

SUBSTRATE EFFECTS ON SEEDLING DYNAMICS IN MANAGED NORTHERN
HARDWOOD FORESTS

By

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ABSTRACT

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In order to sustain themselves within forests any tree species must be able to reproduce. Accomplishing this task is often difficult as trees must pass through a variety of life history stages and transitions in order to reach sexual maturity. Given this complexity, it is often difficult to identify why some certain species regenerate prolifically within forests while others often fail to regenerate. This dissertation investigated how different types of forest substrate (bare mineral soil and decaying coarse woody debris) influence individual species' ability to establish seedlings on the forest floor in the managed northern hardwood forests of the Great Lakes region, where only a small percentage of species are reported to be reproducing successfully. I consider substrate's influence on seedling establishment from three separate starting points: seed added to the forest floor, seed dispersed from local seed sources and seedlings established on bare mineral soil and different types of decaying coarse woody debris. Taking this approach allowed me to investigate not only how substrate influences seedling dynamics, but also how substrate interacted with several factors which could override the influence of substrate including light availability, competing non-tree vegetation, site quality (soil and nutrient availability), local seed source density, and mycorrhizal fungi. Beginning with the presence of a seed (seed additions), bare mineral soil demonstrated a strong influence over smaller seeded species germination, but not larger seeded white pine. In addition, increasing light

availability improved seedling establishment for all species. However, under natural regeneration conditions (without seed additions) the importance of bare mineral soil for smaller seeded species and light for all species' seedling establishment became less apparent as, in many situations, local seed source density and site quality exerted a stronger influence over species' initial establishment. Differing types of forest substrate, however, were strongly influential on individual species growth after establishment, as bare mineral soil and decaying hemlock, northern white cedar and paper birch consistently supported greater seedling growth compared to decaying yellow birch, balsam fir, and sugar maple. In addition, seedlings colonized by mycorrhizal fungi generally shown to positively influence seedling growth across substrates, and in certain situations, were associated with dramatic rank changes in species growth performance on different substrates. Collectively, this dissertation demonstrates how different types of forest substrate can alter seedling layer species composition through its differing effects on individual species' seedling establishment. However, it also demonstrates how a host of other factors can mitigate the influence of substrate, suggesting that managing for substrate alone may not reverse the current reproduction failures experienced by several northern hardwood tree species.

For all those dedicated to forest conservation. Lang lebe der Förster!

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TABLE OF CONTENTS

LIST OF TABLES	ix
LIST OF FIGURES	xi
CHAPTER I.....	1
Introduction	1
Dissertation Structure.....	1
Understory Composition	3
Major Harvesting Events.....	4
LITERATURE CITED	7
CHAPTER II - Scarification and gap size have interacting effects on northern temperate seedling establishment.....	10
Abstract	10
Introduction	12
Methods.....	18
<i>Study site</i>	18
<i>Experiment one</i>	19
<i>Experiment two</i>	21
<i>Statistical analysis</i>	22
Results.....	25
<i>Germination</i>	25
<i>Seedling establishment and survival</i>	25
<i>Temporal changes in seedling density in harvest gaps</i>	26
Discussion.....	26
<i>Germination</i>	26
<i>Seedling establishment and survival</i>	29
Conclusion and Management Recommendations	31
Figures.....	32
Tables	37
LITERATURE CITED	43
CHAPTER III - Does substrate availability alter natural regeneration patterns within harvest gaps?.....	51
Abstract	51
Introduction	53
Methods.....	57
<i>Study area</i>	57
<i>Field methods</i>	58
<i>Field measurements</i>	59
<i>Statistical methods</i>	60
Results.....	62

<i>Seedling establishment</i>	62
Discussion.....	64
<i>Seedling Establishment</i>	64
Conclusion and Management Recommendations	67
Figures.....	68
Tables	71
LITERATURE CITED	76
CHAPTER IV - The effect of substrate type and mycorrhizal fungi on seedling development for northern temperate seedlings.....	84
Abstract	84
Introduction	86
Methods.....	90
<i>Field methods</i>	90
<i>Shade house methods</i>	90
<i>Laboratory methods</i>	93
<i>Statistical methods</i>	94
Results.....	96
<i>Height growth</i>	96
<i>Seedling survival</i>	97
<i>Mycorrhizal colonization patterns and effects</i>	97
<i>Sterilization's effect on performance rankings</i>	98
Discussion.....	98
<i>Height growth</i>	98
<i>Seedling survival</i>	101
<i>Mycorrhizal colonization</i>	102
Conclusions and Management Recommendations	102
Figures.....	104
Tables	111
LITERATURE CITED	117
CHAPTER V - Conclusions	122

LIST OF TABLES

Table 2.1. Results of a generalized linear mixed model for the effects of Scarification, Light Availability, Species, and their interactions on germination for eastern hemlock, yellow birch, paper birch, and white pine. Each combination of factors was considered up to three way interactions in the original model. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).....	37
Table 2.2. Observed germination response of paper birch, yellow birch, eastern hemlock, and white pine in Scarified and Unscarified subplots. SD=standard deviation.....	38
Table 2.3. Summary of environmental conditions across different gap sizes classes.....	39
Table 2.4. Results of a generalized logistic mixed model for the effects of Clipping, Light Availability, Species, and their interactions on germinant establishment (1 st year survival) and second year survival for eastern hemlock, yellow birch, paper birch, and white pine. Each combination of factors was considered up to three way interactions in the original model. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).....	40
Table 2.5. Results of a generalized logistic mixed model for the effects of Clipping, Light Availability, Species, Fencing, and their interactions on third year eastern hemlock and paper birch survival. Each combination of factors was considered up to three way interactions in the original model. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).....	41
Table 2.6. The effect of Clipping on paper birch and eastern hemlock third year survival. SD=standard deviation.....	42
Table 3.1. Results of a generalized logistic mixed model for the effects of Light Availability, Non-Tree Vegetation Density, Habitat Type, Species, and their two way interactions on seedling survival. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).....	71
Table 3.2. Results of a generalized linear mixed model for the effects of Scarification, Light Availability, Habitat Type, Species, Seed Production Potential (SPP) and their two way interactions on seedling establishment. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).....	72
Table 3.3. Species' average seedling density (with standard deviation in parentheses) in 228 plots across 19 northern hardwood stands in the Northern Lower and Eastern Upper Peninsulas of Michigan.....	73

Table 3.4. Species' average seedling density (with standard deviation in parentheses) in 114 scarified and unscarified plots across 19 northern hardwood stands in the Northern Lower and Eastern Upper Peninsulas of Michigan. Asterisks represent statistically significant effects (Prob ChiSq < 05).....	74
Table 3.5. Mean average light availability and competing non-tree vegetation characteristics (with standard deviation in parentheses) across high (AFOCa and AFOA), medium (AFO and AFPo) and low (ParVVb and ATFD) quality habitat types (Burger and Kotar 2004).....	75
Table 4.1. Results of a standard least squares model for the effects of Sterilization, Species, Substrate, and their interactions on height growth.....	111
Table 4.2. F ratio's and $P > F$ from standard ANOVA least squares models for the effects of Sterilization, Substrate, and their interactions on species' height growth.....	112
Table 4.3. Results of a nominal logistic regression model for the effects of Sterilization, Species, Substrate, and their interactions on seedling survival.....	113
Table 4.4. Overall survival rate of individual species at the end of the experiment.....	114
Table 4.5. Results of a standard least squares model for the effects of Species, Substrate and their interaction on mycorrhizal colonization of roots.....	115
Table 4.6. Sterilization's effect on species height growth rankings within individual substrate types. Values of ρ are Spearman's rank correlations between sterilized and unsterilized treatments. Smaller values indicate greater changes in ranks.....	116

LIST OF FIGURES

Figure 2.1. The effects of scarification (SC) and light on eastern hemlock (A), paper birch (B), yellow birch (C), and white pine (D) germination. R^2 applies to the whole model including the main effects of scarification and light availability. P values are displayed for scarification and light in that order.....	33
Figure 2.2. The effect of light availability on eastern hemlock (A), paper birch (B), yellow birch (C), and white pine (D) germinant establishment (1 st year survival). R^2 applies to the whole model including the main effects of light availability. P values represent the effect of light on seedling establishment.....	34
Figure 2.3. Average germination (A) and number of second year surviving seedlings (B) for eastern hemlock (EH), paper birch (PB), yellow birch (YB), and white pine (WP) in unharvested areas (UND) (0m diameter), single tree gaps (ST) (<23m diameter), large group gaps (LG) (24-50m diameter), and patch cut gaps (PC) (>50m diameter).....	35
Figure 2.4. Average number of third year surviving seedlings for eastern hemlock (EH) and paper birch (PB) in unharvested areas (UND) (0m diameter), single tree gaps (ST) (<23m diameter), large group gaps (LG) (24-50m diameter), and patch cut gaps (PC) (>50m diameter).....	36
Figure 3.1. Predicted establishment response of yellow birch (YB), white ash (WA), black cherry (BC), and eastern hemlock (EH) to local (50m) seed production potential ($\sum \text{diameter}^2 / \text{distance}^2$). R^2 and P values represent the fit of the whole model and significance of seed production potential, respectively.....	68
Figure 3.2. Seedling establishment as predicted by local seed production potential in high (AFOCa and AFOA), medium (AFO and AFPO) and low (ParVVb and ATFD) quality habitat types for red maple (A), black cherry (B), sugar maple (C), and white ash (D) (Burger and Kotar 2004).....	69
Figure 3.3. The effect of varying light availability in 114 harvest gaps on red maple (A) and sugar maple (B) seedling establishment.....	70

Figure 4.1. Height growth across balsam fir (BF), eastern hemlock (EH), northern white cedar (NWC), paper birch (PB), sugar maple (SM), mineral soil (MS), and yellow birch (YB) for balsam fir (A), hemlock (B), paper birch (C), and white pine (D) seedlings. Error bars represent one standard error, while substrates not sharing a common letter supported significantly different seedling growth ($P < 0.05$, Tukey-Kramer HSD).....104

Figure 4.2. Height growth across sterilized (Maroon) and unsterilized (Gold) balsam fir (BF), eastern hemlock (EH), northern white cedar (NWC), paper birch (PB), sugar maple (SM), mineral soil (MS), and yellow birch (YB) for red maple (A), northern white cedar (B), white spruce (C), and yellow birch (D) seedlings. Error bars represent one standard error, while asterisks represent statistically significant effects of sterilization on growth (prob $|t| < 0.05$).....105

Figure 4.3. Percent colonization of arbuscular mycorrhizal fungi (AMF) on red maple (A) and northern white cedar (B) seedlings and ectomycorrhizal fungi colonization on yellow birch (C) and white pine seedlings (D) across unsterilized balsam fir (BF), eastern hemlock (EH), northern white cedar (NWC), paper birch (PB), sugar maple (SM), mineral soil (MS), and yellow birch (YB) substrates. Error bars represent one stand error, while substrates not sharing a common letter supported colonization at significantly different rates ($P < 0.05$, Tukey-Kramer HSD).....106

Figure 4.4. The relationship between arbuscular mycorrhizal fungi (AMF) colonization and height growth for red maple (A) and northern white cedar (B) and ectomycorrhizal fungi (EMF) colonization and height growth for yellow birch (C) and white pine (D).....107

Figure 4.5. Effect of sterilization (maroon) on species' height growth performance on balsam fir CWD. Species were ranked from one to eight with one representing the best height growth performance. The Spearman's rank correlation statistic is listed in the top left corner.....108

Figure 4.6. Effect of sterilization (maroon) on species' height growth performance on northern white cedar CWD. Species were ranked from one to eight with one representing the best height growth performance. The Spearman's rank correlation statistic is listed in the top left corner.....109

Figure 4.7. Effect of sterilization (maroon) on species' height growth performance on eastern hemlock CWD. Species were ranked from one to eight with one representing the best height growth performance. The Spearman's rank correlation statistic is listed in the top left corner.....110

CHAPTER I

Introduction

Forestry has been defined as the science and art of cultivating, maintaining and developing forests. Forest regeneration is a critical component of this definition, as forests with characteristics commensurate with human goals can neither be maintained nor developed unless cultivation occurs. In species diverse forests, one of the greatest challenges foresters face is maintaining species diversity, as they must create environmental conditions that will allow species with varying resource requirements the opportunity to reproduce. This process is further complicated by the fact that seedlings, due to their size and lack of resource acquiring structures, are highly vulnerable to a variety of factors which could affect their survival. Forest substrate is one such factor which may influence seedling establishment and survival. In addition, forest substrate is a factor that can realistically be manipulated by forest management. My dissertation investigates how forest substrate interacts with local seed source density, light availability, substrate moisture and nutrient availability, non-tree vegetation, and mycorrhizal fungi to affect seedling establishment and survival in the managed northern hardwood forests of the Northern Great Lakes region.

Dissertation Structure

I begin, in this chapter, by describing the current state of seedling demographics in managed northern hardwood forests and identifying some interesting unexplained patterns.

I'll then briefly review the history of northern hardwood forest exploitation and management in the Northern Great Lakes region and some of the major harvesting events that have contributed to the forest composition and structures we see today. In doing so, I will explain how the legacy of these events may be influencing some of the current regeneration patterns addressed in this dissertation

The second chapter focuses on identifying critical processes which influence seedling establishment and survival within different sized harvest gaps independent of seed supply. In this chapter, I demonstrate how substrate type and light availability influence species germination, and how light availability and exposure to non-tree vegetation (grass, forbs, shrubs, and ferns) affect seedling survival. In addition to identifying important factors and processes, this chapter also demonstrates how, via different patterns for seedling germination and survival, species shift in seedling density across a range of harvest gap sizes over time.

The third chapter investigates seedling establishment within harvest gaps under natural regeneration conditions across a collection of forest stands representing a broad range of northern hardwood forest site qualities and overstory composition. This chapter highlights the effects of local seed sources, site quality, substrate availability, and light on species establishment. It also represents a realistic case study of some of the issues land managers are facing when attempting to regenerate individual species, as it considers how variation in seed availability affects the regeneration process.

The fourth chapter explores species' growth and survival across different types of forest substrate. It also separates the effects of mycorrhizal fungi and substrate mineral nitrogen content as driving mechanisms for this pattern. In addition, this chapter provides

important information for restoring old-growth characteristics in northern hardwood forests.

Understory Composition

Consistent with species demographic trends observed throughout eastern North America, the understories of northern hardwood forests in the Great Lakes region are currently dominated by shade tolerant species (Neuendorff et al. 2007; Fei and Steiner 2009; Matonis et al. 2011.) Among the most common species are ironwood (*Ostrya virginiana* (Mill.) K. Koch), red maple (*Acer rubrum* L.) and sugar maple (*A. saccharum* Marsh.). On the other end of this spectrum are several formerly prominent, shade intolerant to mid-tolerant species including white pine (*Pinus strobus* L.), yellow birch (*Betula alleghaniensis* Britton.) and red oak (*Quercus rubra* L.) which now comprise only a small percentage of the seedling layer. While this pattern suggests that light availability may be exerting a strong influence over seedling layer species composition, extremely shade-tolerant eastern hemlock is also declining in the regeneration layer of northern hardwood forests, (Matonis et al. 2011) suggesting that more is limiting than just light. Consistent with this notion, in trials where light availability has been increased through cutting larger harvest gaps, only modest gains of less tolerant species' seedling layer density have been observed (Shields et al. 2007; Bolton and D'Amato 2011; Kern et al. 2013). Consequently, the processes and mechanisms by which some shade tolerant species have come to dominance and most shade intolerant to mid tolerant species have been replaced remain undefined.

Major Harvesting Events

Containing up to as many as 20 different tree species, northern hardwood forests are one of the most tree species diverse forest types in the eastern deciduous forest. Prior to European settlement, northern hardwood forests could generally be characterized as a mix of early to late successional conifer and deciduous species with white pine, sugar maple, and eastern hemlock occurring at the greatest density (Whitney 1987; Zhang et al. 2000; Schulte et al. 2007). These dominant species, however, became the target of exploitive logging operations and were extracted in great quantities throughout the region in the late nineteenth and early twentieth centuries (Whitney 1987). The effect of this disturbance was, in many locations, compounded by large high intensity fires which arose from the combination of large residual fuel loads and open stand conditions created by the exploitative harvests, which dried the now abundant forest fuels. These fires killed many of the smaller trees ignored by the loggers and eliminated much of the existing advanced regeneration, setting the stage for regional species composition shifts. Among the most dramatic shifts associated with these disturbances was the loss of many formerly prevalent conifer species, which lacked the ability to sprout or colonize disturbed sites at long distances via seed dispersal (Whitney et al. 1989; Schulte et al. 2007). In their absence, many deciduous species possessing these traits such as sugar maple and aspen (*Populus* spp.) became more prominent. Consequently, most conifer species are now less common in the overstory when compared to the late twentieth century and, as a result, may now face strong seed source limitations to their regeneration (Zhang et al. 2000; Friedman and Reich 2005; Schwartz et al. 2005).

Beginning in the 1950's, single-tree selection harvesting became the dominant management paradigm for northern hardwood forests (Arbogast 1957). This system was adopted originally to increase the dominance of economically important shade tolerant species such as sugar maple. It does so by creating small harvest gaps which only marginally and ephemerally increase light at the forest floor (Eyre, and Zillgitt 1953; Klingensporn et al. 2012). As a result, the forests floor has been subjected to decades of low light conditions, which is incompatible with the comparatively higher light demands of intolerant and mid-tolerant species (Kobe et al. 1995; Walters and Reich 2000). Therefore, the scarcity of shade intolerant to mid-tolerant species in the seedling layer may be explained by an inadequate supply of light to support their survival (Webster and Lorimer 2005; Webster and Jensen 2007; Matonis et al. 2011)

Single tree selection may also be constraining seedling layer diversity by reducing important seedling establishment substrates. Decaying coarse woody debris (hereafter referred to as CWD) has been shown to be an important seedling establishment site in several forest types including northern hardwoods (Harmon and Franklin 1989; Mori et al. 2004; Marx and Walters 2008). CWD may be particularly important for smaller seeded species, as thick litter layers have been shown to inhibit their establishment on the forest floor. Unfortunately, CWD is becoming increasingly rare in managed forests, as selection harvests remove older or diseased trees that are likely to become the next generation of CWD (Hura and Crow 2004). Mineral soil represents an alternative safe site for small seeded species to establish; however, its availability has also been diminished by an increased emphasis on gentle harvesting practices which limits surface disturbance by harvesting over snow (Shields et al. 2007). As a result, the rarity of smaller seeded species

in the seedling layer may be explained by a lack of favorable seedling establishment substrate (Caspersen and Saprunoff 2005; Bolton and D'Amato 2011).

Broadly, this dissertation asks whether the availability of mineral soil and/or CWD is a major factor influencing seedling layer species composition. To answer this question, I conduct a series of manipulative experiments at differing points in the seedling establishment process and at differing spatial scales. This approach allows me to not only document mineral soil and CWD's initial influence on seedling layer species composition, but also test a variety of other factors which may override its potential influence. My design also provides land managers with a blueprint for overcoming potential substrate limitations in northern hardwood forests. In Chapter Two, I begin my investigation by following the fate of different species' seeds, dispersed in different types of forest substrate, spread across a range of light environments.

