Factors affecting regeneration-layer dynamics in mixed-pine forest ecosystems of eastern Upper Michigan and implications for forest ecosystem restoration

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By

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Abstract

The structure and composition of mixed-pine forest ecosystems across the Lake States region of the United States have been significantly altered due to changes in the natural fire regime and subsequent logging activities. Legacies of these changes include significant shifts in species composition, inadequate regeneration of historically dominant pine species (e.g., red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.), structurally simplified stands with high stem densities, accumulation of fuels outside of the natural range of variation, and increased dead material such as snags and down woody debris. Many of these changes are the direct result of past management practices (e.g., clearcutting) that favored regeneration of other species such as jack pine (*P. banksiana* Lamb).

Although there are increasing efforts by scientists and land managers to develop restoration prescriptions for these mixed-pine ecosystems, there are considerable knowledge gaps both of our understanding of the effects of fire history on regeneration dynamics in current stands, and the viability of proposed alternative silvicultural techniques to address restoration and fuel reduction objectives. To meet these research needs in mixed-pine forest ecosystems of eastern Upper Michigan, my dissertation examines 1) the role of fire history, fuels, and overstory characteristics on regeneration-layer dynamics, 2) initial (2-year) regeneration and ecosystem responses to variable-retention harvesting as a restoration and fuel-reduction technique, and 3) stand-related factors that influence regeneration-layer dynamics after different harvest treatments.

The role of fire history, fuels, and overstory characteristics was examined by relating seedling and sapling densities to these three groups of factors in both old-growth (reference conditions) and second-growth (altered conditions) stands. The variable-retention harvesting involved retaining 30% of the initial overstory basal area in a stand by manipulating the overstory in two spatial patterns: 1) an aggregate pattern where gaps (~ 0.3 ha) were created within the residual stand; and 2) a dispersed pattern where the

residual trees were relatively uniformly dispersed across the stand. Measured responses included regeneration of target species, reductions in live jack pine fuels, ground-flora cover, and litter decomposition (as a measure of ecosystem productivity). Factors influencing regeneration-layer dynamics following different harvest treatments were also examined in three mixed-pine stands harvested in 1992, 2004, and 2007 respectively. The central question addressed in this study was: are high red pine and eastern white pine seedling and sapling densities associated with 1) areas close to potential seed trees? 2) areas with lower overstory density, overstory basal area and low importance values of species other than red pine and eastern white pine? 3) areas with greater canopy openness? 4) areas characterized by greater harvested volumes and larger gap sizes, and 5) areas with less cover of ground-flora (herbs and shrubs)?

Findings suggest that regeneration-layer dynamics of altered stands are influenced by complex interactions among fire history, current fuel loadings and current overstory characteristics. Fire history particularly seemed to influence regeneration of red pine and eastern white pine by limiting their regeneration in areas that have had longer fire-free periods, and also limiting regeneration in areas that potentially experienced higher-severity fires that favored jack pine. Initial (2-year) responses to the variable-retention harvesting indicated increases in eastern white pine seedling recruitment in treated compared to unharvested control stands, but we observed low red pine densities, suggesting little red pine response to treatments. The harvest treatments significantly reduced jack pine basal area in the overstory. No significant treatment effects were, however, found on ground-flora cover, or litter decomposition over a one-year period. Also, no significant differences in measured responses were found between aggregate and dispersed retention patterns. Examining factors influencing regeneration following harvest treatments, overstory characteristics and ground-flora were found to have negative relationships with regeneration in all three stands (harvested in 1992, 2004 and 2007 respectively). Regeneration of target species was not found to significantly increase with decreasing distance from potential seed trees, higher harvest volumes, or larger harvest gaps. Canopy openness was positively correlated with greater sapling densities only in the 2004 stand.

The results of both descriptive and experimental studies in this dissertation builds on the efforts by scientists and land managers to restore mixed-pine ecosystems across the northern Lake States by 1) advancing our knowledge of fire and fuel issues within the region, 2) enhancing the adoption of emerging restoration techniques as well as integration of ecological forestry principles, and 3) encouraging both monitoring and adaptive management as ways to assess and improve the effectiveness of restoration treatments.

