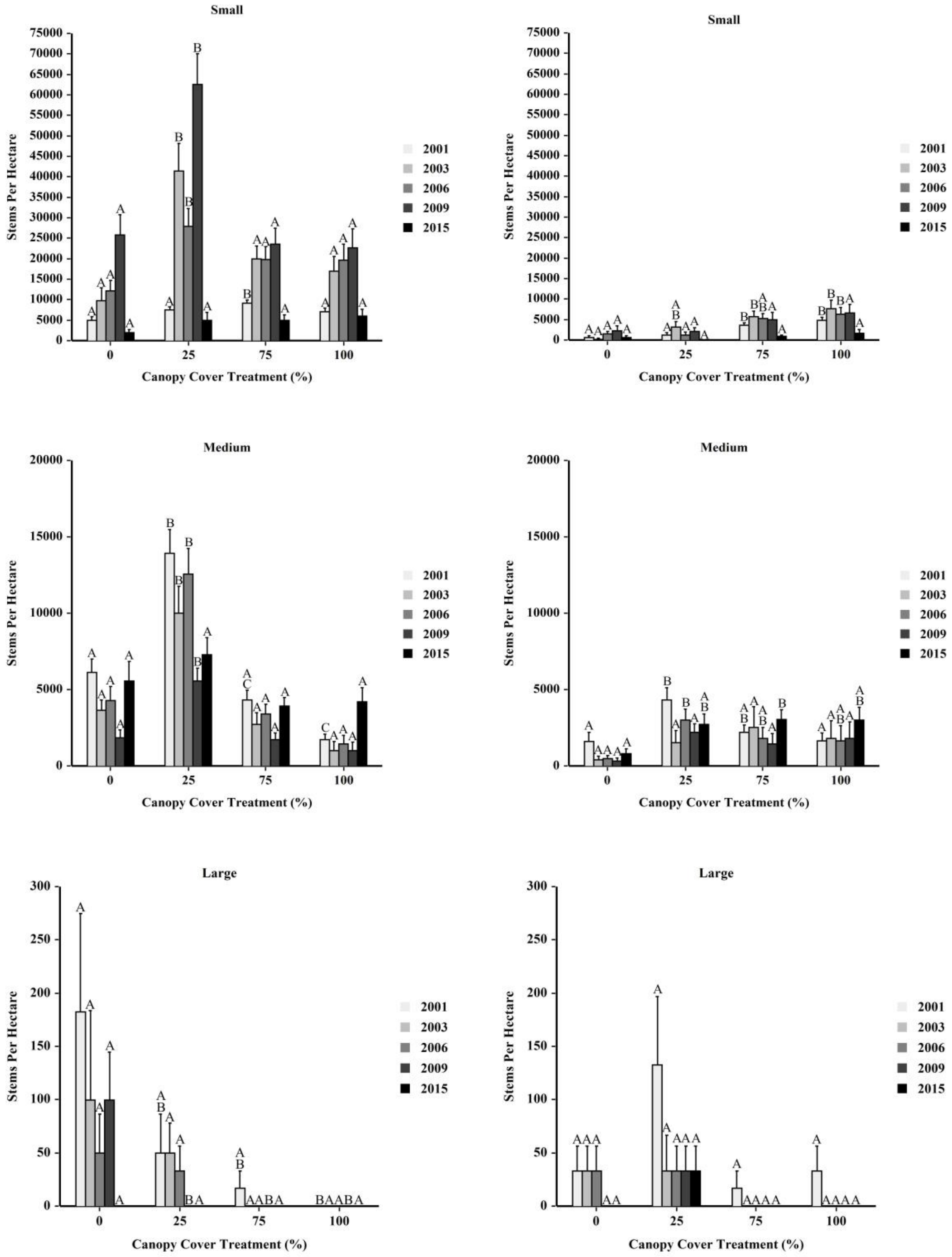


Figure 4.13. Continued.