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CHAPTER II

Scarification and gap size have interacting effects on northern temperate seedling establishment

Abstract

After decades of promoting only the most economically valuable tree species, silvicultural practices in northern temperate forests of North America have increasingly become focused on maintaining tree species diversity. Unfortunately, many formerly prominent tree species including paper birch, yellow birch, eastern hemlock and white pine are now rarely found in the seedling layer, raising concerns about their future sustainability. This study investigates the mechanisms of seedling recruitment failure for these four species in two related seed addition experiments conducted in 45 variably sized harvest gaps (220 to 6500m²) and four unharvested locations in two adjacent mesic northern hardwood stands, located in Emmet County Michigan, USA. In addition to elucidating mechanisms, these experiments provide evidence for what size harvest gap provides the best environment for regenerating this particular group of species. The first experiment uses mixed models to investigate the influence of competing non-tree vegetation, light availability and browsing on seedling survival, while the second experiment uses the same statistical approach to explore the influence of scarification, light availability, and non-tree vegetation on seed germination and seedling establishment. Eastern hemlock, paper birch and yellow birch, all smaller seeded species, were 12, 17 and 95 times more abundant in scarified plots compared to unscarified plots. In contrast, white

pine, the largest seeded species, was unaffected by scarification. Highly shade tolerant hemlock and highly shade intolerant paper birch both germinated at greater densities in lower light environments, while both mid-tolerant species, white pine and yellow birch, were unaffected by light. Each species' initial establishment significantly increased with increasing light availability, and with the exception of yellow birch, each species also survived at a significantly higher rate with increasing light availability. Paper birch and hemlock third year survival also increased with increasing light. However, both species survival was also significantly negatively influenced by competition from non-tree vegetation. At the conclusion of the study, large group selection gaps (24-50m diameter) contained the highest density of each species' except white pine, suggesting that large group selection gaps may provide the best opportunity for reestablishing this particular group of species in the seedling layer.

Introduction

With the human population expected to surpass eight billion in the next decade (United Nations 2012), demand for goods and services from already heavily exploited forest ecosystems will continue to increase. Unfortunately, due to declining tree species diversity and evenness, the variety of goods and services some forest ecosystems can provide may soon decline (Schuler and Gillespie 2000; Lawrence 2004; Amatangelo et al. 2011), as lower diversity forests are oftentimes limited in the range of materials they offer for forest products, the types of habitat they provide wildlife and their resilience to disturbance (Chapin et al. 2000; Folke et al. 2004; Drever et al. 2006; Fischer et al. 2006). Complicating matters further, many forest ecosystems may soon become less productive as several factors, including climate change, are expected to expose species to growing conditions and disturbances to which they are less suitably adapted, and now potentially less resilient (Sturrock et al. 2011; Anderson et al. 2013; Duveneck et al. 2014).

The northern temperate forests of Eastern North America represent one such forest type where species composition shifts may soon threaten the sustainability of certain timber products and elevate the risk of severe disturbance. Some of the most noticeable compositional changes include a decrease in overstory evenness (Zhang et al. 2000), an expansion of shade tolerant species (Schulte et al. 2007; Nowacki and Abrams 2008; Amatangelo et al. 2011; Hanberry 2013), and a near exclusion of conifers (including hemlock and white pine) and shade intolerant species from the understory (including paper birch and yellow birch) (Neuendorff et al. 2007; Matonis et al. 2011). Recognizing the

problems associated with declining tree diversity, forest managers have begun investigating silvicultural means to restore tree species diversity to this forest type.

Imitating natural disturbance is one often suggested approach for promoting tree species diversity in northern temperate forests (Scheller and Mladenoff 2002; Seymour et al. 2002; Bolton and D'Amato 2011). Harvest disturbance using single-tree selection, the dominant silvicultural system in northern hardwood forests for over 60 years, creates a series of environmentally similar small harvest gaps (< 23 meters diameter). Unlike single tree selection, a natural disturbance based harvesting regime creates a range of microenvironments within a stand by varying harvest gap sizes. It is generally believed that the range of environmental conditions produced by a natural disturbance harvesting regime will promote species diversity, as the lower light environments produced in small harvest gaps are thought to favor the establishment of shade tolerant species, while the higher light environments found in progressively larger harvest gaps are thought to promote the establishment of mid-intolerant to shade intolerant species (Ricklefs 1977; Denslow 1980). Nevertheless, evidence from recent gap regeneration studies suggests that gap dynamics are far less predictable, and may be influenced by several factors other than gap size (Shields et al. 2007; Falk et al. 2010; Gasser et al. 2010; Bolton and D'Amato 2011; Matonis et al. 2011; Kern et al. 2012; Fahey and Lorimer 2013; Kern et al. 2013; Klingsporn-Poznanovic et al. 2013). Consequently, there are several potential explanations for why restoration efforts that manipulate gap size alone have failed to produce a more diverse species mix.

Seedling establishment failure is one potential explanation for the variable patterns of tree recruitment within harvest gaps (Wright et al. 1998; Caspersen and Saprunoff

2005). While harvest gap size can be manipulated to give individual species or groups of species a competitive advantage based on their shade tolerance, seed must be present and be able to germinate and establish before any competitive advantage can be realized. As such, manipulating factors that influence declining tree species seed supply, and/or germination and establishment may be more important to their restoration than manipulating factors that affect their growth.

Similar to how tree species vary in their competitive abilities among light environments, tree species vary in their ability to germinate and establish on a variety of forest floor substrates (Perala and Alm 1990; Shields et al. 2007a; Marx and Walters 2006; 2008). For instance, smaller-seeded species are more successful on easily-penetrable, moisture-holding substrates such as decaying coarse woody debris (hereafter referred to as CWD) compared to the undisturbed litter layer (McGee and Birmingham 1997; Cornett et al. 2001; Caspersen and Sapruncoff 2005; Marx and Walters 2008). In contrast, larger seeded species, some of which are now dominating northern temperate forest understories (sugar maple, beech), establish successfully on undisturbed leaf litter substrates (Caspersen and Sapruncoff 2005; Neuendorff et al. 2007; Matonis et al. 2011). Unfortunately, in managed northern hardwood forests, undisturbed leaf litter substrates dominate and CWD is becoming increasingly rare, as mortality of large trees has been greatly diminished by harvest removals (Hura and Crow 2004). As such, smaller-seeded species recruitment failures within harvest gaps in managed northern temperate forests may actually be the product of substrate limitation rather than low light availability.

One obvious solution to this potential recruitment bottleneck is to increase the availability of favorable establishment sites. While CWD may take decades to develop

naturally, and is prohibitively labor intensive to restore artificially, bare mineral soil/humus establishment sites are relatively easy to create and may provide similar establishment opportunities. For example, the forest floor could be scarified, a silvicultural technique which disturbs the litter layer and understory vegetation by dragging chains or disks across the forest floor, to increase bare mineral soil/humus availability. Scarification has even been shown to be effective at increasing light-seeded species establishment in boreal and sub-boreal forest biomes with more recalcitrant litter layers (Raymond et al. 2003; Lorenzetti et al. 2008; Prévost et al. 2010), but little is known about whether scarification will increase small-seeded species seedling establishment in more productive northern temperate forests. Furthermore, little is known about how gap size might interact with scarification in affecting the establishment of tree seedlings. Given the move toward using variable harvest gap sizes in northern temperate forest management, these interactions are important to understand if scarification is to be employed operationally. Another potential explanation for inconsistent patterns of harvest gap recruitment is the interaction between harvest gap size and non-tree vegetation (forbs, shrubs, ferns, and graminoids). By absorbing and/or acquiring light, moisture, and nutrients, non-tree vegetation can modify growing conditions at the forest floor and potentially minimize environmental differences that exist between different sized harvest gaps (Royo and Carson 2006). Large gaps created by the removal of groups of trees (group selection or patch selection harvesting) may experience the greatest degree of modification as highly competitive early successional species like raspberry (*Rubus idaeus*), black berry (*Rubus occidentalis*), and sedge (*Carex* sp.) have been shown to increase in larger sized harvest gaps (Shields and Webster 2007; Matonis et al. 2011, Kern 2012; Walters et al. in preparation).

Consequently, intense competition for resources from non-tree vegetation may shift the competitive balance in large harvest gaps from resource demanding shade intolerant species to more resource conserving shade tolerant species that can withstand being overtopped and shaded by competing vegetation (Montgomery et al. 2010). Smaller group harvest gaps, on the other hand, may provide a more favorable environment for shade intolerant species to establish. While lower light availability may constrain shade intolerant species' growth potential, early successional non-tree vegetation expansion may also be muted in the lower light environment of smaller group harvest gaps. As such, some tree species, perhaps including those that are shade intolerant to mid-tolerant, may actually have greater access to light in smaller group harvest gaps as a result of reduced competition if their growth is less sensitive to lower light availability than is competing non-tree vegetation. This, in turn, may lead to shade intolerant to mid-tolerant species being most abundant in smaller group harvest gaps.

In addition to substrate limitations and competition from non-tree vegetation, browsing from white-tailed deer (*Odocoileus virginianus* (Zimmermann)) could also limit the efficacy of varying gap size to increase tree diversity. In order to reach the canopy, seedlings must first pass through the browsing range of deer (to ~ 1.5m tall) (Walters et al. in preparation). Within this range, seedlings are subject to repeated browsing, which has been shown to constrain seedling development and survival. Nevertheless, escaping the browsing range may challenge some species more than others, as deer have been shown to browse certain species preferentially, and certain species have demonstrated a greater tolerance to browsing (Horsley et al. 2003; Rooney and Waller 2003; Long et al. 2007; Witt and Webster 2010; Kain et al. 2011; Randall and Walters 2011; Nuttle et al. 2014;

Walters et al. in preparation). On the other hand, newly germinated seedlings may not be apparent or desirable to foraging deer, as the effects of browsing have been shown to increase with seedling size (Randall and Walters 2011, Nuttle et al. 2013). Therefore, even if silvicultural treatments are successful at overcoming establishment substrate and light/non-tree competition barriers to regeneration, recruitment in harvest gaps may still ultimately depend on local deer density (Millington et al. 2010.)

In summary, manipulating harvest gap size is an increasingly common silvicultural strategy aimed at increasing tree diversity in northern temperate forests. However, unexpected patterns of tree recruitment observed in several gap regeneration experiments suggest that gap size may not be the only factor affecting tree species recruitment. Given the combined effects of declining CWD availability and a recent shift to gentle harvesting practices which minimize surface disturbance (Shields et al. 2007), bare mineral soil availability may be an important component to the regeneration failures of several small seeded species. Here, we report how substrate availability, harvest gap size, and exposure to non-tree vegetation and deer interact to affect the germination, establishment (1 year), and short-term survival (up to 3 years) of four species that are declining in northern temperate forests (eastern hemlock, white pine, paper birch, yellow birch) across a gradient of light availability in a mesic northern hardwood stand. Specifically we predict: 1) small seeded species germination will be restricted by a lack of bare mineral substrate across harvest gaps, 2) competition from non-tree vegetation will negatively affect seedling survival, especially for shade-intolerant species in large group selection gaps, 3) browsing will not affect seedlings due to their small stature 4) sufficient resource availability and

modest competition from non-tree vegetation will allow all species' seedling survivorship to be maximized in medium sized harvest gaps.

To test these predictions we established two experiments that collectively tracked the germination and survival of eastern hemlock (*Tsuga Canadensis* L.), yellow birch (*Betula. alleghaniensis* Britton.), paper birch (*B. papyrifera* Marsh), and white pine (*Pinus strobus* L.) seedlings for up to three years in subplots that were unfenced or fenced to exclude deer, unscarified or scarified to create bare mineral soil/humus substrate, and unclipped or clipped to control non-tree vegetation across 45 harvest gaps of varying size and 4 unharvested areas in two adjacent recently harvested northern hardwood stands. In the first experiment, annual seedling censusing over three years allowed us to develop a longer term pattern of how light availability and exposure to deer and non-tree vegetation affect paper birch and hemlock seedling survivorship. In the second experiment, bi-weekly censusing coupled with annual censusing allowed us higher resolution data of germination and seedling survivorship over two years for each of the four species. Collectively, the information presented in these experiments allow us to accurately depict patterns of seedling germination and survival within different sized harvest gaps and gain mechanistic insights into why harvest gap recruitment failures occur for four species declining in the northern temperate forest.

Methods

Study site

Our experimental sites were located in two adjacent northern hardwood stands in Emmet County, Michigan, USA (N45.574624 -W85.074373). The stands feature post-

glacial moraine topography and a mesic, rich to very rich habitat moisture and habitat type (AFOca) (Burger and Kotar 2003). Both stands are dominated by sugar maple (*Acer saccharum* (Marsh.)) with white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), paper birch (*Betula papyrifera* (Marsh.)), black cherry (*Prunus serotina* (Ehrh.)), and American beech (*Fagus grandifolia* (Ehrh.)) representing minor components of the overstories. In total, 45 harvest gaps ranging in size from 220 to 6500m² and four unharvested areas were selected from the two stands (stand 1: 40 gaps + 4 unharvested areas, stand 2: 5 gaps). To ensure gap independence, each gap was located at least 50m from another harvest gap. Logging slash was removed from the interior of each gap and piled along the borders.

Experiment one

The goal of this experiment was to identify the effects of light availability, non-tree vegetation and deer herbivory on seedling survival. Beginning in the spring of 2011, we located main plots (13x13m) in the center of each harvest gap and four unharvested areas. All existing advanced regeneration (existing seedlings and saplings) were then removed with a brush saw from each main plot. Main plots were then either fenced to exclude deer (30) or left unfenced (14). Plots were chosen randomly for non-fencing from within bins of gap sizes (0m diameter), single-tree gaps (<23m diameter), large group gaps (24-50m diameter), and patch cut gaps (PC) (>50m diameter) to ensure our fencing/non-fencing treatment occurred across the full range of gap sizes. Four subplots (4m²) were nested within each main plot. Each subplot was assigned one of four treatments: control, surface scarification, competing non-tree vegetation (forb, graminoids, ferns, shrubs) removal, and

surface scarification with vegetation removal. Scarification was conducted in the spring and was accomplished by raking away the litter layer to create a bare mineral soil/humus seedbed. Vegetation removal was accomplished by clipping all non-tree vegetation monthly throughout the growing season. After scarification, 500 cold-stratified seeds of eastern hemlock (Michigan source, Michigan Department of Natural Resources, Wyman Nursery, Manistique Michigan) yellow birch (Pennsylvania source, Sheffield's seeds, Locke, New York) and paper birch (Michigan source, Sheffield's seeds Locke, New York), (of each species) were sown in late May in each subplot. Prior to sowing, we conducted germination tests on each species to ensure seed viability. Despite yellow birch demonstrating adequate germination in the test, poor germination was observed in the field prompting us to remove yellow birch results from this report.

For each subplot, we assessed non-tree vegetation cover and height, light availability above non-tree vegetation, and light availability at the forest floor (beneath non-tree vegetation). Non-tree vegetation density was determined by visually estimating subplot coverage to the nearest five percent (looking down) and by measuring its height (cm) at nine pre-determined locations. Canopy openness, a proxy for canopy gap light availability (Kobe and Hogarth 2007), was determined from analyses of hemispherical photographs (taken at a height above the non-tree vegetation layer 1.5m) using Gap Light Analyzer v 2.0 (Frazier et al. 1999) with an automatic threshold value determined for each photo from Sidelook v. 1.1.01 (Nobis and Hunziker 2005). The light environment at the forest floor (1cm) was estimated by taking readings with a LAI 2000 plant canopy analyzer (LI-COR Incorporated, Lincoln, Nebraska) to determine diffuse non-interceptance (DIFN), which is the fraction of the sky visible to the sensor. This was done to quantify the impact

of competing non-tree vegetation on light availability to developing seedlings. To obtain this measurement, we first took a reading above the competing vegetation layer (1.5m) to get a maximum light value for the subplot, then three readings from random locations beneath the non-tree vegetation layer (1cm) to characterize its impact on light diminishment. The percentage of light available beneath the non-tree vegetation layer was then multiplied by the canopy openness value to determine light availability to seedlings established on the forest floor. Each seedling was given a colored tag denoting its cohort year at the time of its germination. Seedling survivorship for sown species was then monitored within subplots at the end of September for three years.

Experiment two

The goals of this experiment were to a) acquire higher resolution information than in Experiment One on how light, substrate availability, and competing non-tree vegetation affect the germination and survival via more frequent censusing, and b) assess the effects of these factors on a greater number of species than those that successfully germinated in Experiment One (paper birch, yellow birch, eastern hemlock, and white pine). To accomplish this, in spring 2012, we established four additional subplots adjacent to the main plot in 13 of the 40 harvest gaps and two understory locations. Gaps were selected from gap size strata in order to assure we captured the entire range of gap sizes. Subplots were also established in five additional single-tree gaps, located in an adjacent recently harvested stand (summer 2011), as a lack of available gap space prevented us from locating subplots outside of the main plot in the single-tree gaps used in Experiment One. Each of the four new subplots was randomly assigned one of the treatment options

described above in Experiment One. After scarification, 500 cold-stratified seeds of eastern hemlock (Michigan source, Michigan Department of Natural Resources, Wyman Nursery, Manistique Michigan), yellow birch (Pennsylvania source, Sheffield's seeds, Locke, New York), paper birch (Michigan source, Sheffield's seeds Locke, New York), and white pine (Michigan source, Michigan Department of Natural Resources, Wyman Nursery, Manistique Michigan) were spread evenly throughout each subplot. Due to a shortage in seed, white pine was only added to subplots in 12 of the 20 gaps.

In each subplot in each location, we assessed non-tree vegetation cover and height, light availability above non-tree vegetation, and light availability below non-tree vegetation using the same protocol described in Experiment One. In addition, we also quantified substrate (bare mineral soil/humus mix or hardwood litter) availability by visually estimating its cover (looking down upon subplots) to the nearest 5%. Germination was surveyed within each subplot on a bi-weekly basis from early-May through September. We increased the sampling intensity in this experiment to get a more accurate measurement of germination and early survival as high seedling mortality was observed in Experiment One prior to our lone September census. A seed was considered successfully germinated and established once its first true leaves expanded. Each established seedling was then tagged and monitored for survival over the next two years.

Statistical analysis

For statistical analysis, we kept the results of each experiment separate. This was done to exclude potential confounding factors including differences in cohort age, sampling intensity and variation in climate between years. As such, we used the cohort

from Experiment Two (greater sampling intensity and larger species population) to compare species' germination, establishment (1st year survival) and second year survival, while the cohort established in Experiment One (less intense sampling, smaller species population but greater cohort age) was used to compare third year survival.

We examined the effects of scarification/unscarified, light availability, species, and their interactions on seed germination for each of our four species (Experiment Two) with Generalized Linear Mixed Models (GLMM) assuming a Poisson distribution with a logarithmic link function. This method was adopted because our data were heavily right skewed due to the large number of plots with few or no germinants. Clipping was not considered as a factor for germination as the competing vegetation was already altered in subplots receiving scarification treatments.

To examine seedling establishment (1st year survival) and second and third year survival we used Generalized Logistic Mixed Models assuming a binomial distribution. For establishment and second year survival of each of our four species, we considered the effects of clipping/unclipped, light availability, species, and their interactions. Fencing was not included as a factor at these intervals because seedling establishment and second year survival were only evaluated in unfenced subplots (Experiment Two). Fencing was, however, considered along with each previously mentioned factor in the third year survival of paper birch and hemlock, as seedling survivorship was evaluated in subplots which had been either fenced or left unfenced (Experiment One). However, we do not report on the effect of fencing in this report, as we did not observe browsing effects on seedlings.

Model selection was accomplished through backwards elimination until only statistically significant ($p < .05$) factors and/or interactions remained in the model.

Significant species interactions were investigated by examining the response of each individual species to the significant interacting factor. Once we arrived at a final model, we checked the model for dispersion of the distribution, goodness of fit, and the existence of potential outliers. Model dispersion was estimated by calculating an over-dispersion factor ($\hat{c} = \text{chi-square} / \text{df}$). Models whose dispersion factors exceeded one were considered over-dispersed. In such cases, parameter estimates were obtained using a *quasi-likelihood* approach which inflated the standard errors of each factor estimate by $\sqrt{\hat{c}}$. The model was then re-run and checked for significance. Model fit and potential outlier detection was accomplished by examining plots of studentized deviance residuals. Model fit was evaluated by visually inspecting how evenly the residuals were distributed around zero. Points on the plot exceeding two standard deviations of the mean were identified as potential outliers. To evaluate the influence of such points, we used Cook's distance statistic. Distance statistics exceeding one were identified as potentially having strong leverage effects on the model. To investigate these effects, we removed the potential outlier from the data set and re-ran the model. If all parameters in the model remained significant, the potential outlier was kept as part of the data set. However, if changes in parameter significance occurred without the outlier, the point was then removed (Ramsey and Schafer 1997). All analyses were performed in (JMP 9.0, SAS Institute, Cary, NC).