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Fields of Study

Major Field: Environment and Natural Resources

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Chapter 1: Introduction

Significant changes in the structure and composition of mixed-pine forest ecosystems within the Lake States region of the United States (Cleland et al., 2004; Corace et al., 2012; Drobyshev et al., 2008b; Frelich, 1995) have necessitated restoration efforts across the ecoregional landscape (Corace et al., 2009; Palik et al., 2005; Palik and Zasada, 2003). Field-based experimental studies that inform these efforts can benefit from strong theoretical frameworks, allowing scientists to link theory and practice to enhance the utility of findings. In this chapter, I discuss the theoretical concepts underpinning my research in the mixed-pine forest ecosystems of eastern Upper Michigan and their applicability to forest management.

Alternative states theory and the role of fire in mixed-pine forest ecosystems

The theory of locally stable alternative states, and its relationship with ecological thresholds and the resilience of ecological systems have been increasingly recognized as having important applications in the management and restoration of complex natural ecosystems (Beisner et al., 2003; Groffman et al., 2006; Nowacki and Abrams, 2008). Through a ball-in-cup analogy, the theory is used to explain how ecosystems can shift from one state to another depending on the kind of disturbance it experiences (see Figure 1 in Beisner et al., 2003, and Figure 6 in Nowacki and Abrams, 2008). Briefly, Beisner et al., (2003) proposed that the ball represents the state of the community, while the basins (cups) represent the stability domains or domains of attraction across the landscape. Under disturbances normal to the ecosystem, the ball movement is constrained within the domain of attraction (i.e., within the boundaries of the basin) (Beisner et al., 2003). This means that the dynamics of the ecosystem are kept within the natural range of variability (Landres et al., 1999), thereby maintaining the ecosystem in that state (Beisner et al., 2003). A significant shift in biotic factors (e.g., species composition) or abiotic factors (e.g., environmental drivers such as fire), however, may result in the ball being pushed out of the current domain to another domain, meaning the dynamics of the ecosystem are pushed beyond the natural range of variability, thereby resulting in an alternative state. This alternative state theory has been adopted to examine how changes to the natural fire regimes have contributed to "mesophication" of many fire-adapted ecosystems in the eastern United States (Nowacki and Abrams 2008).

We can apply and examine the relevance of the alternative state theory in the mixed-pine forest ecosystems of the northern Lake States to investigate how changes in the natural fire regime can potentially result in altered ecosystems, and how this knowledge can be used to inform management and restoration efforts (Figure 1.1). The mixed-pine ecosystems of the northern Lake States were historically dominated by red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.) (Heinselmann, 1973; Whitney, 1987; Zhang et al., 2000). In eastern Upper Michigan, the occurrence of relatively frequent (a mean FRI of 32.7±19.2 years for pre-EuroAmerican settlement period) mixed-severity surface fires are believed to have maintained mixed-pine ecosystems dominated by the two pine species (State 1 in Figure 1.1) and reduced fire-sensitive species such as red maple (*Acer rubrum* L.) (Drobyshev et al., 2008a). According to alternative states theory, changes in the characteristics of this fire regime (e.g., fire exclusion or occurrence of more frequent higher-severity fires) are likely a major cause for changes in the structure and composition of these stands, potentially leading to alternative states (State 2 in Figure 1.1) in the absence of restoration interventions. I hypothesize that the occurrence of both longer fire-free periods (due to fire suppression and severe fires that are outside the natural range of variability) are likely leading to two potential scenarios in current stands: 1) fire suppression causing increases in fire-sensitive shade-tolerant species (such as red maple); and 2) severe fires favoring short-lived fire-adapted species such as jack pine (*P. banksiana* Lamb.).