Table 4.2. Natural oak regeneration. Stems are per hectare by size class, stand type, and canopy cover treatment. Bold p-values indicate statistical differences between years 2001 and 2015 following two prescribed fires. These values are based on two-tailed t-tests at α= 0.05 significance. N = 48 sampling plots per canopy treatment.

Size Class	Stand Type	Canopy Cover Treatment (%)	Start 2001	End 2015	Difference (2015-2001)	*p-value*
Small	Oak	0	5,000.00	1,875.00	-3,125.00	**0.0058**
		25	7,500.00	5,000.00	-2,500.00	0.1988
		75	9,166.67	5,000.00	-4,166.67	**0.0062**
		100	7,083.33	6,041.67	-1,041.67	0.5639
	Pine	0	625.00	625.00	0.00	1.0000
		25	1,250.00	0.00	-1,250.00	**0.0127**
		75	3,541.67	833.33	-2,708.33	**0.0004**
		100	4,791.67	1,666.67	-3,125.00	**0.0121**

Table 4.2. Continued.

Size Class	Stand Type	Canopy Cover Treatment (%)	Start 2001	End 2015	Difference (2015-2001)	*p-value*
Medium	Oak	0	10,610.67	10,345.40	-265.27	0.8719
		25	23,542.42	11,870.68	-11,671.73	**0.0000**
		75	6,432.72	4,774.80	-1,657.92	0.1502
		100	1,790.55	5,437.97	3,647.42	**0.0038**
	Pine	0	1,591.60	795.80	-795.80	0.2144
		25	4,310.58	2,718.98	-1,591.60	0.0521
		75	2,188.45	3,050.57	862.12	0.1803
		100	1,657.92	2,984.25	1,326.33	0.1148
Large	Oak	0	182.37	0.00	-182.37	0.0546
		25	49.74	0.00	-49.74	0.1825
		75	16.58	0.00	-16.58	0.3224
		100	0.00	0.00	0.00	.

Table 4.2. Continued.

Size Class	Stand Type	Canopy Cover Treatment (%)	Start 2001	End 2015	Difference (2015-2001)	*p-value*
	Pine	0	33.16	0.00	-33.16	0.1595
		25	132.63	33.16	-99.47	0.1351
		75	16.58	0.00	-16.58	0.3224
		100	33.16	0.00	-33.16	0.1595

Table 4.3. Red maple regeneration. Stems are per hectare by size class, stand type, and canopy cover treatment. Bold p-values indicate statistical differences between years 2001 and 2015 following two prescribed fires. These values are based on two-tailed t-tests at α= 0.05 significance. N = 48 sampling plots per canopy treatment.

Size Class	Stand Type	Canopy Cover Treatment (%)	Start 2001	Ending 2015	Difference (2015-2001)	*p-value*
Small	Oak	0	2,708.33	110,000.00	107,291.67	**0.0011**
		25	5,000.00	8,125.00	3,125.00	0.1043
		75	7,708.33	10,416.67	2,708.33	0.2079
		100	9,791.67	42,291.67	32,500.00	**0.0000**
	Pine	0	208.33	208.33	0.00	1.0000
		25	1,041.67	1,875.00	833.33	0.3767
		75	1,250.00	1,250.00	0.00	1.0000
		100	4,166.67	16,875.00	12,708.33	**0.0164**

Table 4.3. Continued.

Size Class	Stand Type	Canopy Cover Treatment (%)	Start 2001	Ending 2015	Difference (2015-2001)	*p-value*
Medium	Oak	0	9,350.65	8,289.58	-1061.07	0.4341
		25	23,476.10	24,404.53	928.43	0.6507
		75	22,481.35	30,107.77	7,626.42	**0.0018**
		100	16,114.95	16,579.17	464.22	0.8250
	Pine	0	66.32	66.32	0.00	1.0000
		25	5,902.18	1,127.38	-4,774.80	**0.0082**
		75	795.80	397.90	-397.90	0.2243
		100	331.58	397.90	66.32	0.7097
Large	Oak	0	2287.85	994.72	-1,293.13	**0.0023**
		25	1823.65	547.10	-1,276.56	**0.0012**
		75	646.57	66.31	-580.25	**0.0009**
		100	116.05	16.58	-99.47	0.1825

Table 4.3. Continued.