Results

Germination

Scarification had strong overall effects on germination, but significant species and Scarification interactions indicate that species responded differently to Scarification (Table

2.1). Eastern hemlock, paper birch and yellow birch, all smaller seeded species, were 12, 17 and 95 times more abundant in scarified plots when compared to unscarified plots (Table 2.2). In contrast, white pine, the largest seeded species, was unaffected by scarification (Table 2.2). Light availability, which increased along with harvest gap size, also had strong effects on germination, but a significant interaction with species also indicated that species responded differently to Light (Figure 2.1) (Tables 2.1 & 2.3). Highly shade tolerant hemlock and highly shade intolerant paper birch both germinated at greater densities in lower light environments, while both mid-tolerant species, white pine and yellow birch, were unaffected by Light (Figure 2.1).

Seedling establishment and survival

Seedling establishment (1st growing season survival) and second year survival were strongly affected by the main effects of species and Light availability and modestly affected by their interaction (Table 2.4). Each species' initial establishment increased with increasing Light availability, however, the strength of response varied among species, as hemlock demonstrated the most dramatic increase in survival in response to increasing light (Figure 2.2). Similar increases in second year survival were observed at higher light availabilities for hemlock, paper birch and white pine. Yellow birch survival, however, did not respond significantly to light by the end of the second year (Data not shown). In the third year, seedling survival was most strongly influenced by the main effects of Clipping, Light and species (only hemlock and paper birch tested) (Table 2.5). Clipping (Table 2.6) and Light (data not shown) both had positive effects on each species, while paper birch exhibited overall higher third year survivorship (65%) compared to hemlock (21%).

Temporal changes in seedling density in harvest gaps

No particular gap size proved to be an optimal germination environment. Among species, white pine and hemlock germination was maximized in unharvested closed canopy areas, while paper birch and yellow birch favored single tree and large group selection gaps, respectively (Figure 2.3a). Similar to germination, no particular gap size was shown to maximize seedling density after two growing seasons. However, in contrast to germination, only white pine could be found surviving in subplots beneath unharvested areas. Among species, white pine and hemlock shifted their gap size of maximum density from unharvested areas to single tree gaps; while paper birch and yellow birch remained most dense in single tree and large group selection gaps respectively (Figure 2.3b). In the third and final year, large group selection gaps supported the highest seedling density of hemlock and paper birch (Figure 2.4).

Discussion

Germination

Since the seed to seedling transition is one of the earliest steps in the natural regeneration process, factors affecting germination have the potential to strongly influence forest stand dynamics. Smaller seeded species (yellow birch, paper birch, and hemlock) germinants were overwhelmingly more abundant in scarified subplots compared to unscarified subplots, demonstrating the strong influence of bare mineral soil/humus on seedling layer composition (Table 2.2). These results support our initial hypothesis of

substrate limitation for smaller seeded species, and are consistent with germination patterns found in other forest types (Valkonen and Maguire 2005), seedling substrate associations found in northern hardwood forests (Caspersen and Saprunoff 2005; Bolton and D'Amato 2011; Matonis et al. 2011; Bèland and Chicoine 2013), and post scarification seedling layer composition from other forest types (Raymond et al. 2003; Lorenzetti et al. 2008; Beguin et al. 2009; and Prévost et al. 2010). Collectively, these findings suggest that substrate related germination failures are likely contributing strongly to the scarcity of smaller seeded species seedlings reported by Neuendorff et al. (2007) and Matonis et al. (2011). However, it should also be noted that a reduction in local seed sources may also be contributing strongly to natural regeneration patterns, and were not considered in this seed addition study (Investigated in Willis et al. Ch2).

In contrast to the germination response of smaller seeded species, white pine was unaffected by the scarification treatment (Table 2.2). This finding supports our non-substrate limitation hypothesis for larger seeded species and the findings of Cornett et al. (1998), who also found white pine emergence to be insensitive to forest floor disturbance, but differs with the findings of Raymond (2003) who found white pine germination improved following scarification. One potential explanation for this discrepancy may come from a difference in litter depth at both sites. First, with the exception of American beech (a minor overstory component), the overstory at our site is composed almost exclusively of species (sugar maple, white ash, basswood) which produce relatively nutrient rich quickly decomposing litter (Melillo and Aber 1982). In contrast, the dominant overstory species in Raymond et al. (2003) was white pine (38% volume) which, due to its lower litter quality, likely produced a more recalcitrant litter layer than the one existing at

our site (Melillo and Aber 1982; Rustad and Cronan 1988). This suggests that the litter layer at our site may have presented a less significant physical barrier to white pine germination than the one reported by Raymond et al. (2003). Consequently, scarification may have had a larger effect on seed bed conditions at the site used by Raymond et al. (2003). Nevertheless, Smith (1951) found that white pine was capable of penetrating up to 5cm of needle litter within two weeks of germination suggesting that differences in litter depth may not entirely account for observed differences in white pine establishment.

Another factor which may have minimized scarification's influence on white pine germination is seed predation. White pine seeds are a preferred food for small mammals (Abbott 1961; Martell 1979), and have demonstrated greater germination when excluded from seed predators Cornett et al. 1998; Raymond et al. 2003). In this study, no attempts were made to exclude seed predators and white pine germinant density was the lowest among our experimental species (Table 2.2) (Figure 2.3a). Thus, we cannot eliminate the possibility that seed predation may have overridden any positive effects that scarification may have had on white pine germination.

In addition to scarification, species responded differently to light availability (Table 2.1) (Figure 2.1). While hemlock's germination decline in higher light environments was unsurprising considering its extreme shade tolerance and late successional status, paper birch's preference for lower light environments is surprising given its extreme intolerance of shade and reputation as an early successional pioneer species (Figure 2.1) (Burns and Honkala 1990). Nevertheless, this finding is consistent with earlier studies which reported greater hemlock and paper birch germination in shade (Hough 1960; Goerlich and Nyland 2000).

In contrast to hemlock and paper birch, light availability had no effect on white pine and yellow birch germination (Figure 2.1). As previously mentioned, seed predation may account for the overall low germination observed for white pine; however, yellow birch's lack of response is surprising considering that light has been shown to lessen the effect of a water soluble germination inhibitor present on its seed-coat (Redmond and Robinson 1954). Nevertheless, previous work has also shown light to have little effect on yellow birch germination (Houle 1992).

While the limited range of species investigated in this study restricts our ability to comment on general trends among species, these results do suggest that lower light availability (associated with single-tree gaps (Table 2.3)) is not a strong constraint on germination for this particular group of declining species (Figure 2.3a). Thus, moving away from single-tree selection towards a natural disturbance based silvicultural system is unlikely to increase these species' initial representation in harvest gaps.

Seedling establishment and survival

Within harvest gaps, increasing light availability (larger harvest gaps) had a positive influence on each species' initial establishment (Figure 2.2) and, with the exception of yellow birch, each species' second year survival (Table 2.4). This finding is unsurprising considering that other work has shown light to be highly limiting in rich-mesic growing environments like the one which exists at our site (Putz and Canham 1992; Burger and Kotar 2004). It also supports the notion that canopy gaps provide important regeneration opportunities in forest systems where large scale disturbances are uncommon (Runkle 1982; McCarthy 2001). The combination of yellow birch's mid-tolerance of

shade and the short time period for which we tracked its survival (2 years) may account for the lack of response (Burns and Honkala 1990; Kobe et al. 1995). Nevertheless, white pine, a species of similar shade tolerance, responded positively to increasing light availability, suggesting that another unmeasured factor(s) may be obscuring the influence of light availability on yellow birch survival.

Consistent with our expectations, seedlings established in unclipped subplots were quickly overtopped by non-tree vegetation, and experienced dramatically reduced light environments compared to seedlings established in clipped subplots in all but the smallest harvest gaps and unharvested areas (Table 2.3). In partial agreement with our hypothesis, clipping non-tree vegetation had a positive influence on third year seedling survivorship (Tables 2.5 & 2.6). However, the lack of a significant interaction with light indicates that clipping was equally effective across all gap sizes. Eastern hemlock's positive response to clipping was also unexpected given its extremely high tolerance of shade (Burns and Honkala 1990; Kobe et al. 1995). While limited to just two species (hemlock and paper birch), this finding suggests that competition from non-tree vegetation can influence seedling layer composition even at the earliest stages of seedling development. It also supports the notion that competition for light is more important than competition for moisture and nutrients on fertile sites (Putz and Canham 1992; Montgomery et al. 2010), given our site conditions (rich-mesic habitat type) and the fact that our clipping treatment only controlled aboveground competition. It is our opinion, however, that yellow birch and white pine's non-response to clipping is likely more related to the short duration of time in which they were exposed to non-tree vegetation (2 years) than an indicator of understory competitiveness, as other investigators have reported negative effects of non-tree

vegetation on these species in experiments conducted over greater time intervals (Gasser et al. 2010; Kern et al. 2012).

Conclusion and Management Recommendations

The collective findings from the two manipulative experiments conducted in this investigation provide several important insights for natural disturbance based silviculture in managed northern temperate forests. Central among these findings is the importance of bare mineral soil/humus for smaller seeded species germination. While we cannot predict whether seedlings established in scarified plots will ultimately gain dominance in the understory and capture canopy growing space, scarification should increase the odds of small seeded species successfully recruiting in harvest gaps simply by increasing their initial density. Thus, our findings support the notion put forth by Bolton and D'Amato (2011) suggesting that germination substrate may override the influence of harvest gap size for smaller seeded species, and demonstrate the importance of incorporating surface disturbance into silvicultural prescriptions. However, it should be emphasized again that seed supply issues may override the influence of substrate under natural regeneration conditions.

Variation in harvest gap size also affected seedling demographics. Although no harvest gap size provided the optimal environment for seed germination (Figure 2.3a), large group harvest gaps supported the highest densities of seedlings for all species except white pine, which germinated at low initial densities (Figure(s) 2.3B & 2.4). Taken together, our results suggest that large group selection harvest gaps may represent the best management option for restoring this particular group of species, as they provide generally

favorable environments for seed germination (Figure 2.3A) and encourage greater seedling establishment and survival (Figure 2.2). This pattern also provides initial support for adopting an expanding gap harvesting system where harvest gaps are expanded once advanced regeneration has been achieved (Raymond et al. 2009). Nevertheless, our results also indicate that non-tree vegetation had a negative effect on seedling survival. As such, restoration efforts may need to consider vegetation control options if they are attempting to regenerate this collection of species in harvest gaps on high quality sites.

Figure 2.1- The effects of scarification (SC) and light on eastern hemlock (A), paper birch (B), yellow birch (C), and white pine (D) germination. R^2 applies to the whole model including the main effects of scarification and light availability. P values are displayed for scarification and light in that order.

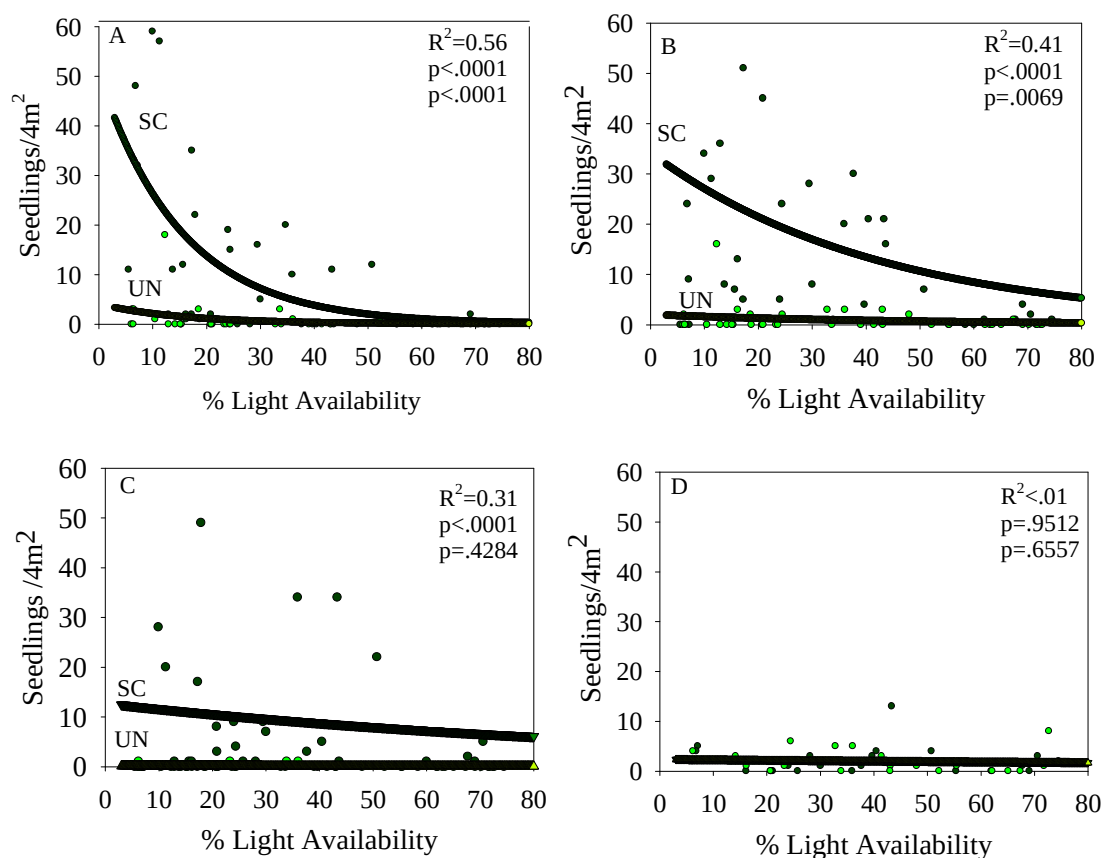


Figure 2.2- The effect of light availability on eastern hemlock (A), paper birch (B), yellow birch (C), and white pine (D) germinant establishment (1st year survival). R^2 applies to the whole model including the main effects of light availability. P values represent the effect of light on seedling establishment.

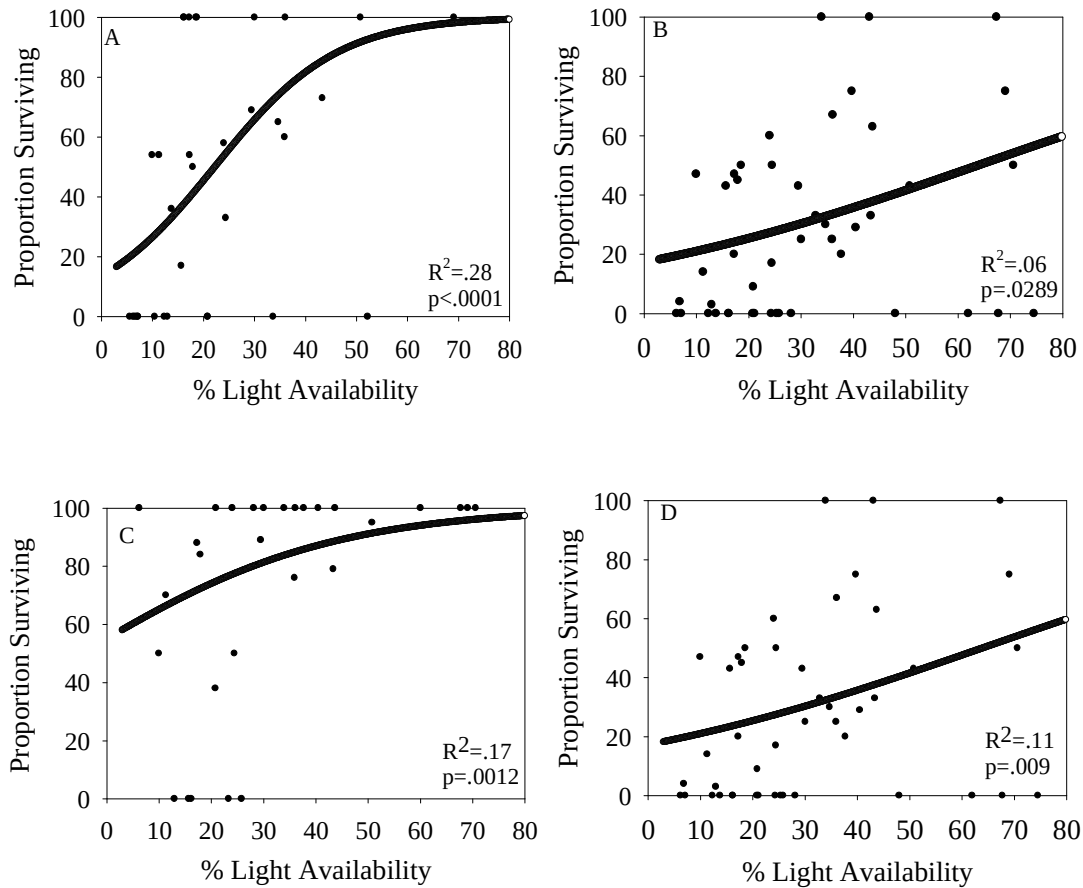


Figure 2.3- Average germination (A) and number of second year surviving seedlings (B) for eastern hemlock (EH), paper birch (PB), yellow birch (YB), and white pine (WP) in unharvested areas (UND) (0m diameter), single tree gaps (ST) (<23m diameter), large group gaps (LG) (24-50m diameter), and patch cut gaps (PC) (>50m diameter).

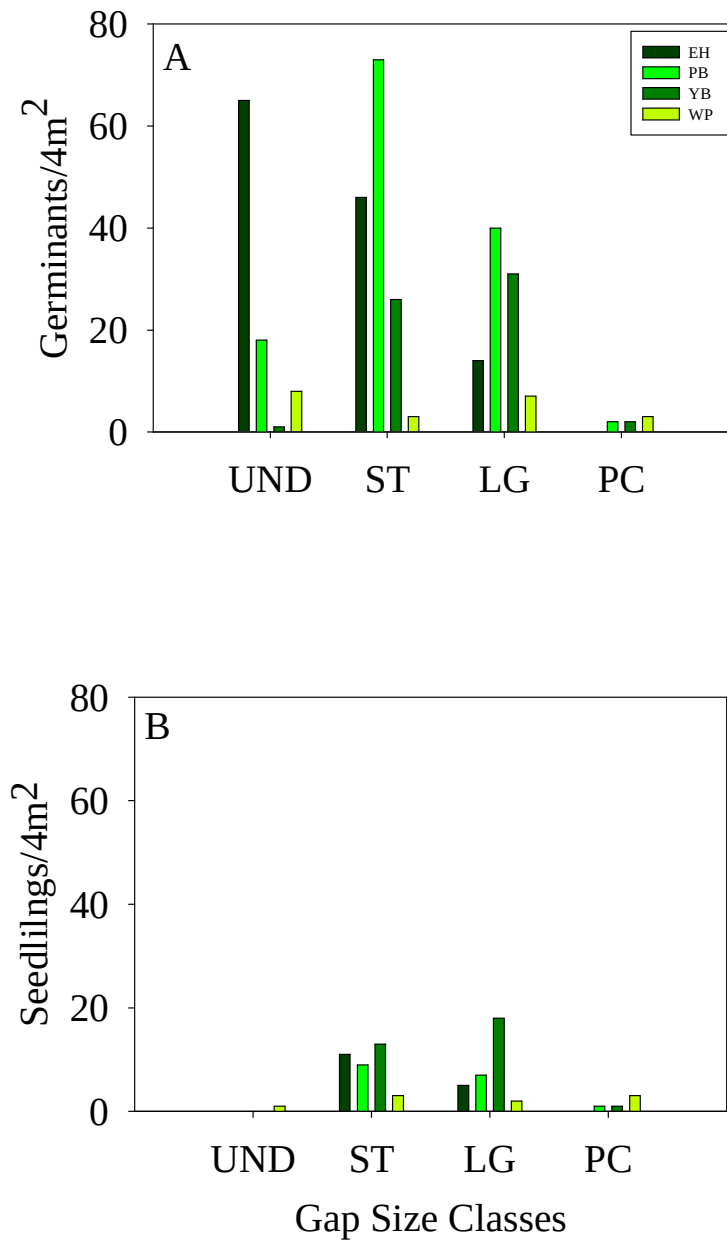


Figure 2.4- Average number of third year surviving seedlings for eastern hemlock (EH) and paper birch (PB) in unharvested areas (UND) (0m diameter), single tree gaps (ST) (<23m diameter), large group gaps(LG) (24-50m diameter), and patch cut gaps (PC) (>50m diameter).