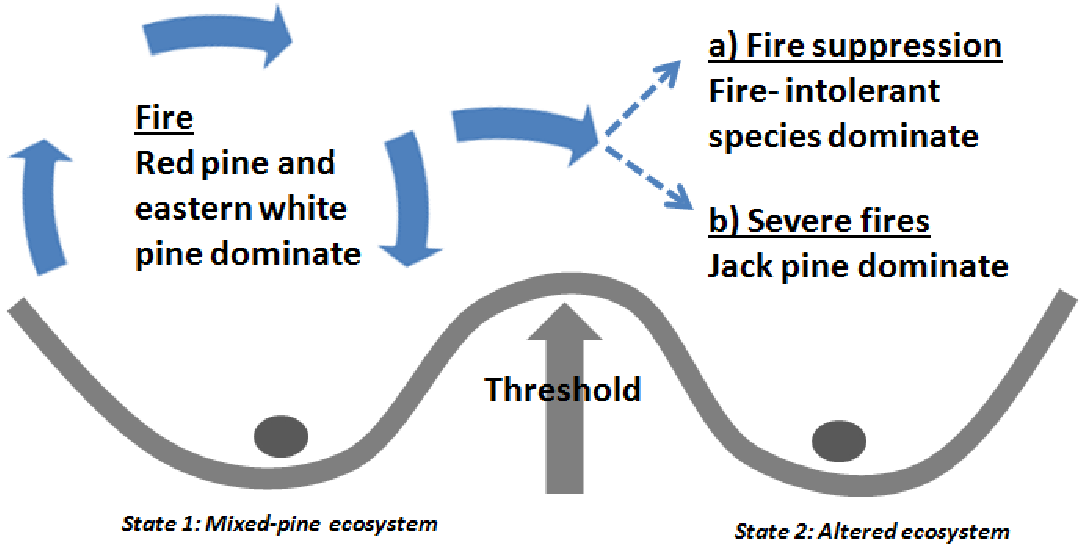

Figure 1.1 Alternate stable state conceptual diagram (modified from Beisner et al., 2003) illustrating the role of fire in maintaining mixed-pine forest ecosystems (State 1) of the eastern Upper Michigan, and how changes to the natural fire regime results in altered ecosystems (State 2) characterized by significant shifts in species composition. The ball represents the state of the system and the cups (basins) represent the domains of attraction within the landscape.

The transition from state 1 to state 2 only occurs where changes to the ecological driver pushes the ecosystem beyond a critical ecological threshold to result in alternative states. Groffman et al. (2006) define an ecological threshold as the point at which there is an abrupt change in an ecosystem quality, property or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem. Ecological resilience, defined as the amount of change an ecosystem can absorb while maintaining functional processes (Holling, 1973; Gunderson, 2000), is an important factor in this transition process. The ecological resilience of the original community and its relationship with characteristics of the basin (e.g., steepness of the slope and the width of the basin) will influences how easy or difficult it is to cross the ecological threshold (Peterson et al., 1998). The occurrence of ecological thresholds is particularly of significance to managers because alterations in the natural disturbance regime may cause the original ecosystem to transition to an altered ecosystem that is significantly different from the original ecosystem in composition and/or function (Hobbs et al., 2009). It is also likely that these same ecological thresholds could become restoration thresholds that prevent return to a less altered state without significant management input (see Figure 1 in Hobbs et al., 2009).

In terms of applications of this theory to forest management, Scheffer et al. (2001) suggested that one way to reduce the risk of unwanted shifts between states is by addressing the gradual changes that affect the resilience of the original ecosystem (State 1 in Figure 1.1). While the changes in the natural fire regime, and shifts in species composition have been documented for mixed-pine ecosystems (Corace et al., 2012; Drobyshev et al., 2008a, b), there are considerable gaps in our knowledge about the effects of the legacies of these changes on regeneration dynamics in current altered ecosystem across the northern Lake States. Regeneration is an important process in the development of any forest stand, and restoration initiatives that increase regeneration of target species are often important strategies that can help redirect the development of the stands towards desired reference conditions. Consequently, the overall goal of my dissertation research was to explore how legacies of change in the natural fire regime of the mixed-pine forests influence regeneration patterns, with the long-term outcome of informing the design of restoration treatments that would help restore natural processes in these forests.

Framework for emerging restoration alternatives for mixed-pine ecosystems

Due to the recognition of the role of fire in fire-dependent forest ecosystems across North America, and the significant shifts in stand structure and composition stemming from changes in the natural fire regime, a variety of restoration techniques have been proposed to help move disturbed fire-dependent ecosystems towards reference conditions. Over the last decade, scientists and land managers have been designing and implementing restoration treatments that: 1) are ecosystem-based, addressing multiple ecosystem components rather than single species focused; 2) more closely emulate natural processes and patterns created by those disturbance events for the given ecosystem type; and 3) are designed within a larger spatial context, emphasizing landscape scales and spatial heterogeneity (Corace et al., 2009; 2012; Franklin, 1993; Franklin and Johnson, 2012; Franklin et al., 2007; Hunter 2005). The theoretical framework underlying the design and application of restoration techniques that would meet the above criteria in addressing a variety of restoration and management objectives are based on our understanding of ecological restoration and its relationship to natural disturbance processes (Dobson et al., 1997), as presented in Figure 1.2.