Size Class	Stand Type	Canopy Cover Treatment (%)	Start 2001	Ending 2015	Difference (2015-2001)	*p-value*
	Pine	0	0.00	0.00	0.00	.
		25	66.31	0.00	-66.31	0.2093
		75	0.00	0.00	0.00	.
		100	0.00	0.00	0.00	.

Figure 4.14. Small, medium, and large red maple regeneration within oak and pine stands by year and canopy cover treatment. Canopy cover treatment codes are as described in Figure 4.1. Within a year, means with the same letter are not statistically different among canopy treatments based on Tukey's HSD (α = 0.05). Error bars represent one standard error of the mean.

Red maple regeneration in oak stands: **Red maple regeneration in pine stands:**

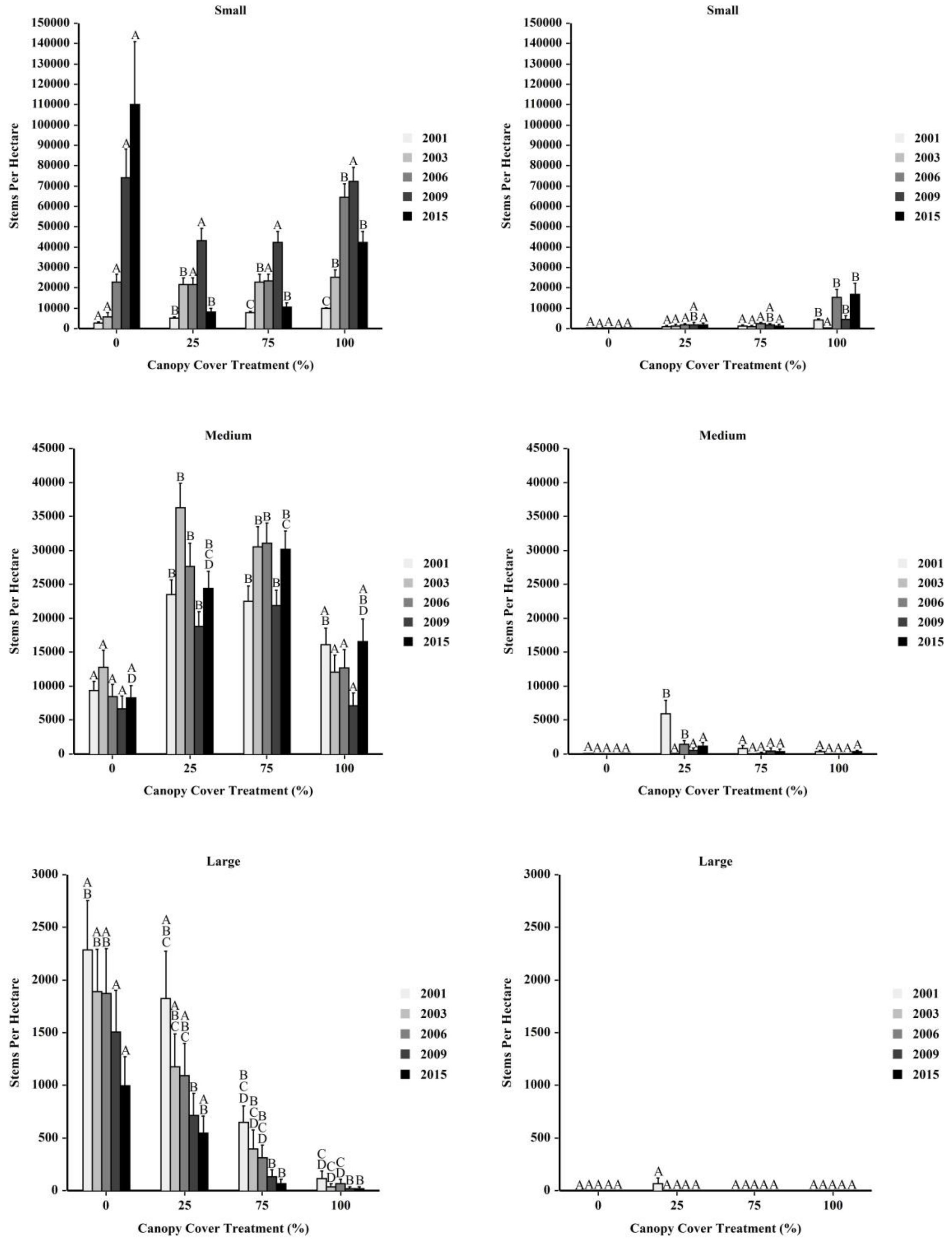


Figure 4.14. Continued.

CONCLUSION

Eastern North America's forests provide a wealth of ecosystem services and functions for both humans and other organisms. However, alterations to past disturbance regimes, global transportation of pests and pathogens, over utilization, and modifications in land use are all human-induced factors hindering the stability of forest ecosystems. Unless conservation needs are recognized and successfully addressed, many forest species face an uncertain future. My dissertation was designed to highlight the regeneration needs of several eastern North American species (i.e., ashes (*Fraxinus* spp.), mountain stewartia (*Stewartia ovata*), and oaks, (*Quercus* spp.) and fill gaps in the knowledge base required for their conservation. Each group and species faces its own unique set of challenges. The ashes are suffering significant population losses across their ranges as a result of an incidentally introduced insect pest. My research on ashes assisted in benchmarking current ash and competing woody vegetation regeneration levels and provides information for prioritizing the conservation of both major and minor ash species throughout the eastern United States. Throughout the past century, poor levels of regeneration have been documented for numerous oak species, especially upland oaks. My research evaluated