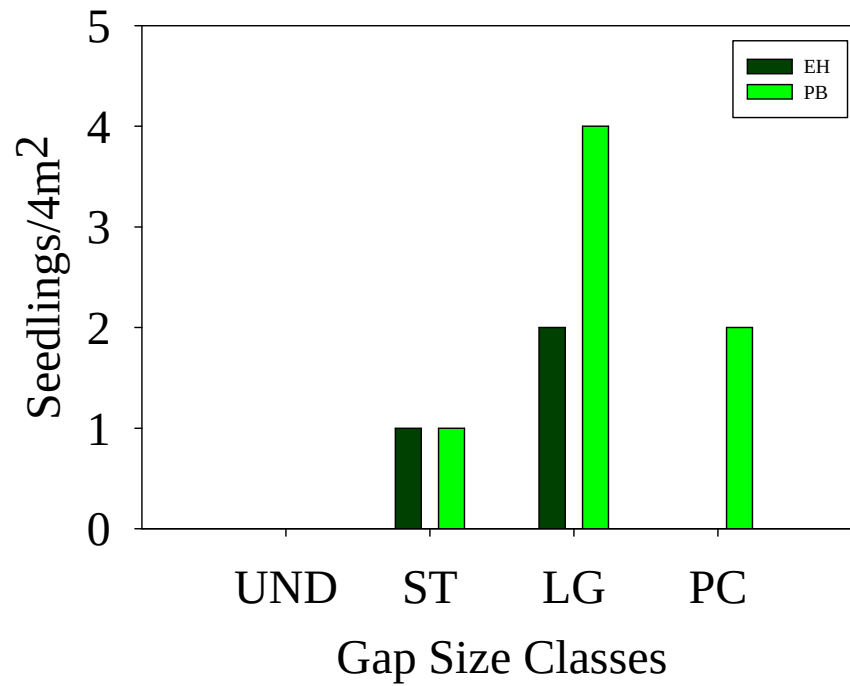


Table 2.1- Results of a generalized linear mixed model for the effects of Scarification, Light Availability, Species, and their interactions on germination for eastern hemlock, yellow birch, paper birch, and white pine. Each combination of factors was considered up to three way interactions in the original model. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).

	Factor	L-R ChiSquare	Prob>ChiSq
Germination	Scarification	38.31	<.0001
	Species	3.96	0.2659
	Scarification x Species	11.17	0.0108
	Light	14.14	0.0002
	Species x Light	12.26	0.0066
	R ² =.44		

Table 2.2- Observed germination response of paper birch, yellow birch, eastern hemlock, and white pine in Scarified and Unscarified subplots. SD=standard deviation.

Species	Treatment	Sub-plot s	Mean seedlings/4m 2	Media n	Rang e	SD
Paper birch	Scarified	40	17.15	7.5	0-128	24.97
Yellow birch	Scarified	40	9.53	1	0-113	20.38
Hemlock	Scarified	40	10.98	2	0-59	16.02
White pine	Scarified	24	2.04	1	0-13	2.84

Species	Treatment	Sub-plot s	Mean seedlings/4m 2	Media n	Rang e	SD
Paper birch	Unscarified	40	0.98	0	0-16	2.65
Yellow birch	Unscarified	40	0.1	0	0-1	0.3
Hemlock	Unscarified	40	0.88	0	0-18	2.93
White pine	Unscarified	24	2	1	0-8	2.19

Note¹- White pine was seeded in fewer subplots due to seed shortages.

Table 2.3- Summary of environmental conditions across different gap sizes classes.

Variable	Understory (0m dia)	Single Tree (<23m dia)	Large Group (24-50m dia)	Patch Cut (>50m dia)
Gaps/Understory (n=49)	4	13	24	8
Canopy Openness (%)	7.18	17.21	35	74.12
Non-Tree Vegetation Cover (%)	10	12	66	76
Non-Tree Vegetation Height (cm)	3	4	27	44
<i>Rubus</i> spp. Cover (%)	0	1	15	50
Forest Floor Light (%)	6.98	16.15	21.06	36.16

Table 2.4- Results of a generalized logistic mixed model for the effects of Clipping, Light Availability, Species, and their interactions on germinant establishment (1st year survival) and second year survival for eastern hemlock, yellow birch, paper birch, and white pine. Each combination of factors was considered up to three way interactions in the original model. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).

	Factor	L-R ChiSquare	Prob>ChiSq
Establishment (1st year)	Species	100.2	<.0001
	Light	34.92	<.0001
	Species x Light	8.85	0.0314
	R ² =.43		
Survival (2nd year)	Species	82.69	<.0001
	Light	19.28	<.0001
	Species x Light	9.37	0.0247
	R ² =.36		

Table 2.5- Results of a generalized logistic mixed model for the effects of Clipping, Light Availability, Species, Fencing, and their interactions on third year eastern hemlock and paper birch survival. Each combination of factors was considered up to three way interactions in the original model. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).

	Factor	L-R ChiSquare	Prob>ChiSq
Survival (3rd year)	Clipping	16.55	<.0001
	Species	15.98	<.0001
	Light	12.85	0.0003
	Clipping x Species	3.1	0.0784
	R ² = .39		

Table 2.6- The effect of Clipping on paper birch and eastern hemlock third year survival. SD=standard deviation.

Species	Cohort Age	Treatment	Subplots	Mean (%)	Median	Range	SD
Paper birch	3	Clipped	26	68	82	0-100	39
Hemlock	3	Clipped	32	27	6	0-100	37

Species	Cohort Age	Treatment	Subplots	Mean (%)	Median	Range	SD
Paper birch	3	Unclipped	19	33	0	0-100	46
Hemlock	3	Unclipped	28	15	0	0-100	32

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Chapter III

Does substrate availability alter natural regeneration patterns within harvest gaps?

Abstract

Balancing timber production and non-timber attributes like biodiversity has increasingly become a goal of forest management. By nature, this is a more challenging task than timber centric management, as silvicultural prescriptions must account for the regeneration requirements of several different tree species rather than just those species which are most economically valued. In the managed northern hardwood forests of the Great Lakes region, low light availability, resulting from decades of single-tree selection management, has been implicated as a potential cause of regeneration failures of several shade intolerant to mid-tolerant species. However, evidence from several harvest regeneration studies have shown that increasing light availability through the creation of larger harvest gaps has been only modestly successful in altering seedling layer composition. This study uses mixed models approach to investigate the influence of local seed source density, substrate availability, site quality (moisture and nutrient availability), and harvest gap size (75-650m²) on sugar maple, red maple, white ash, white pine, yellow birch, paper birch, eastern hemlock, and black cherry seedling establishment over three years in 19 upland hardwood stands located throughout the Northern Lower and Eastern Upper Peninsula's of Michigan. In general, larger seeded shade tolerant to mid-tolerant species dominated the seedling layer, as sugar maple, red maple, and white ash were at

least twice as abundant as any other species. The five other species' comparatively lower density was not related to harvest gap size as only sugar maple (lower establishment with increasing light availability) and red maple (increasing establishment with increasing light availability) establishment significantly responded to differences in harvest gap size. In contrast, local seed source density strongly influenced yellow birch, eastern hemlock, black cherry, and white ash seedling layer presence, as each species significantly and uniquely increased in density with increasing local seed source production potential. In a similar fashion, white pine and paper birch also experienced a significant increase in seedling establishment in plots that had been scarified (bare mineral soil/humus dominated) when compared to unscarified plots (hardwood litter dominated). Finally, site quality was an important contributing factor to seedling establishment, as at a given level of seed production potential, white ash and sugar maple occurred at higher densities in gaps with higher moisture and nutrient availability, while red maple and black cherry were more abundant in gaps with lower moisture and nutrient availability. Collectively, these results suggest that local seed production, substrate availability and site quality may be exerting a stronger influence on shade tolerant species seedling layer dominance than is light availability.

Introduction

Balancing timber production and non-timber attributes like biodiversity has increasingly become a goal of forest management (Lindenmayer et al. 2000; Lindenmayer et al. 2006; Heller and Zavaleta 2009). By nature, this is a more challenging task than timber centric management, as silvicultural prescriptions must account for the regeneration requirements of several different tree species rather than just those species which are most economically valued. Further complicating matters, silvicultural techniques aimed at increasing species diversity remain untested in several forest ecosystems.

One such community where concern over tree species diversity is growing and experimentation with alternative silvicultural tools is needed is the managed northern hardwoods forests of the Great Lakes region. Here, for nearly six decades, silvicultural practices have concentrated on regenerating economically valuable shade tolerant species by using the single-tree selection system. The single-tree selection system relies on natural regeneration to fill the spaces created by the harvest of individually marked trees at 10-15 year harvest intervals (15-20% reduction in basal area per harvest) (Arbogast 1957; O'Hara 2002; Neuendorff et al. 2007). In the process, harvesting typically creates small harvest gaps, which only marginally and ephemerally increase light availability to regenerating tree seedlings (Eyre, and Zillgitt 1953; Klingsporn et al. 2012). Thus, it is widely believed that the low light environments created in single-tree selection harvests have likely contributed to the expansion of shade tolerant species and the decline of less shade tolerant species in this forest type (Zhang et al. 2000; Schwartz et al. 2005; Neuendorff et al. 2007; Amatangelo et al. 2011; Matonis et al. 2011).

Recognizing that declining diversity could lead to decreased forest resilience and sustainability, operational and experimental efforts have been made to increase the representation of less shade tolerant species by creating larger, higher-light harvest gap sizes by selecting groups of trees for harvest. However, these trials have been generally unsuccessful, as the same shade tolerant species dominating small gaps generally dominate large gaps as well (Shields et al. 2007; Bolton and D'Amato 2011; Kern et al. 2012; Kern et al. 2013; Klingsporn-Poznanovic et al. 2013). This suggests that factors in addition to light availability are constraining the recruitment of some species within harvest gaps. Among these factors, seedling substrate availability, local seed sources, advanced regeneration, and competition from non-tree vegetation may be some of the most important.

Due to a decline in coarse woody debris (Hura and Crow 2004), and an increase in gentle harvesting practices which seek to minimize surface disturbance (e.g. winter harvesting), bare mineral soil/humus often covers only a small fraction of the forest floor in harvest gaps (Shields et al. 2007). Among substrates, bare mineral soil/humus may be particularly important for some species regeneration, as its combination of adequate nutrient availability, moisture holding capacity and receptiveness to root penetration provide a favorable environment for seedling establishment (Collis-George and Sands 1959; Gray et al. 1997; Prescott et al. 2000; Oleskog and Sahlén 2000). Smaller seeded species in particular may be dependent on bare mineral soil, as their stored carbohydrate reserves provide little energy for the development of roots to find reliable moisture and nutrient supplies whilst establishing through leaf litter (Burton et al. 1969; Kidson and Westoby 2000; Moles and Westoby 2004). Therefore, the regeneration of smaller seeded

species, several of which are less shade tolerant (e.g. yellow birch, paper birch) but also eastern hemlock, which is extremely shade tolerant (Kobe et al. 1995), may be limited more by seedling establishment substrates than low light environments (Casperson and Saprunoff 2005; Willis et al. ch1).

Lack of local seed production may also limit the regeneration of several species in northern hardwood forest harvest gaps. While overstory species richness has remained largely unchanged over the past century, several factors including exploitative logging, invasive pests and pathogens, and decades of poor recruitment by several species have combined to reduce canopy layer evenness at the landscape scale (Zhang et al. 2000; Schulte et al. 2007; Amatangelo et al. 2011). As such, several previously abundant species are now likely contributing less seed to the annual seed rain within stands. Three such species which have experienced sharp long-term declines are eastern hemlock (*Tsuga canadensis* L.), white pine (*Pinus strobus* L.) and yellow birch (*Betula alleghaniensis* Britton.) (Whitney 1987; Frelich 1995; Woods 2000; Zhang et al. 2000; Schulte et al. 2002; Friedman and Reich 2005; Schulte et al. 2007; Rhemtulla et al. 2009). While their reduction in the overstory likely results in local reductions of seed availability, the effects likely vary by species because dispersal characteristics vary among species. For instance, compared to birch, hemlock and white pine seeds are less broadly dispersed by wind and thus, unless vectored by wildlife, are more likely to be locally dispersal limited (Ribbens et al. 1994). Therefore, the lack of conifer representation within harvest gaps may be facilitated to a greater extent by a lack of local seed sources rather than a lack of favorable establishment substrate or light availability.

Competition from non-tree vegetation (shrubs, forbs, graminoids and ferns) may represent an additional explanation for failed species recruitment within harvest gaps. By occupying establishment sites and competing for light, moisture, and nutrients, non-tree vegetation has been shown to influence seedling survival (George and Bazzaz 1999; Beckage and Clark 2003; Royo and Carson 2006; Royo and Carson 2008; Montgomery et al. 2010). Shade intolerant to mid-tolerant species may be the functional group most threatened by dense layers of non-tree vegetation, as the low light levels created by competing vegetation may prevent them from energetically offsetting their comparatively higher respiration costs (Bazzaz 1979; Walters and Reich 2000; Crane and Reich 2005; Valladares and Niinemets 2008). However, competition may not be a significant factor in all harvest gaps, as non-tree vegetation cover and height have been shown to positively correlate with increasing gap size (Shields et al. 2007; Matonis et al. 2011; Kern et al. 2012). Likewise, competition intensity may vary geographically, as local soil moisture and nutrient regimes (site quality) may modify non-tree vegetation's response to increasing light availability. Therefore, larger harvest gaps on lower quality sites may provide better recruitment opportunities for shade intolerant to mid-tolerant species than larger harvest gaps on higher quality sites if competition intensity varies with site quality (Davis et al. 1999).

In conclusion, low light availability created by small harvest gaps has been considered as the primary factor driving the expansion of shade tolerant species in the Great Lakes region. However, attempts to restore seedling diversity by varying only harvest gap size to affect light availability have been largely unsuccessful at promoting less shade tolerant species and other declining species, suggesting that other factors within

harvest gaps may be preventing their regeneration. In this report, we examine the effects of local seed tree density, mineral soil substrate availability, light availability, and non-tree vegetation on seedling establishment and first-year survival of eight tree species in 114 harvest gaps located in 19 different stands of varying site quality in the Northern Lower and Eastern Upper Peninsulas of Michigan. Specifically we predict: 1) local seed source proximity will limit seedling establishment for conifers and larger seeded species 2) bare mineral soil/humus availability will limit the establishment of lighter seeded species 3) competition from non-tree vegetation will limit shade intolerant species establishment in large harvest gaps on high quality sites but not on lower quality sites.

Methods

Study area

In May, 2011, 11 upland hardwood or mixed-upland forest stands entering their first growing season following a winter harvest were located throughout the Northern Lower and Eastern Upper Peninsula's of Michigan with the aid of a harvest database maintained by the Michigan Department of Natural Resources (MDNR). Eight additional stands fitting the same criteria were located in May of 2012. Overstory composition in most stands was dominated by sugar maple (*Acer saccharum* Marsh.) with lesser and varying amounts of red maple (*A. rubrum* L.), white ash (*Fraxinus americana* L.), American basswood (*Tilia americana* L.), white pine (*Pinus strobus* L.), red oak (*Quercus rubra* L.), eastern hemlock (*Tsuga canadensis* L.), yellow birch (*Betula alleghaniensis* Britton.), paper birch (*Betula papyrifera* Marsh), and black cherry (*Prunus serotina* Ehrh.). Habitat type, a classification system that uses assemblages of understory vegetation as a

proxy for nutrient and moisture availability, was used to classify the site quality of each harvest gap (Burger and Kotar 2003). This method was chosen due to the logistical challenges of quantifying moisture and nutrient availability across 19 sites, and due to the demonstrated correspondence of this system to *in situ* measurements of nitrogen and moisture availability (Walters and Reich 1997). It was also chosen for its relevance to forest management, as the habitat type classification system is commonly used as a management tool throughout the Great Lakes region. The three habitat classes encountered in the Northern Lower Peninsula in this study are AFOCa (mesic to very-mesic soil moisture availability; rich-very rich nutrient availability), AFO (dry-mesic to mesic; medium to rich), and ParVVb (dry to dry-mesic; poor to medium); while the three encountered in the Eastern Upper Peninsula include AFOA (mesic to wet-mesic; medium to rich), AFPo (dry-mesic to mesic; medium), and ATFD (dry-mesic to mesic; poor to medium).

Field methods

Within each stand, six harvest gaps were selected to track seedling establishment and survival. Gaps were selected non-randomly with the goal of varying gap size and maximizing local seed source (within 50m radius) diversity. Gap size was determined by measuring the tree bole to tree bole distance for edge trees using the methods of Runkle (1981). Two additional requirements for gap selection were that they were of harvest origin (i.e. at least one tree harvested) and at least 50m from a forest edge or another gap included in the study. Once gaps were chosen, all advanced regeneration was removed from the gap with a brush saw. Two plots (3x3m) were then established within each gap, with one

randomly selected to receive a soil disturbance treatment. In late May, treated plots were scarified with rakes until the forest floor was dominated by a combination of bare mineral soil and humus.

Field measurements

Within each plot, we visually estimated coverage of bare mineral soil/humus (combined), litter, forbs, shrubs, *Rubus spp.*, grass/sedge, and non-receptive substrate (e.g. rocks) to the nearest 5%. In addition, we measured non-tree vegetation height (cm) at nine pre-determined locations to calculate an average non-tree vegetation height value for each plot. In order to estimate seed dispersal within harvest gaps, local seed production potential was determined for each species included in this study in each gap by summing the quotient of the squared diameter-at-breast-height (1.4m) and the squared distance (m) to plot center of each tree greater than 25.4 (cm) in diameter and within 25m of the gap center, but outside of the gap itself ($\sum \text{diameter}^2 / \text{distance}^2$) (Ribbens et al. 1994; Matonis et al. 2011). Species determined to be declining from previous demographic studies conducted in the region (Zhang et al. 2000; Friedman and Reich 2005; Schwartz et al. 2005; Schulte et al. 2007; Amatangelo et al. 2011; Matonis et al. 2011) (yellow birch, white pine and hemlock) or shade intolerant species (paper birch and black cherry) were measured within 50m of gap center to consider a greater range of local seed production potential and also to account for *Betula*'s greater seed dissemination distance potential (Ribbens et al. 1994). Canopy openness, a proxy for light availability (Kobe and Hogarth 2007), was determined for each plot by taking a hemispherical photograph at 1.5 m (which was always above the understory vegetation layer) above plot center during overcast

conditions or twilight. (Canham et al. 1990). Each photo was analyzed with Gap Light Analyzer v. 2.0 (Frazer et al. 1999) using an automatic threshold value provided by Side-Look v. 1.1.01 (Nobis and Hunziker 2005). Seedling establishment, forest floor coverage, and non-tree vegetation height were then assessed in each plot at the end of the growing season (September). All established seedlings were tagged and checked in September for survival. Each plot was then revisited annually to check for the establishment of new seedlings, changes in substrate coverage, non-tree vegetation coverage and height, and the survival of previously established seedlings for three (2011 established sites) or two (2012 established sites) growing seasons.

Statistical methods

We examined the effects of species, substrate availability, canopy openness, local seed production potential, site quality and their two way interactions on seedling establishment with Generalized Linear Mixed Models (GLMM) assuming a Poisson distribution with a logarithmic link function. We selected this approach to account for the high number of biologically significant zeroes which prevented us from transforming the data to meet the assumption of normality for general linear modeling. Stand was not incorporated as a factor despite gaps being nested within stands. This was done for two reasons. First, considering stands as a factor would have severely limited degrees of freedom for testing the factors of interest. Second, gap plots can reasonably be considered experimental units as all measurements we took (habitat class, seed sources) were gap specific. Prior to modeling, site quality was standardized by categorizing individual habitat types into high (AFOCa and AFOA), medium (AFO and AFPo), and low site

quality (ParVVb and ATFD) groups, and analyzed as a continuous variable. While we recognize that habitat type could also be categorized as an ordinal variable, which would avoid the potentially invalid assumption of a continuous relationship of moisture/nutrient availability among habitat types, we chose to treat habitat type as a continuous variable in order to preserve degrees of freedom, allowing us to examine a broader collection of species. The influence of each factor and their two-way interactions were then investigated in a full factorial modeling design. Three and four-way interactions were not considered due to a loss of degrees of freedom. Model selection was accomplished through backwards elimination. Insignificant interactions $\text{ProbChiSq} > 0.25$ were pooled with the error term and rerun as a new model until only statistically significant factors ($\text{ProbChiSq} < .05$) and interactions ($\text{ProbChiSq} < 0.25$) could be reached (Bancroft 1964). Once we arrived at a final model, we checked the model for dispersion of the distribution, goodness of fit and potential outliers. Model dispersion was estimated by calculating an over-dispersion factor ($\hat{c} = \text{chi-square} / \text{df}$). Models with dispersion factor values > 1 were considered over-dispersed. In such cases, parameter estimates were obtained using a *quasi-likelihood* approach which inflated the standard errors of each factor estimate by $\sqrt{\hat{c}}$. The model was then re-run and checked for significance. Model fit and potential outlier detection was accomplished by examining plots of studentized deviance residuals. Model fit was evaluated by visually inspecting how evenly the residuals were distributed around zero. Points on the plot exceeding two standard deviations of the mean were identified as potential outliers. We evaluated the influence of such points with Cook's distance statistic. Values > 1 indicate points potentially having significant effects on the model. To investigate these effects, we removed the potential outlier from the data set and re-ran the

model. If all parameters in the model remained significant, the potential outlier was kept as part of the data set. If changes in parameter significance occurred while the outlier was excluded, we removed the observation from the model (Ramsey and Schafer 1997). This issue, however, was not encountered.

The effects of species, canopy openness, non-tree vegetation density, site quality, and their two-way interactions on seedling survivorship were investigated through Generalized Logistic Mixed Models assuming a binomial distribution with a logit link function. The same model fitting and model diagnostic procedures that were used to model seedling establishment were repeated for seedling survival. While statistically significant relationships were found for seedling survival, our final model predictive strength was low overall (Table 3.1). Furthermore, no compelling main effects or meaningful interactions were discovered during the analysis. As such, we will not discuss seedling survival in this report. All analyses were performed in JMP 9.0 (SAS Institute, Cary, NC).

Results

Seedling establishment

The eight species examined in this study varied strongly in their rates of seedling establishment (Table 3.2). In general, larger seeded shade tolerant to mid-tolerant species dominated the seedling layer as sugar maple, red maple, and white ash were at least twice as abundant as any other species (Table 3.3). This pattern, however, was not related to the interaction between Local Seed Production Potential (SPP) and Habitat Type (site quality) as, at a given level of SPP, all species were found at higher densities on higher quality

Habitat Types (Table 3.2). Species also responded similarly to the interaction of Light and Habitat Type, as at a given level of Light Availability, seedling establishment was consistently greater on higher quality Habitat Types (Table 3.2). Similar responses were also observed among species to the interaction of Light and SPP, as seedling density was consistently higher for low light environments at a given level of SPP for all species (Table 3.2). However, Species did differ strongly in their interactions with SPP and Habitat Type, respectively (Table 3.2). Local seed source density was an important constraint on eastern hemlock, white ash, black cherry, and yellow birch establishment, as each species increased significantly but uniquely with increasing SPP (Figure 3.1). Independent of Local Seed Production Potential, black cherry and red maple established at greater densities on lower quality sites, while sugar maple and white ash were found in greater abundance on higher quality sites (Figure 3.2). This relationship for black cherry and white ash, however, was largely driven by variation in SPP (Figure 3.2). In addition to Local Seed Production Potential and Habitat Type, Species also differed significantly in their response to Scarification (bare mineral substrate) and Light Availability (Table 3.2). Scarification was a significant factor for paper birch and white pine, as seedling density increased for both species in scarified compared to unscarified plots (Table 3.4). Light, on the other hand, strongly influenced red maple and sugar maple, as red maple seedling density increased along with increasing Light Availability, while sugar maple seedling density decreased with increasing Light Availability (Figure 3.3).

Discussion

Seedling establishment

One of the basic assumptions of gap based silviculture is that targeted tree species will have the opportunity to establish within harvest gaps. While logistical constraints prevented us from measuring seed rain in harvest gaps directly, local seed production potential exerted a strong influence on seedling establishment for several species including eastern hemlock, white ash, yellow birch and black cherry (Figure 3.1). These findings are in agreement with our initial hypothesis of seed limitation for larger seeded or conifer species and, with the exception of white ash, are also consistent with seed dispersal trends reported in the literature (Burns and Honkala 1990; Ribbons et al. 1994; Casperson and Saprunoff 2005; Pairon et al. 2006). In contrast to our hypothesis, however, local seed production potential was also a significant seedling establishment constraint for yellow birch. This finding was surprising considering *Betula*'s reported ability to disperse seeds long distances by wind over air or snow (Matlack 1989; Ribbons et al. 1994). Nevertheless, in forests, low wind velocity has been shown to constrain yellow birch's seed dispersal over snow (Greene and Johnson 1997), and seed density has also been shown to be vastly reduced at a distance beyond 125(m) (Hughes and Fahey 1988). Consequently, our finding of local seed source limitation for yellow birch is consistent with the seed dispersal findings of Greene and Johnson (1997) and Hughes and Fahey (1988), and may help explain the low rates of seedling recruitment reported by other investigators at the gap and landscape scales (McEuen and Curran 2004; Shields et al. 2007; Bolton and D'Amato 2011; Kern et al. 2013).

Independent of local seed source production potential, site quality (habitat type) also factored strongly into individual species seedling establishment (Table 3.2). White ash and sugar maple established at higher densities in gaps that were of higher site quality while red maple and black cherry established at greater densities in gaps of lower site quality (ParVVb and ATFD) (Figure 3.2). Collectively, this pattern corresponds with each species' reported regeneration requirements (Burns and Honkala 1990) and is consistent with other studies which have reported enhanced performance of sugar maple and white ash on high quality sites and/or moister topographic positions (Host et al. 1987; Walters and Reich 1997; Shreeg et al. 2005; Frey et al. 2007), and red maple and black cherry's reported tolerance of more xeric sites and landscape positions (Abrams 1998; Burger and Kotar 2004; Frey et al. 2007).

Bare mineral soil/humus availability was yet another factor which modestly influenced seedling establishment (Table 3.2). Consistent with our expectations, and the results of other forest regeneration studies, scarification significantly increased paper birch seedling establishment in harvest gaps (Raymond et al. 2003; Beguin et al. 2009; Prévost et al. 2010; Willis et al. Ch1) (Table 3.4). However, contrary to our expectations, and our previous report (Willis et al.) Ch1, white pine seedling establishment also significantly increased in scarified plots (Table 3.4). One potential explanation for these seemingly contradictory patterns may be related to a difference in organic layer depth in the high quality (AFOca) gaps examined in Willis et al. (ch1) and the mostly medium (AFO and AFPo) to lower ParVVb and ATFD quality gaps where white pine established in this study (Data not shown), as the potential combination of a greater proportion of slowly decomposing nutrient deficient litter and drier soil moisture conditions may have slowed

decomposition in harvest gaps on medium and lower quality sites, resulting in deeper, more recalcitrant organic layers. In support of this theory, Raymond et al. (2003) reported a similar increase in white pine establishment following scarification in lower quality harvest gaps than the ones reported in Willis et al. (ch1). As such, scarification may have a more significant impact on larger seeded species establishment in harvest gaps on lower quality sites. Nevertheless, no other larger seeded species demonstrated a significant increase in scarified plots in lower quality gaps following scarification, and white pine establishment was low overall compared to most other species (Table 3.3).

Light availability was the final factor which had modest significance on seedling establishment (Table 3.2). Independent of local seed source productivity, red maple established at greater abundance in high light environments, while sugar maple was more abundant in low light environments (Figure 3.3). This pattern coincides with each species' reported shade tolerance (Burns and Honkala 1990; Kobe et al. 1995) and provides limited support for the notion that gap size can be manipulated to control species composition based on their differing functional abilities (Messier et al. 1999). Nevertheless, several species of lesser or equal shade tolerance including paper birch, black cherry, yellow birch, white ash and white pine did not establish at greater density in higher light environments. This suggests that creating larger harvest gaps may not increase the representation of declining shade intolerant to mid-tolerant species unless advanced regeneration is already present. It also adds to a growing body of evidence in the Great Lakes region which indicates that the effect of gap size can be marginalized by several different potentially interacting factors (Shields et al. 2007; Bolton and D'Amato 2011; Matonis et al. 2011; Kern et al. 2013; Walters et al. in preparation). However, it is also possible that the range

of harvest gaps (75-650m²) (Table 5) encountered in this report was too small to incite significant seedling establishment response from shade intolerant to mid tolerant species, as Willis et al. (ch1) reported increasing rates of seedling establishment with increasing light availability across a larger range of gap sizes (220 to 6500m²).

Conclusions and Management Recommendations

Gap regeneration is a complex process involving several steps from seed creation all the way up through sapling and pole growth. Due to seedling establishment being one of the earliest steps in this process, the factors which affect its outcome have the potential to alter regeneration outcomes. Managing for biodiversity complicates this process further, as land managers must account for each species' particular regeneration requirements.

Above all, the results of this study emphasize the importance of local seed sources and site quality for individual species' seedling establishment. In managed northern hardwood forests, locating harvest gaps in proximity to seed sources may prove challenging, as several species are currently less abundant in the overstory compared to previous decades (Zhang et al. 2000; Schwartz et al. 2005; Schulte et al. 2007; Amatangelo et al. 2011). In such situations, planting seedlings (Walters et al. in press) or artificial seeding (Willis et al. Ch1) may help overcome potential seed source limitations. These actions may also be aided greatly by prior knowledge of site quality and the stress tolerance of the targeted species. In conclusion, management efforts which ignore these critical factors, and simply alter harvest gap sizes to manipulate species composition, may be setting the stage for future regeneration failures unless advanced regeneration is already established.

Figure 3.1- Predicted establishment response of yellow birch (YB), white ash (WA), black cherry (BC), and eastern hemlock (EH) to local (50m) seed production potential ($\sum \text{diameter}^2 / \text{distance}^2$). R^2 and P values represent the fit of the whole model and significance of seed production potential, respectively.

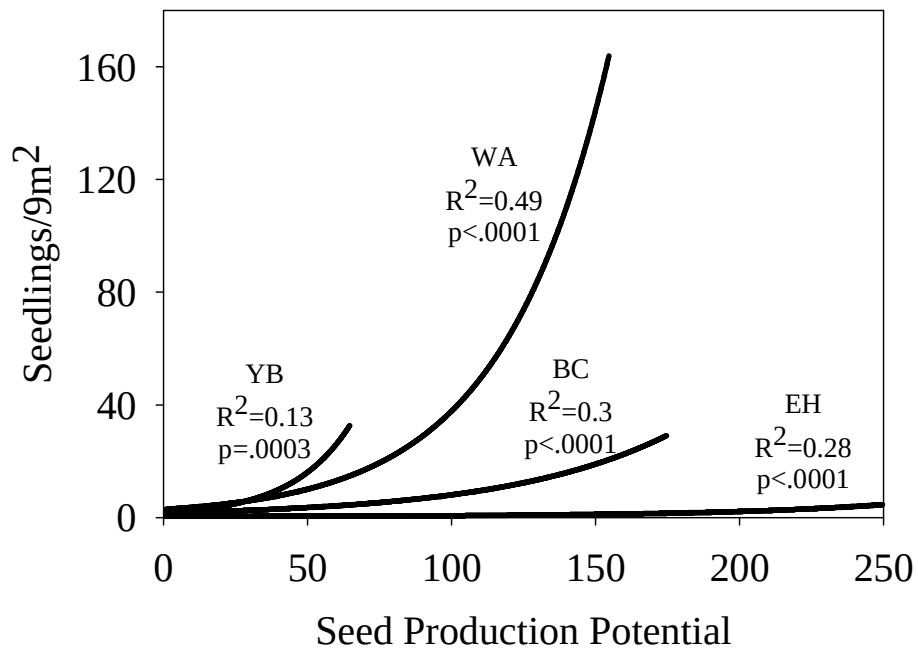
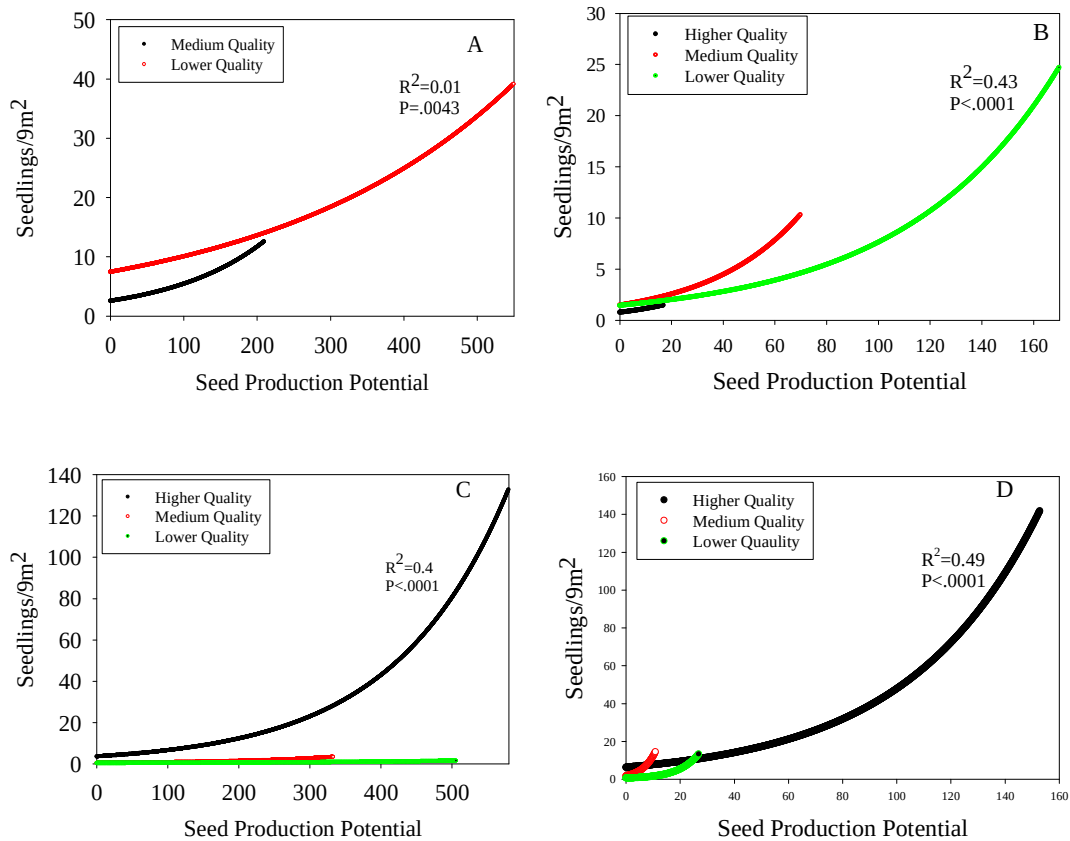


Figure 3.2- Seedling establishment as predicted by local seed production potential in high (AFOCa and AFOA), medium (AFO and AFPO) and low (ParVVb and ATFD) quality habitat types for red maple (A), black cherry (B), sugar maple (C), and white ash (D) (Burger and Kotar 2004).



Note⁻¹ Higher quality sites were not included in this analysis for red maple, as it only had a viable seed production potential in one harvest gap.

Figure 3.3- The effect of varying light availability in 114 harvest gaps on red maple (A) and sugar maple (B) seedling establishment.

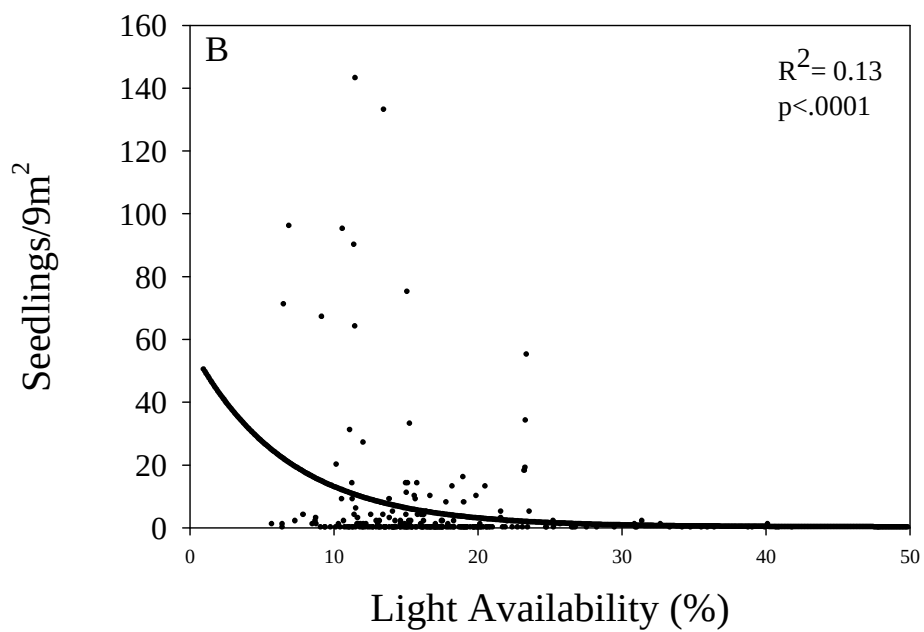
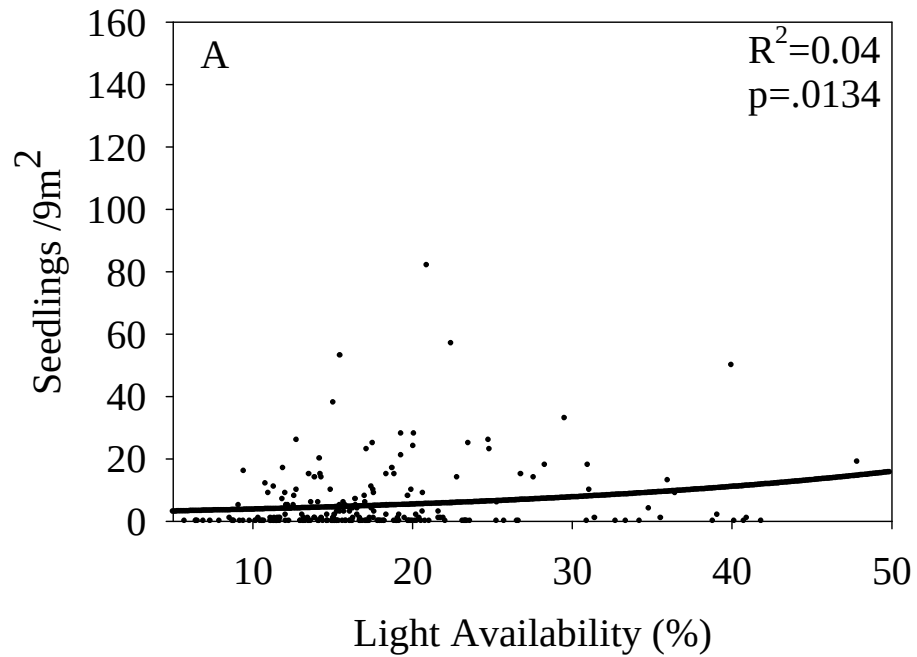


Table 3.1- Results of a generalized logistic mixed model for the effects of Light Availability, Non-Tree Vegetation Density, Habitat Type, Species, and their two way interactions on seedling survival. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).