a novel approach of intercropping oaks with pine plantations with canopy reduction treatments for advancing both natural and artificial oak regeneration. Overall, treatment combinations were identified that would maximize oak regeneration in similar forests. The mountain stewartia research should inform conservationists of the needs and conservation issues of this relatively unknown and rare southeastern United States species. With little else known about the species besides physical and geographical descriptions, my research quantified microsites supporting mountain stewartia populations. Collectively, the findings in this dissertation should benefit attention of forest managers and conservationists alike, by advancing the scope of knowledge related to the regeneration of some of our more rare and imperiled hardwood species.

VITA

Joshua J. Granger was born in central Nebraska in 1983. He graduated as valedictorian from Sargent Public Schools in May 2001. Joshua earned two undergraduate degrees at the University of Nebraska at Kearney, receiving a Bachelor of Arts degree in German with a minor in Health Science in May 2008 and a Bachelor of Science degree in Biology with a minor in Philosophy in December 2009. Following graduation, Joshua began his graduate studies at the University of Nebraska. After receiving a Master of Science degree in Biology May 2013, Joshua began his doctoral studies at the University of Tennessee, Knoxville. His Doctor of Philosophy in Natural Resources from the Department of Forestry, Wildlife and Fisheries and his Master of Science in Statistics from the Department of Statistics, Operations and Management Science, were completed in the spring of 2017.

Joshua is a member of the Society of American Foresters, International Oak Society and Phi Kappa Phi, Gamma Sigma Delta, Gamma Beta Phi, Sigma Xi, and Alpha Mu Gamma honor societies. He enjoys traveling, reading, traditional woodworking, gardening, fishing, day-hiking, hunting, and most importantly, spending time with his friends and family.