	Factors	L-R Chi Square	Prob>Chisq
Survival	Light	1.86	0.1726
	Non-Tree Vegetation	12.71	0.0004
	Habitat Type	3.12	0.0771
	Species	8.98	0.2539
	Light x Non-Tree Vegetation	13.14	0.0003
	Light x Species	13.87	0.0536
	Non-Tree Vegetation x Habitat		
	Rank	10.34	0.0013
	Habitat Type x Species	11.93	0.1029
	R ² = .09		

Table 3.2- Results of a generalized linear mixed model for the effects of Scarification, Light Availability, Habitat Type, Species, Seed Production Potential (SPP) and their two way interactions on seedling establishment. All interactions Prob ChiSq > 0.25 were pooled with the error term and the models rerun (Bancroft 1964).

		L-R Chi Square	Prob>Chisq
Seedling Establishment	Scarification	2.45	0.1177
	Light	0.02	0.9025
	Habitat Type	1.8	0.1799
	SPP	2.14	0.1436
	Species	192.29	<.0001
	Scarification x Light	3.46	0.0628
	Scarification x SPP	3.18	0.0747
	Scarification x Species	25.25	0.0007
	Light x Habitat Type	9.88	0.0017
	Light x SPP	4.64	0.0312
	Light x Species	17.67	0.0135
	Habitat Type x SPP	4.88	0.0272
	Habitat Type x Species	237.7	<.0001
	SPP x Species	223.56	<.0001
	R ² = .50		

Table 3.3- Species' average seedling density (with standard deviation in parentheses) in 228 plots across 19 northern hardwood stands in the Northern Lower and Eastern Upper Peninsulas of Michigan.

Species	Mean± SD	Range
Eastern Hemlock	0.12 (0.7)	0-8
Yellow Birch	1.78 (7.78)	0-71
Paper Birch	0.88 (3.48)	0-32
Red Maple	5.07 (10.43)	0-82
Sugar Maple	6.08 (19.46)	0-143
White Pine	0.2 (.69)	0-4
Black Cherry	2.16 (6.03)	0-73
White Ash	5.26 (19.98)	0-118

Table 3.4- Species' average seedling density (with standard deviation in parentheses) in 114 scarified and unscarified plots across 19 northern hardwood stands in the Northern Lower and Eastern Upper Peninsulas of Michigan. Asterisks represent statistically significant effects (Prob ChiSq < 05).

Scarified	Mean $\pm$ SD	Range
Eastern Hemlock	0.12 $\pm$ 0.6	(0-5)
Yellow Birch	2.4 $\pm$ 8.32	(0-56)
Paper Birch *	1.5 $\pm$ 4.73	0-32)
Red Maple	5.44 $\pm$ 12.2	(0-82)
Sugar Maple	7.03 $\pm$ 23.51	(0-143)
White Pine*	0.28 $\pm$ 0.88	(0-4)
Black Cherry	1.6 $\pm$ 3.17	(0-21)
White Ash	4.27 $\pm$ 16.43	(0-103)
Unscarified	Mean	Range
Eastern Hemlock	0.11 $\pm$ 0.79	(0-8)
Yellow Birch	1.15 $\pm$ 7.17	(0-71)
Paper Birch	0.25 $\pm$ 1.05	(0-9)
Red Maple	4.68 $\pm$ 8.33	(0-50)
Sugar Maple	5.12 $\pm$ 14.38	(0-75)
White Pine	0.11 $\pm$.39	(0-2)
Black Cherry	2.7 $\pm$ 7.89	(0-73)
White Ash	6.25 $\pm$ 2.16	(0-118)

Table 3.5- Mean average light availability and competing non-tree vegetation characteristics (with standard deviation in parentheses) across high (AFOCa and AFOA), medium (AFO and AFPO) and low (ParVVb and ATFD) quality habitat types (Burger and Kotar 2004).

	High Quality	Medium Quality	Low Quality
Stands	5	7	7
Gaps	30	42	42
Canopy Openness Range (%)	5.73-23.42	7.91-26.66	6.45-50.32
Canopy Openness (%)	14.37 (4.03)	16.7 (3.89)	21.58 (10.43)
Vegetation Cover (%)	51.16 (37.62)	37.14 (36.09)	28.39 (31.89)
Vegetation Height (cm)	28.63 (36.49)	8.84 (14.47)	8.98 (16.24)

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Chapter IV

The effect of substrate type and mycorrhizal fungi on seedling development for northern temperate seedlings

Abstract

Gaining access to light and soil resources is a challenging task for seedlings on the forest floor. Due to their high moisture holding capacity and elevated position off the forest floor, decaying coarse woody debris (CWD) is thought to provide seedlings a favorable environment to establish and develop. Nevertheless, species of CWD have been shown to differ in their ability to support seedling development, and seedlings have been shown to differ in their ability to develop on individual species of CWD. This study investigates mycorrhizal fungi as a potential explanation for this pattern in a potted pot experiment where 11 tree species (yellow birch, paper birch, red maple, white ash, eastern hemlock, balsam fir, white spruce, northern white cedar, white pine, and red oak) were established on seven different types of substrate (bare mineral soil, yellow birch, sugar maple, paper birch, eastern hemlock, northern white cedar, and balsam fir CWD) that had either been sterilized or left unsterilized. In general, species grew better on bare mineral soil, paper birch, eastern hemlock, and northern white cedar CWD compared to sugar maple, yellow birch, and balsam fir CWD. Seedling survivorship was high for all conifer species (>90%), but varied widely among deciduous species with yellow birch (89%) surviving at the highest rate, and white ash (28%) surviving at the lowest rate. Mycorrhizal colonization had a positive effect on red maple, northern white cedar, white pine, and yellow birch's height growth, and was positively associated with large changes in species' performance

rankings on individual species of CWD. Collectively, this research demonstrates that individual species of CWD differ strongly in their ability to support seedling development, and thus should be considered at the species level, rather than a generic substrate on the forest floor. In addition, it identifies mycorrhizal colonization as an important factor contributing to seedling development on CWD.

Introduction

The transition between seedling and sapling is one of the most uncertain stages in the natural regeneration process. In order to pass through this vulnerable period, seedlings must gain access to adequate amounts of light and soil resources needed for constructing additional structural and resource acquiring biomass. For young seedlings, acquiring adequate resources may be particularly challenging as they often lack the necessary root system and or canopy area needed to exploit resources beyond their immediate proximity. As such, the resource environment of a seedlings initial establishment site may play an important role in determining whether a seedling successfully develops into a sapling.

Heavily decayed coarse woody debris (hereafter referred to as CWD) is one type of establishment site which may be particularly conducive to seedling development given its easily penetrated surface and high moisture holding capacity. (Harmon 1986; Cornett et al. 2001; Caspersen and Saprunoff 2005; Shields et al. 2007; Marx and Walters 2008; Bolton and D'Amato 2011). In addition to its role as a moisture source, CWD may increase seedling survival through elevating seedlings off the forest floor and thus providing refuge from many of the factors which limit seedling development there; i.e. competition from established vegetation, leaf litter smothering, high water tables, and potentially any species specific pests or pathogens which may be more abundant on the forest floor/mineral soil (Harmon and Franklin 1989; Packer and Clay 2000 & 2003; Simard et al. 2003; O'Hanlon-Manners and Kotanen 2004; Wang and Kembell 2005). Indeed, CWD has been documented as an important resource for seedling establishment/development in forests throughout the world (Harmon and Franklin 1989; McGee and Birmingham 1997; Simard

et al. 2003; Mori et al. 2004; Marx and Walters 2008; Sanchez et al. 2009). Nevertheless, compelling evidence also exists indicating that, despite all its beneficial properties, species differ in the capability for CWD to support seedling development, and that not all tree species are capable of long term survival on CWD (Marx and Walters 2006; Marx and Walters 2008). Consequently, management efforts seeking to promote old-growth structural characteristics by creating/maintaining CWD on the forest floor may need to focus more intently on conserving or restoring individual species CWD rather than considering it as a generic entity if maintaining/restoring ecosystem function is the primary objective.

Variation in CWD's ability to supply seedlings with nutrients is one potential explanation for the conflicting patterns of seedling development, as species have been shown to differ in their decay rates, nutrient ratios, nutrient concentrations, and rate at which nutrients become mineralized for seedling consumption (Arthur et al. 1993; Takahashi et al. 2000; Marx and Walters 2006; Strukelj 2013; Shorohova and Kapitsa 2014; Klockow et al. 2014). As such, certain species of CWD may simply be more capable of supporting development for all seedlings, no seedlings or only certain seedlings based on their nutrient environments and the nutrient demands/growth strategies of individual seedlings (Grime 1977; Chapin 1980). If true, seedling growth/survival on CWD may proceed in a predictable manner where fast growing nutrient demanding strategies demonstrate the greatest growth on nutrient rich CWD, but also experience the lowest survival and growth on nutrient poor CWD, reflecting a potential trade-off between maximizing growth potential versus stress tolerance (Grime; 1977; Chapin 1980; Aerts 1999). In partial support of this hypothesis, Marx and Walters (2006 & 2008) found that

fast growing yellow birch survived and grew best on eastern hemlock (*Tsuga canadensis* L.) CWD, which also had the highest nitrogen mineralization rates compared to sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) CWD. Nevertheless, the trends developed by Marx and Walters (2006 & 2008) are based on the performance of only a small range of species' seedlings growing on a small range of CWD species, and thus provide little generality and only limited evidence for the existence of a nutrient induced trade-off response.

Differences among seedlings in their ability to access nutrients via a symbiotic relationship with mycorrhizal fungi may also account for observed differences in seedling growth on CWD independent of differences in measured mineral N dynamics. In exchange for carbon from the seedling, mycorrhizal fungi improve seedling access to nutrients by increasing the substrate volume in which a seedling can forage for nutrients and by breaking down previously insoluble compounds (Smith and Read 1996; Perez-Moreno and Read 2000). Furthermore, mycorrhizal fungi are frequently found within CWD, suggesting that species' colonization is not limited by mycorrhizal presence (Harvey et al. 1979; Amaranthus and Perry 1994; Tedersoo et al. 2008). Provided this nutrient acquisition advantage, colonized seedlings may grow faster and survive at higher rates than uncolonized seedlings (Marx and Walters 2006). This, in turn, could cause species to grow and survive at rates that differ from those which would be predicted by a nutrient trade-off alone. Indeed, Marx and Walters (2006) also reported seedlings growing on CWD achieved greater mass when colonized with mycorrhizal fungi compared with uncolonized seedlings, but did not observe rank changes in performance.

One factor which may determine the importance of seedlings becoming colonized is the type of mycorrhizal fungus individual tree species associate with. Due to their limited saprophytic capabilities, arbuscular mycorrhizae (AMF) may be less abundant in CWD than ectomycorrhizal fungi (EMF), which are saprophytic (Treseder et al. 2005; Smith and Smith 2011). Species which associate with EMF may also receive a greater increase in nutrient availability. Via their production of oxidative extracellular enzymes, EMF associated species can access nitrogen and phosphorous from a variety of pools which are inaccessible to AMF fungi (Turner 2008; Courty et al. 2010; Phillips et al. 2013). Consequently, seedlings associated with EMF may have a higher probability of becoming colonized and may also gain a greater functional advantage as a result.

In this shade house potted plant experiment, we investigate the effect of nutrient availability and mycorrhizal colonization on 11 tree species established across seven substrates (six species of CWD and soil) that have either have or have not been sterilized to kill naturally-occurring mycorrhizae. This approach allows us to not only develop a broader pattern of seedling development across different seedling establishment sites, but also allow us to experimentally separate the effects of nutrient availability and mycorrhizal colonization on seedling development. Specifically we predict: 1) seedling height growth will reflect mineral nitrogen availability on sterilized substrates with fast growing tree species demonstrating the greatest growth on nitrogen rich substrates 2) height growth will depend on mineral nitrogen availability and mycorrhizal association type on unsterilized substrates, with EMF colonized seedlings demonstrating greater growth than non-colonized seedlings at a given level of nitrogen availability, leading to possible rank changes in species growth between sterilized and unsterilized substrates.

Methods

Field methods

In summer 2012, CWD of sugar maple, yellow birch, paper birch (*B. papyrifera* Marsh), eastern hemlock, northern white cedar (*Thuja occidentalis* L.), and balsam fir (*Abies balsamifera* (L.) Mill.) were located in four locations in the northern Lower and eastern Upper Peninsula's of Michigan. The four locations included an old growth hemlock hardwood dominated forest preserve (The Huron Mountain Club), two managed lowland conifer swamps and a sugar maple dominated managed upland hardwood stand (Michigan Department of Natural Resources. All CWD was in decay stage 3 or 4 (Graham and Cromack 1982) and was identified to species by bark and branching pattern. Samples of CWD were bagged and transported to the Tree Research Center at Michigan State University for temporary storage (4°C). With the exception of cedar, for which only 11 logs could be located, at least 16 different logs of each species were sampled. In addition to CWD, soil was also obtained from each site using soil cores (20cm).

Shade house methods

In late May 2013, CWD and soil samples were divided into two equally sized populations (by species for CWD) with one being randomly selected for a gamma irradiation sterilization treatment (30-60kGy) (Sterigenics Inc., Schaumburg, IL, USA). Sterilized and unsterilized substrate was then embedded in pots (Stuewe and Sons Inc., Corvallis Oregon) with sterilized coarse silica sand (Best Sand Inc., Chardon Ohio) (2/3

substrate). Sand sterilization was accomplished by drying the sand at 110 °C for 72 hours. Each pot was then seeded with sterilized pre-stratified seeds of sugar maple, red maple (*A. rubrum* L.), northern white cedar, eastern hemlock, yellow birch, paper birch, white pine (*Pinus strobus* L.), white ash (*Fraxinus americana* L.), red oak (*Quercus rubra* L.), white spruce (*Picea glauca* (Moench)), and American elm (*Ulmus americana* L.). Seed sterilization was accomplished by submerging seeds in a water bleach mixture (10% bleach) for one minute. All seeds were obtained from the Michigan Department of Natural Resources (MDNR) or Sheffield's Seed Company Inc, (Locke, New York, USA). Unfortunately, germination was poor for sugar maple, American elm, white ash, and red maple. To overcome this issue we transplanted newly germinated wildings of red maple and white ash seedlings into pots and removed sugar maple from the experiment. Prior to transplant the root systems of each seedling was sterilized in 10% bleach. In addition to the planted/seeded plots, three pots of each unique substrate treatment combination were left empty for inorganic nitrogen extractions (methods described in forthcoming laboratory methods).

The experiment itself was located in three hoop houses built within a lath house (~50% shade). Each hoop house was covered with clear plastic to exclude rain water. To quantify the light environment we measured photosynthetically active radiation (PAR) within each house with a quantum sensor (Apogee Instruments Inc., Logan Utah). PAR ranged from 254-344 $\mu\text{mol m}^{-2}\text{s}^{-1}$ across houses under cloudless mid-morning conditions. To mitigate any potential issues associated with differences in PAR, we spread all unique treatment combinations equally across houses. Seedlings were also rotated across houses to further mitigate environmental differences. In addition, all pots were kept at least five

meters from the edge of each house to minimize edge effects. Throughout the experiment, seedlings were watered as needed with deionized water (DI). DI was chosen to minimize the addition of external nutrients to the pots.

Initial heights (cm) of germinated/planted seedlings were taken after planting in early July 2013. Seedling growth was then reassessed and survival checked at the end of September. At this time, four replicates of yellow birch, paper birch and red oak and three replicates of each species except sugar maple and red pine (due to low sample size) were randomly selected from each unique treatment substrate combination and destructively harvested to examine mycorrhizal colonization and biomass development (methods described in forthcoming laboratory methods). This was done to preserve our ability to examine mycorrhizal colonization as a potential mechanism, and to accurately depict biomass development in case high mortality occurred over winter. Harvest intensity was greatest for birch and oak because these species had already shown large differentiation in height growth, thus providing us with the most data to investigate the effects of nutrients and mycorrhizae on 1st year growth for these species. Fewer replicates of the other species were harvested in order to preserve our ability to detect future (2nd year) changes in growth and survival, as seedlings had yet to differentiate by the end of the first growing season. By this same logic, we decided against investigating 1st year mycorrhizal colonization for this latter group of species.

Harvested seedlings were placed in plastic bags and kept frozen until final processing for mycorrhizae. The remaining seedlings were overwintered in the hoop houses and allowed to grow until the end of June 2014. At that time, all seedlings were assessed for survival, height, and total mass. Seedlings dead at the time of final harvest

were not collected for further analysis. At that time we also selected four species for mycorrhizal analysis (yellow birch, white pine, red maple, and northern white cedar). Selection criteria was based on observed patterns of height development, type of mycorrhizal association (AMF vs EMF) and growth strategies (ranging from rapidly growing nutrient demanding to slow growing nutrient conserving). Four replicates of each unique unsterilized substrate combination and one replicate of each unique sterilized substrate combination were randomly selected from this group of species for colonization analysis.

Laboratory methods

To analyze substrate inorganic nitrogen ($\text{NH}_4^+\text{-N}$, and NO_3^-N) concentration we obtained two 10g samples from each of the three unplanted pots from each unique sterilization substrate combination. On each sample, we determined gravimetric moisture content by drying the first sample at 105° C in a container of a known volume. The second sample was extracted with 50mL of 2 M KCL and analyzed colorimetrically for NH_4^+N , and NO_3^-N content. Following the logic of Marx and Walters (2006) we chose to express the initial [N] content on a volume basis based on the fact that soil is denser than wood and because roots forage a given volume of substrate.

For each seedling selected for mycorrhizal colonization analysis, we first carefully removed all residual CWD and/or soil from the root system by floating them in water. Fine roots (<2mm) were then randomly harvested from the entire root system for colonization analysis. Before analysis, all fine roots were first cleared with KOH and stained with black ink (Sheaffer Incorporated, Ft. Madison, Iowa) to identify AMF

colonization. Roots were then mounted on slides and examined for colonization beneath a compound microscope. AMF colonization was investigated at intersections between an inserted hairline graticule and the root at 200x magnification, while EMF colonization was examined at individual root tips at 100x magnification. At least 50 root intersections/tips were examined for each seedling. Both EMF and AMF colonization was examined for each seedling as several species included in this study have been shown to support both AMF and EMF colonization (Personnel Communication Sarah Newman).

To quantify biomass development, each seedling was separated into above (leaves and stems) and below ground biomass (roots) and dried for 48 hours at 65 °C. Seedlings were then weighed to determine the dry weight biomass of each section. This work is currently ongoing and will be reported in a future publication of this study. In addition, foliar nutrient analysis will also be performed and reported in a future publication.

Statistical methods

We examined the effects of Species, Sterilization and Substrate on height growth using a one-way ANOVA. In order to standardize our analysis, all seedlings that died or were harvested prior to the final harvest in June 2014 were removed from consideration. We also removed red pine, white ash, and red oak from the analysis due to poor representation across all substrates/treatments. For the remaining species, final height growth measurements were log-transformed to meet the assumption of normality prior to the analysis. Model selection was accomplished through backwards elimination. Interaction terms exceeding the suggested threshold for pooling variances ($F > .25$) were removed from the model and pooled in the error term (Bancroft, 1964). The model was

then re-run until a final model containing only significant factors ($F < .05$) and interactions ($F < 0.25$) could be reached. Once we arrived at a final model, significant differences among means were explored using Tukey-Kramer Honestly Significant Difference Test (HSD). This same statistical approach was also used to investigate the effects of Substrate, Species and their interaction on mycorrhizal colonization for the four species in which we investigated root colonization in 2014 (red maple, yellow birch, northern white cedar, white pine). To gain further insight into mycorrhizae's influence (EMF and AMF separately) on seedling development, we examined species height growth vs. colonization rates using linear regression. Finally, to gauge Sterilization's effect on species performance ranks, we compared the mean height growth of individual species growing on Sterilized vs. Unsterilized substrate on each type of Substrate. Spearman's Rho correlations were used to determine height growth rank changes between sterilized and unsterilized substrate, where lower correlation values corresponded to larger changes in ranks. Finally, we examined the influence of Species, Sterilization and Substrate on seedling survivorship using nominal logistic regression models. Model selection was accomplished using the same procedures described for seedling height. Seedlings that died within the first 6 weeks following transplant were removed from the analysis. Red pine was not considered in this analysis due to low sample size. All statistical analysis was performed in JMP 9.0 (SAS Institute, Cary, NC). All graphics were produced in Sigma Plot version 11 (Systat Software Incorporated, San Jose, California).

Results

Height growth

Height growth varied significantly among Species (Table 4.1). In general, fast growing shade intolerant to mid-tolerant species (paper birch, yellow birch, white pine and red maple) outgrew the more shade tolerant conifer species (Figure 4.1). In addition to differing in height growth, Species also responded differently to the combination of Sterilization and Substrate treatments (Tables 4.1 & 4.2). Independent of Sterilization effects, Substrate type was the strongest factor affecting balsam fir, eastern hemlock, paper birch and white pine, as each species grew best on bare mineral soil (Figure 4.1) (Table 4.2). Paper birch and northern white cedar CWD also consistently supported greater height growth for this group of species compared to sugar maple, balsam fir and yellow birch CWD (Figure 4.1). For red maple, northern white cedar, yellow birch and white spruce, height growth depended significantly on the interaction of Substrate Type and Sterilization (Table 4.2). Sterilization had strong negative effects for red maple growth on all substrates except northern white cedar and balsam fir (Figure 4.2). In a similar fashion, Sterilization had strong negative effects on northern white cedar's growth across all substrates except northern white cedar CWD (Figure 4.2). Sterilization also produced significantly less growth on mineral soil for white spruce (Figure 4.2). Yellow birch demonstrated a mixed response to Sterilization as its growth was negatively affected on eastern hemlock CWD but strongly positively affected on balsam fir CWD (Figure 4.2).

Seedling survival

Species differed significantly in their survival (Table 4.3). In general, shade tolerant to mid-tolerant conifer species experienced the greatest survival, as balsam fir, hemlock, white pine, northern white cedar and white spruce survival equaled or exceeded 90% (Table 4.4). In contrast, among the deciduous species, only yellow birch and paper birch survived at greater than 75% (Table 4.4). The lowest survival occurred in red oak and white ash which each survived at 30 and 18%, respectively (Table 4.4). Nevertheless, no factor or interaction significantly predicted these patterns (Table 4.3).

Mycorrhizal colonization pattern and effects

Root colonization was strongly influenced by Substrate and Species by Substrate interactions (Table 4.5). With the exception of white pine, which was colonized most frequently on cedar CWD, root colonization was highest on mineral soil (Figure 4.3). For primarily AMF associated species (red maple and northern white cedar), mycorrhizal colonization was also consistently higher on balsam fir and hemlock CWD than on any other species of CWD (Figure 4.3). For primarily EMF associated species (yellow birch and white pine), colonization was consistently higher on mineral soil and northern white cedar CWD than any other substrate (Figure 4.3). Across species, increasing root colonization was positively associated with increasing height growth, with northern white cedar showing the strongest correlation between colonization and height growth (Figure 4.4).

Sterilization's effect on performance rankings

Sterilization's influence on species' height growth performance rankings varied across substrates (Table 6). Strong rank changes were observed on balsam fir CWD, as shade mid-tolerant EMF associated deciduous species dominated the Sterilized treatment, while primarily shade mid-tolerant to tolerant AMF associated conifer species gained dominance in the Unsterilized treatment (Figure 4.5). In contrast, Sterilization had very little influence on species' height growth on northern white cedar CWD, as shade intolerant to mid-tolerant EMF associated species dominated both treatments (Figure 4.6). For each of the five remaining substrates, Sterilization led to only modest changes in height growth rankings (Table 4.6).

Discussion

Height growth

While we are currently limited in our abilities to identify mechanisms, our results demonstrate that different types of forest substrate have a strong effect on species height growth. Among species, height growth was generally better on mineral soil, and significantly so for balsam fir, eastern hemlock, paper birch and white pine (Figure 4.1). This finding is not surprising, considering that soil has been shown to support higher rates of nitrogen mineralization (N_{min}) and inorganic nitrogen concentrations $[N]$ compared to yellow birch, eastern hemlock and sugar maple CWD (Marx and Walters 2006). In addition, by removing seedlings from several of the factors which influence seedling

access to resources on the forest floor our experimental design likely enhanced a nutrient influence effect.

Among species of CWD, seedling height growth was also generally higher on northern white cedar, paper birch and hemlock compared to balsam fir, yellow birch and sugar maple (Figure 4.1). This finding again concurs with the growth trends reported by Marx and Walters (2006), and strengthens the notion that individual species of CWD vary in their availability to support seedlings, and thus should be considered individually rather than a generic forest floor resource. In addition, these findings also align with the observations of Bolton and D'Amato (2011) and Cornett et al. (2001) who reported northern white cedar and paper birch as important substrates for seedling establishment.

Contrary to our initial hypothesis, mycorrhizal colonization appears to be an important factor for red maple and northern white cedar (AMF associated species). Evidence supporting this conclusion includes both species' generally negative response to sterilization (Figure 4.2) and significantly positive response to increasing AMF % colonization (Figure 4.4). In addition, cedar also grew best on the substrate where it was colonized most often (mineral soil) (Figure 4.3) and experienced a dramatic height growth decline (2nd best to worst) in response to sterilization on balsam fir (Figure 4.5), where it was also frequently colonized (Figure 4.3). The one exception to this pattern for northern white cedar came when it was growing on its own CWD, where growth increased in response to sterilization (Figure 4.2). While, at this point, we cannot dismiss the possibility that this pattern was driven by a treatment related increase in available nutrients, it is also possible that cedar growth is limited on its own CWD by specialized host specific pathogens. Nevertheless, it should also be pointed out that northern white cedar's

mycorrhizal colonization rate was lowest on cedar CWD, thus a lack of mycorrhizal fungi in cedar CWD may also be driving this pattern (Figure 4.3).

In addition to red maple and northern white cedar, mycorrhizal colonization was also important for yellow birch. Much like northern white cedar, yellow birch grew best on the two substrates where it was most likely to be colonized (mineral soil and cedar CWD) (Figures 4.2 & 4.3), and responded positively to increasing EMF% colonization. Moreover, supporting the findings of Marx and Walters (2006 & 2008) and our initial hypothesis, yellow birch grew significantly better on unsterilized hemlock CWD, where it was third most likely to be colonized (Figures 4.2 & 4.3). Mycorrhizal colonization was potentially so important for yellow birch development that sterilization caused a shift in ranks from best growing species on unsterilized hemlock CWD to second best on sterilized hemlock CWD (Figure 4.7). Despite the fact that it generally forms a different type of association (AMF vs. EMF), red maple experienced a similar dramatic shift, where it went from the second best growing species on sterilized hemlock CWD to fifth best on the unsterilized treatment (Figure 4.7). Yellow birch's response to sterilization, however, was not consistent across substrates, as height growth was unaffected by sterilization on cedar CWD, where it remained dominant (Figure 4.6), and was strongly positively affected by sterilization on balsam fir CWD, where it went from the species that grew least in the unsterilized treatment to species that grew best in sterilized treatment (Figure 4.5). While we are still unsure as to the exact mechanism for this dramatic shift on balsam fir, a lack of mycorrhizal fungi is less likely to be the cause, as colonization on balsam fir were neither high nor low for yellow birch (Figure 4.3). Collectively, these findings demonstrate that

mycorrhizal fungi may not be as important on all substrates, and may be strongly differing effects on different species of CWD.

Seedling survival

Large differences occurred in individual species survival (Table 4.3). Corresponding with their slow growing nutrient conserving growth strategy, each conifer species experienced high survival (Grime 1977; Chapin 1980). Consistent with our observations of seedling demographics on CWD in the field, red maple survival was low compared to the majority of other species (Table 4.3). While, not surprising to us, this result does contradict red maple's reputation in the literature as a "super generalist" which can tolerate a variety of environmental conditions (Abrams 1998). Nevertheless, it is hard to say whether red maple's low survival was related to it being a largely transplanted species, as the majority of seedlings survived through the first growing season, but failed to emerge the following spring. White ash, our other transplanted species, followed a similar pattern of survival. Again, however, this result is consistent with our personal observations of white ash rarely surviving on CWD in the field. Red oak followed a similar pattern of high initial survival followed by low spring emergence. This result was surprising, however, considering that red oak was not transplanted, has a moderately conservative growth strategy (Crow 1988; Kolb et al. 1990; Kaelke et al. 2001) and was not shaded at any point during this experiment. Interestingly, paper birch and yellow birch, our two smallest-seeded, fastest-growing species (Walters et al. 1993; Beaudet and Messier 1998), survived at relatively high rates. While we cannot make any definitive statements about substrate nutrient content at this point, this finding demonstrates that even our most

nutrient depauperate substrate was able to support our most nutrient demanding species for more than a single growing season.

Mycorrhizal colonization

For the four species examined in 2014, mycorrhizal colonization was consistently higher on mineral soil than CWD (Figure 4.3). Although no attempt was made to quantify root density or surrounding vegetation proximity at our substrate collection sites, this pattern may reflect mineral soil containing a higher density of mycorrhizal infected roots than CWD. Root density, in turn, may correlate with substrate nutrient concentrations, as roots have been shown to respond to differences in resource availability (Gersani and Sachs 1992; Robinson 1994; Hutchings and John 2004). This theory may also contribute to the differing rates of mycorrhizal colonization observed across different species of CWD (Figure 4.3).

Conclusions and Management Recommendations

Oftentimes one of the greatest challenges in regenerating or restoring tree species is promoting their transition from the seedling to the sapling stage. Although our results indicate that bare mineral soil typically supported the greatest development of species, species face several challenges to their development on the forest floor (Shields et al. 2007; Matonis et al. 2011; Kern et al. 2013; Willis et al. ch1 & 2; Walters et al. in preparation). CWD offers refuge from several of these factors; however, our results indicate that individual species of CWD can have strongly differing effects on seedling development. This both echoes the results of Marx and Walters (2006 & 2008) and calls for a change in

perception of CWD being a generic resource. One of the challenges in making this transition is the legacy of reduced mortality in managed stands. In such situations CWD may already be in decline (Goodburn and Lorimer 1998; Hura and Crow 2004). Furthermore, restarting this cycle naturally could take decades naturally and, in most situations, would be prohibitively labor intensive to attempt artificially. As a result, greater efforts need to be put forth to identify important species of CWD and restart their natural formation if shortages are to be avoided in the future.

Figure 4.1- Height growth across balsam fir (BF), eastern hemlock (EH), northern white cedar (NWC), paper birch (PB), sugar maple (SM), mineral soil (MS), and yellow birch (YB) for balsam fir (A), eastern hemlock (B), paper birch (C), and white pine (D) seedlings. Error bars represent one standard error, while substrates not sharing a common letter supported significantly different seedling growth ($P < 0.05$, Tukey Kramer HSD).

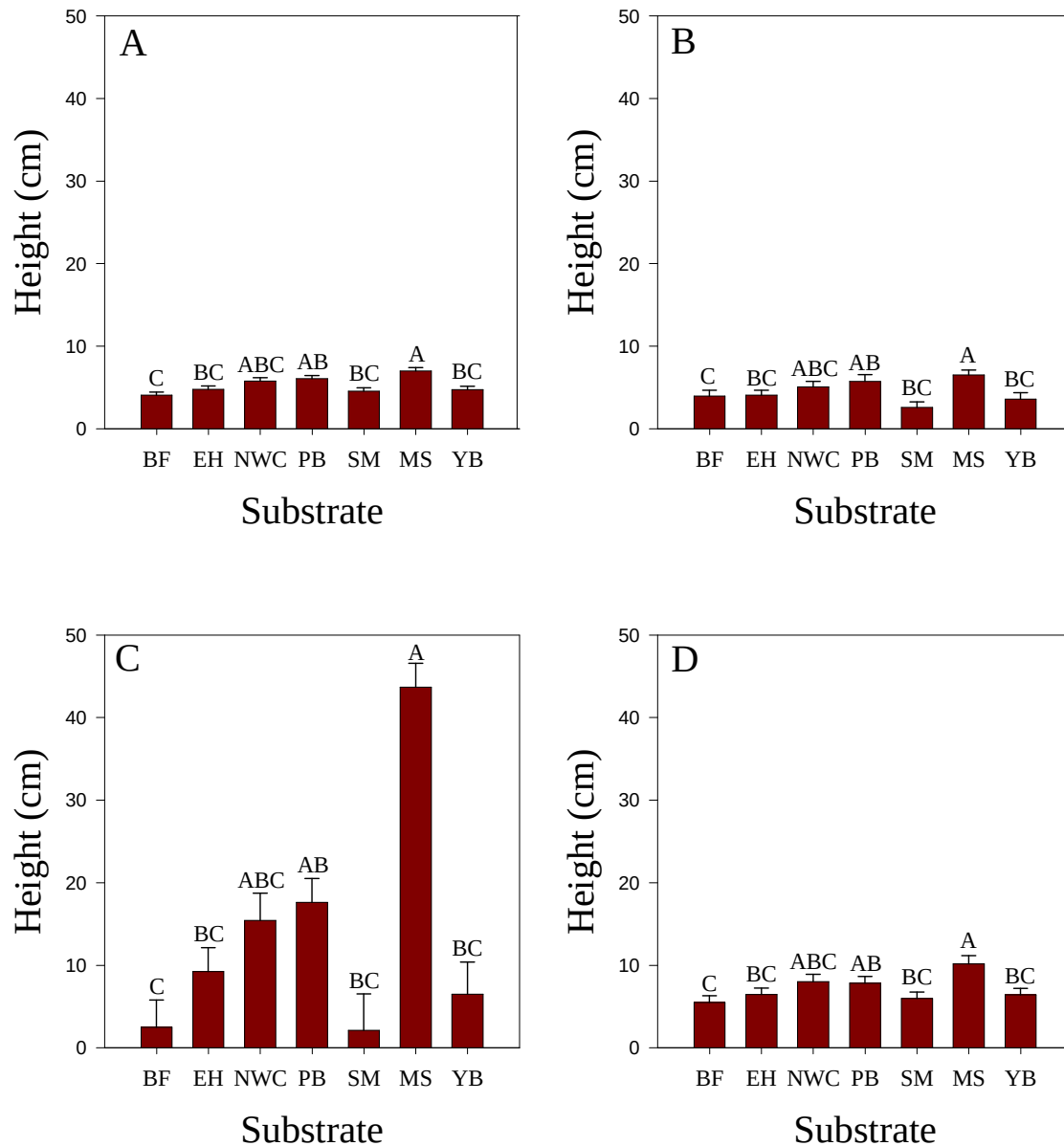


Figure 4.2- Height growth across sterilized (Maroon) and unsterilized (Gold) balsam fir (BF), eastern hemlock (EH), northern white cedar (NWC), paper birch (PB), sugar maple (SM), mineral soil (MS), and yellow birch (YB) for red maple (A), northern white cedar (B), white spruce (C), and yellow birch (D) seedlings. Error bars represent one standard error, while asterisks represent statistically significant effects of sterilization on growth (prob $|t| < 0.05$)

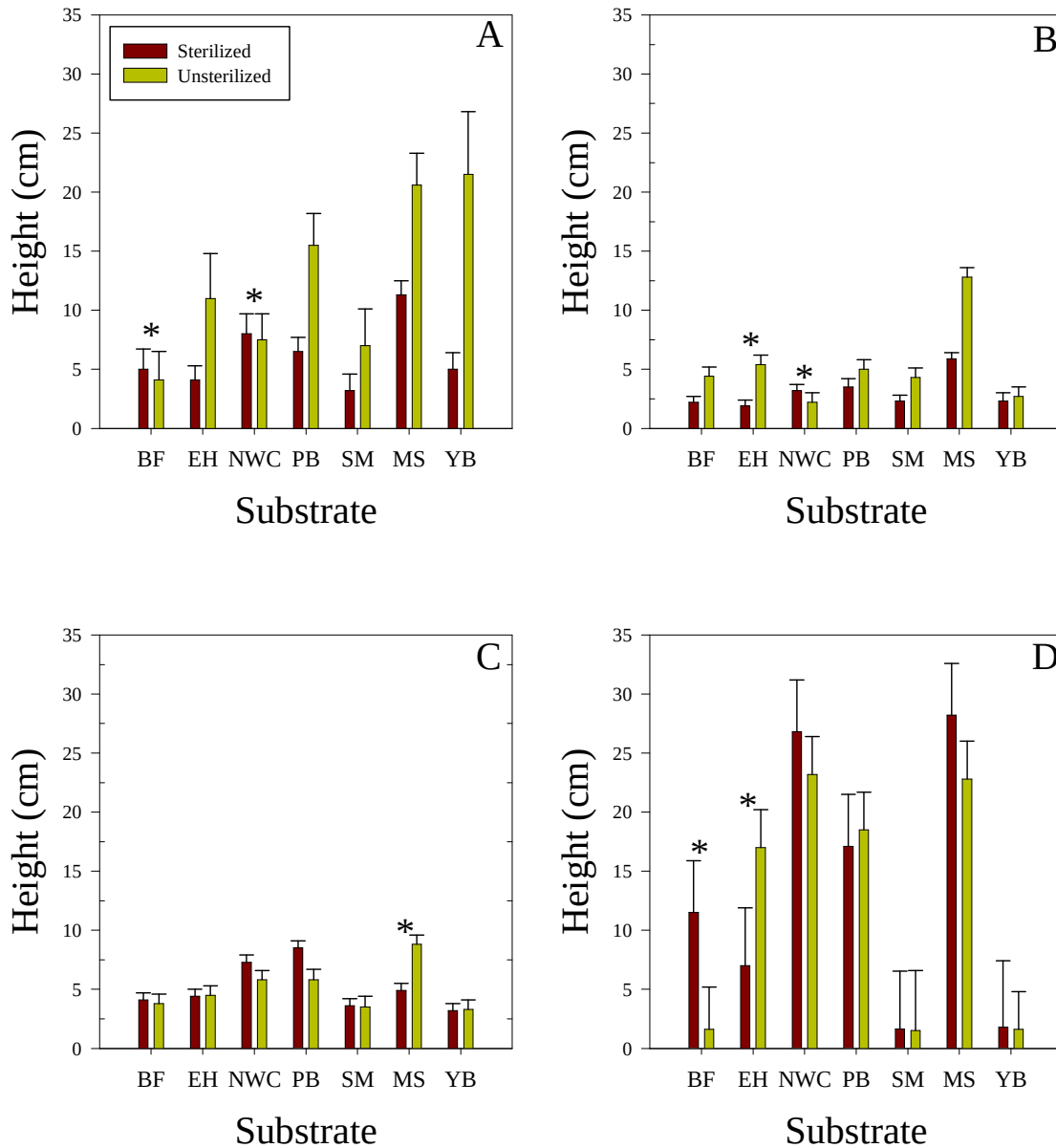
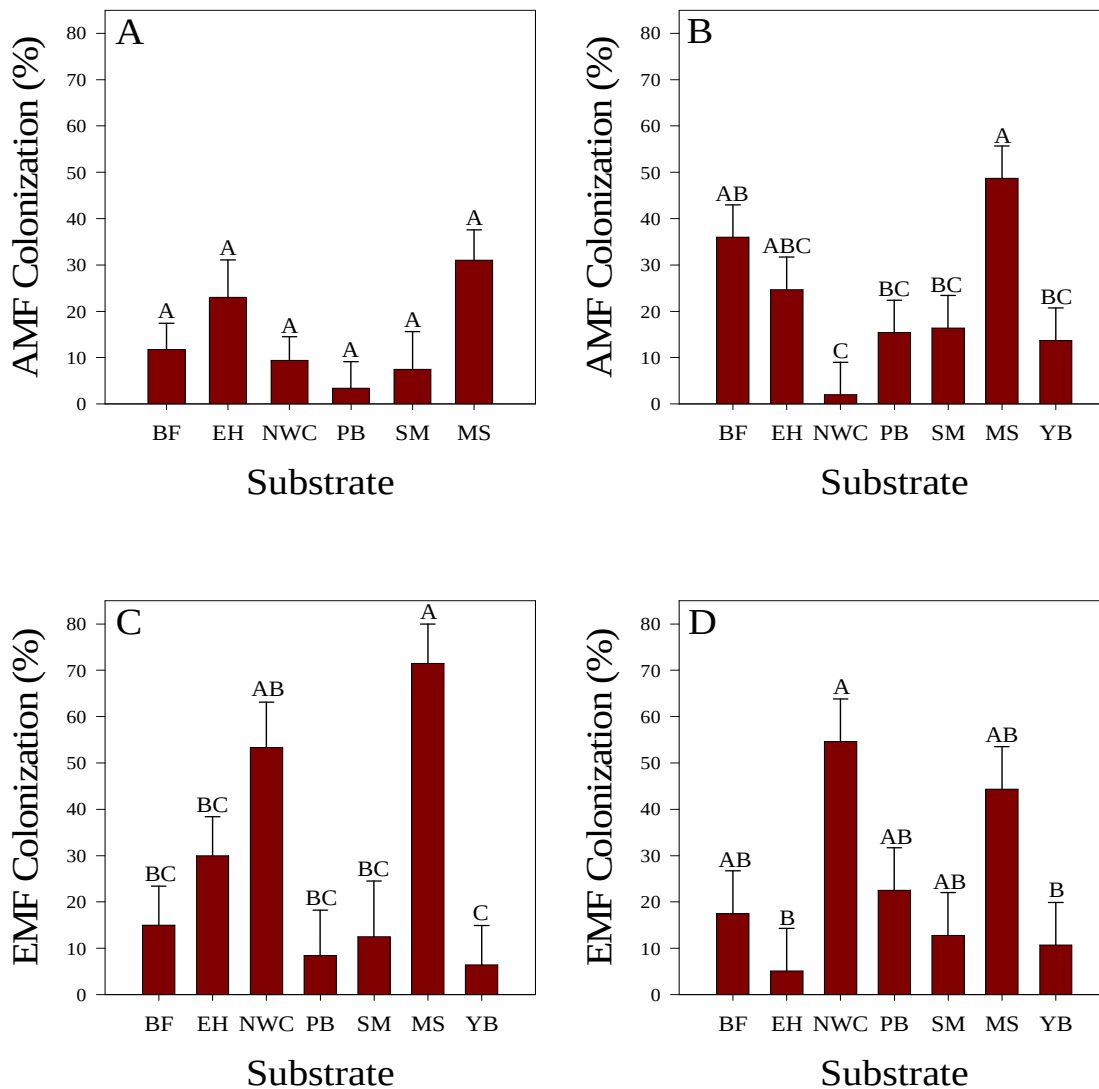


Figure 4.3- Percent colonization of arbuscular mycorrhizal fungi (AMF) on red maple (A) and northern white cedar (B) seedlings and ectomycorrhizal fungi colonization on yellow birch (C) and white pine seedlings (D) across unsterilized balsam fir (BF), eastern hemlock (EH), northern white cedar (NWC), paper birch (PB), sugar maple (SM), mineral soil (MS), and yellow birch (YB) substrates. Error bars represent one stand error, while substrates not sharing a common letter supported colonization at significantly different rates ($P < 0.05$, Tukey-Kramer HSD).



Note²- Yellow birch was not analyzed a substrate for red maple due to our randomly sample population failing to meet the minimum number of intersections to be considered for analysis.

Figure 4.4- The relationship between arbuscular mycorrhizal fungi (AMF) colonization and height growth for red maple (A) and northern white cedar (B) and ectomycorrhizal fungi (EMF) colonization and height growth for yellow birch (C) and white pine (D).

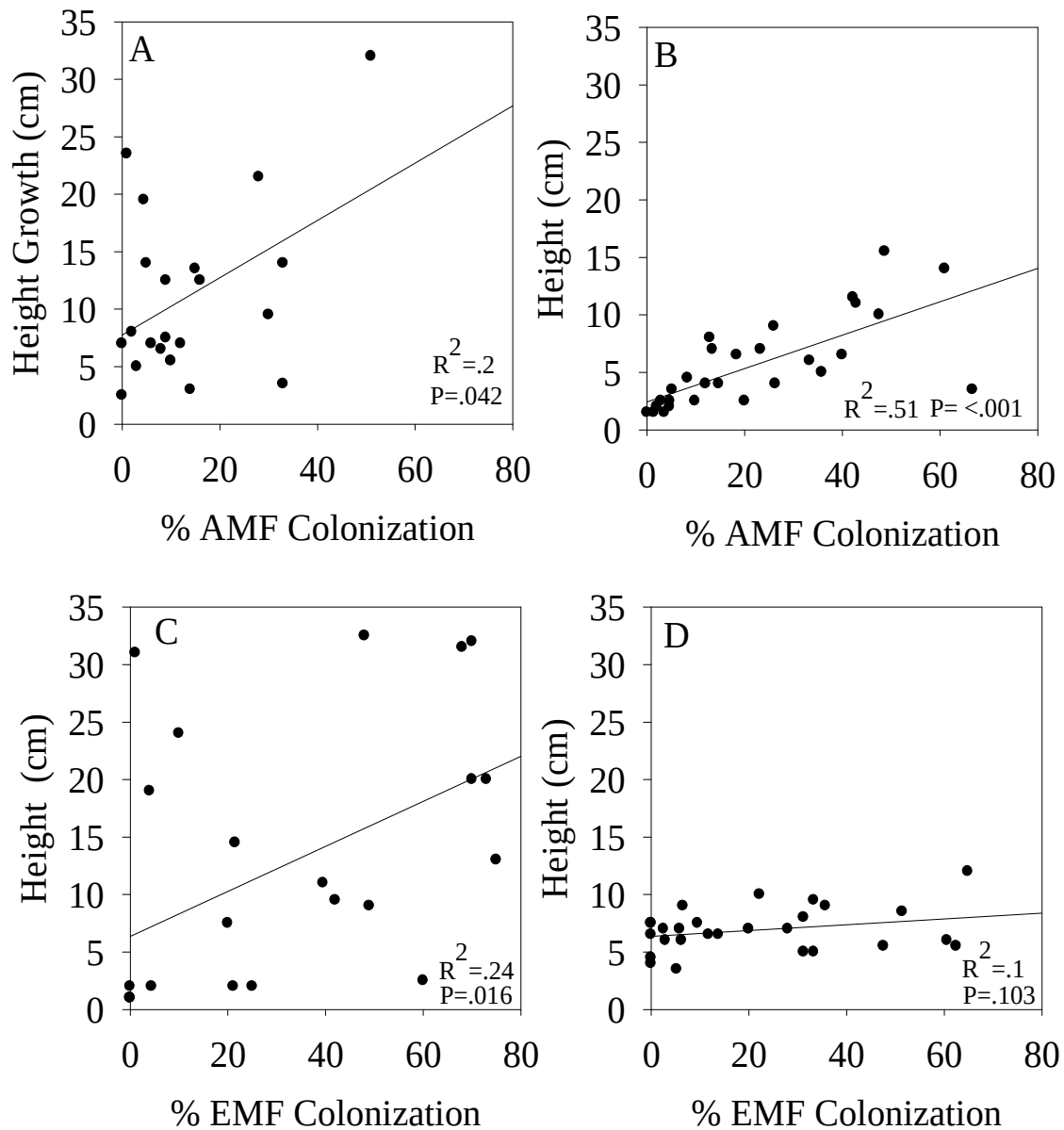


Figure 4.5- Effect of sterilization (maroon) on species' height growth performance on balsam fir CWD. Species were ranked from one to eight with one representing the best height growth performance. The Spearman's rank correlation statistic is listed in the top left corner.

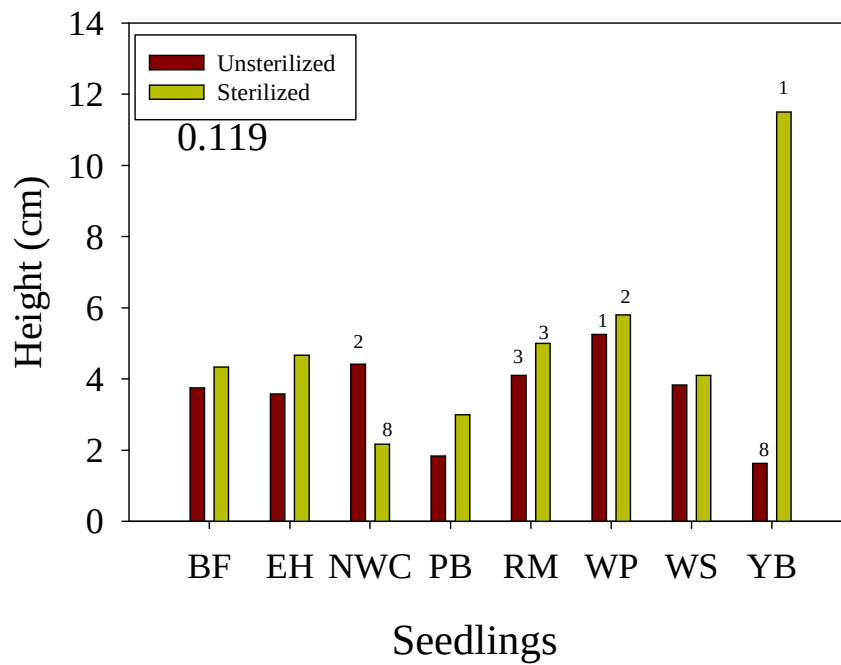


Figure 4.6- Effect of sterilization (maroon) on species' height growth performance on northern white cedar CWD. Species were ranked from one to eight with one representing the best height growth performance. The Spearman's rank correlation statistic is listed in the top left corner.

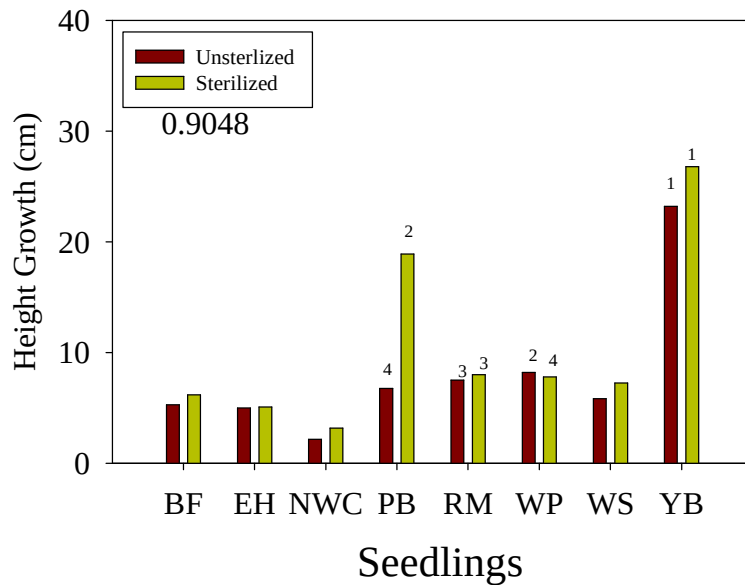


Figure 4.7- Effect of sterilization (maroon) on species' height growth performance on eastern hemlock CWD. Species were ranked from one to eight with one representing the best height growth performance. The Spearman's rank correlation statistic is listed in the top left corner.

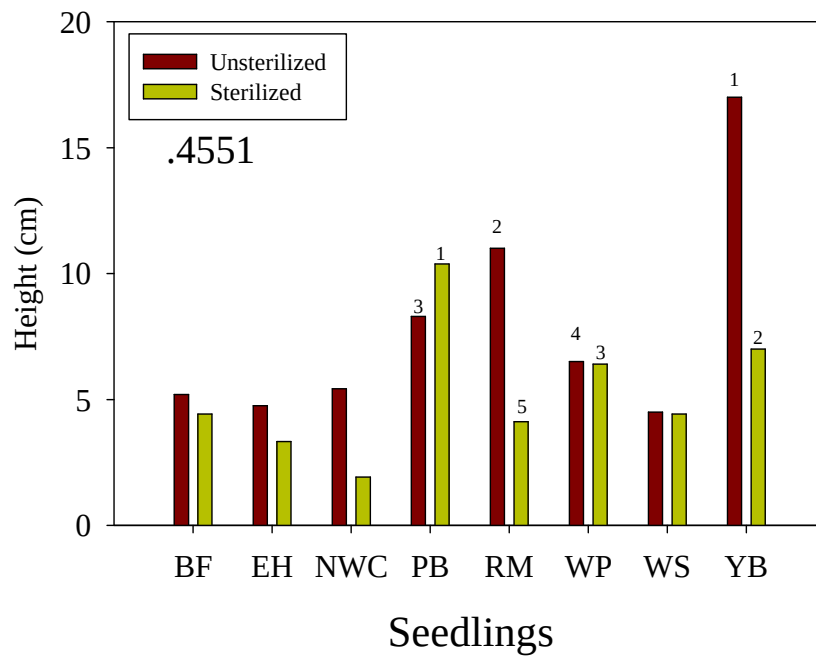


Table 4.1- Results of a standard least squares model for the effects of Sterilization, Species, Substrate, and their interactions on height growth.

		Sum of Squares	F Ratio	Prob > F
Height Growth (cm)	Sterilization	1.03	5.42	0.0203
	Species	35.89	26.91	<.0001
	Sterilization x Species	7.65	5.73	<.0001
	Substrate	80.68	70.57	<.0001
	Sterilization x Substrate	10.25	8.97	<.0001
	Species x Substrate	71.26	8.9	<.0001
	Sterilization x Species x Substrate	21.06	2.63	<.0001
	R Square Adj = .75			

Table 4.2- F ratio's and P > F from standard ANOVA least squares models for the effects of Sterilization and Substrate, and their interactions on species' height growth.

Species	Sterilization	Substrate	Sterilization x Substrate
	0.41	5.59	0.66
BF	0.5256	<.0001	0.6856
	0.02	4.09	2.03
EH	0.8824	0.002	0.0789
	21.63	13.41	2.68
NWC	<.0001	<.0001	.0218
	1.05	12.96	2.31
PB	0.3113	<.0001	0.0546
	22.92	7.22	2.88
RM	<.0001	<.0001	0.0229
	2.71	2.82	0.93
WP	0.1049	0.0175	.4744
	0.24	11.22	2.88
WS	0.623	<.0001	0.0148
	0.5466	28.83	4.21
YB	0.4633	<.0001	.0018

Table 4.3- Results of a nominal logistic regression model for the effects of Sterilization, Species and Substrate, and their interactions on seedling survival.

	Factor	L-R	Prob>ChiSq
		Chi Square	
Survival	Sterilization	0	1
	Species	244.29	<.0001
	Sterilization x Species	>.01	1
	Substrate	>.01	1
	Sterilization x Species	2.95	0.81
	Species x Substrate	67.88	0.13
	Sterilization x Species x Substrate	52.68	0.52
	R Square Adj = .54		

Table 4.4- Overall survival rate of individual species at the end of the experiment.

Species	Total	Living	Dead	Survival (%)
Balsam Fir	83	81	2	98
Eastern Hemlock	77	69	8	90
Northern White Cedar	82	80	2	98
Red Oak	69	21	48	30
Paper Birch	66	50	16	76
Red Maple	80	47	33	59
White Ash	67	19	48	28
White Pine	84	78	6	93
White Spruce	86	82	4	95
Yellow Birch	70	62	8	89

Table 4.5- Results of a standard least squares model for the effects of Species, Substrate and their interaction on mycorrhizal colonization of roots.

	Factor	Sum of Squares	F Ratio	Prob > F
Root Colonization (%)	Species	1359	1.84	0.1476
	Substrate	14269	9.65	<.0001
	Species x Substrate	13260	2.99	0.0005
	R Square Adj = .51			

Note⁻¹ Mycorrhizal colonization was not observed on Sterilized substrate.

Table 4.6- Sterilization's effect on species height growth rankings within individual substrate types. Values of ρ are Spearman's rank correlations between sterilized and unsterilized treatments. Smaller values indicate greater changes in ranks.

Substrate	Spearman's ρ	Prob > $ \rho $
Balsam Fir	0.119	0.7789
Hemlock	0.4551	0.2572
Northern White Cedar	0.9048	0.002
Paper Birch	0.6905	0.058
Sugar Maple	0.6429	0.0856
Bare Mineral Soil	0.5952	0.1195
Yellow Birch	0.6946	0.0559

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CHAPTER V

Conclusions

Elucidating the factors involved with seedling establishment is important for advancing our understanding of forest stand dynamics and is essential for maintaining species diversity in managed forest systems. Forest substrate is a particularly important factor to understand, as it has the potential to influence species composition by affecting which species become established in the seedling layer. Moreover, substrate availability can easily be manipulated by existing silvicultural techniques, making understanding substrate's effect on seedling dynamics highly relevant to forest management.

In this study, bare mineral soil/humus was critical for the germination of smaller seeded species provided the availability of seed on the forest floor. This is an important finding, as forest management can simply scarify the forest floor or harvest in the absence of snow to increase bare mineral soil availability. Light availability is another such factor that can be easily manipulated by management and was influential to seedling establishment; species generally germinated best in lower light environments, but established and survived at higher rates in higher light environments. Nevertheless, providing bare mineral soil/humus and creating a favorable light environment by cutting a particular harvest gap size may not guarantee seedling recruitment, as several species' initial establishment was also influenced by local seed source density (50m), competition from non-tree vegetation, and site quality (soil moisture and nutrient availability). In such scenarios, forest management could turn to artificial seeding or planting, herbicides, and local site knowledge to overcome these regeneration obstacles.

Decaying coarse woody debris (CWD) is another type of substrate on which seedlings often develop. In this study, conifer species demonstrated the highest survival across substrates (bare mineral soil and six types of CWD), while deciduous species survival was more variable. This suggests that CWD may be more important seedling establishment substrate for conifers in northern hardwood forests. Nonetheless, individual species' of CWD varied strongly in their ability to support seedling development, as paper birch (*Betula. papyrifera* Marsh), northern white cedar (*Thuja occidentalis* L.) and eastern hemlock (*Tsuga canadensis* L) CWD generally supported greater height growth (cm) than yellow birch (*B. alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.) and balsam fir (*Abies balsamifera* (L.) Mill.). This finding suggests that scientists and forest managers should take into consideration the specific type of CWD that is available on the forest floor, much like we consider the particular type of soil that exists at a site, rather than consider CWD as a generic seedling establishment substrate. Mycorrhizal colonization was also shown to strongly influence seedling development across substrates. In addition, seedling colonization was also shown to vary across substrate, providing at least correlative evidence that mycorrhizal fungi may be strongly contributing to the differing patterns of seedling growth across different substrates.

Seedling establishment is a complex process in which species must pass through a number of developmental stages before they can develop into saplings. This complexity is magnified in forests where several factors can inhibit development at each stage. The evidence presented in this dissertation demonstrates that substrate can have strong effects over seedling layer composition at the germination stage. However, it was also shown that several factors, acting on stages before and after germination, may override substrate's

influence. Collectively, these findings suggest that a lack of bare mineral soil/humus or eastern hemlock, paper birch, and northern white cedar CWD is contributing to the regeneration failures reported for several tree species in the northern hardwood forests of the Great Lakes region. However, these findings also suggest that manipulating substrate availability alone may not be enough to reestablish many of these species to the seedling layer.