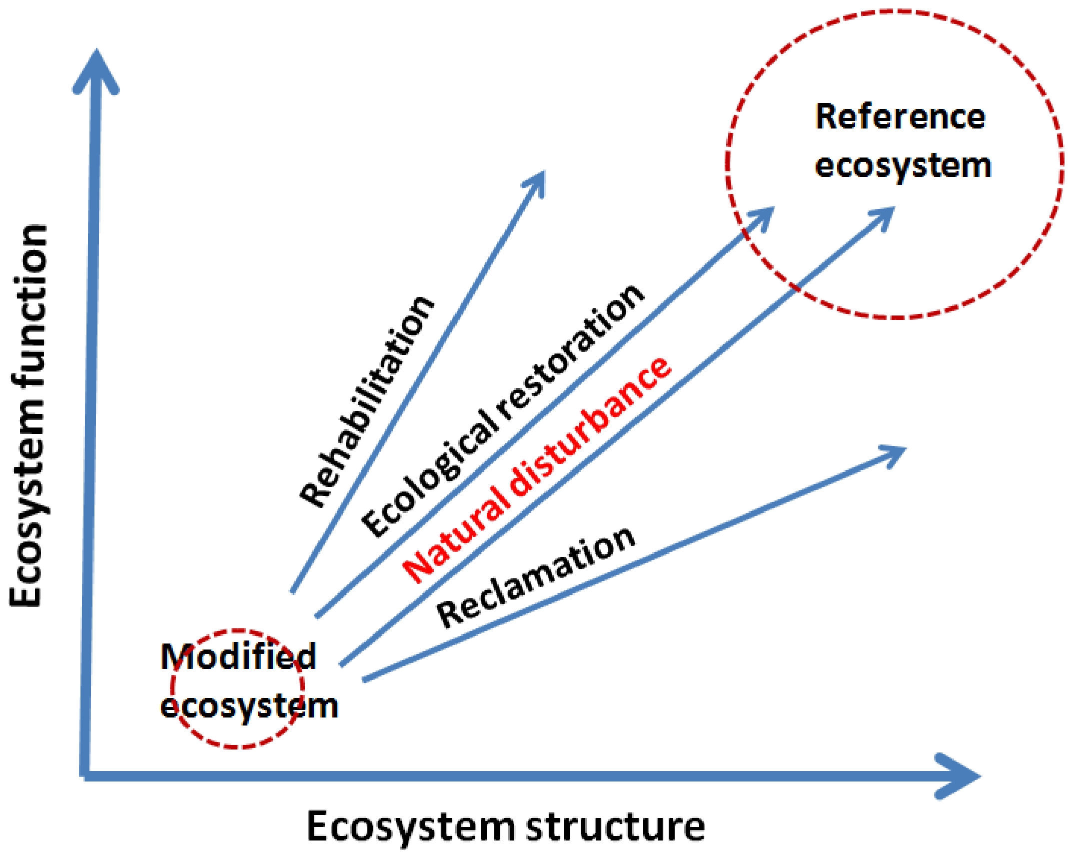

Figure 1.2 Diagram (modified from Dobson et al., 1997) illustrating the relationship between ecological restoration and natural disturbance processes in moving a modified, more simplified ecosystem towards reference conditions by enhancing both structure and function. The dotted circles on each ecosystem type are used to show the size of the natural range of variation, representing the range of acceptable states for defined management objectives.

Where conditions allow for their reintroduction, natural disturbance processes characteristic of a given ecosystem type are believed to be the best alternative to restore modified ecosystems (Dobson et al., 1997). Ecological restoration also provides opportunities to move a more simplified and modified ecosystem along an often non-linear ecological trajectory towards relatively larger, more structurally complex reference conditions, by enhancing both structure and function (Allen et al., 2002; Landres et al., 1999; SER, 2004). In this way, ecological restoration should parallel natural disturbance (Figure 1.2) in terms of restoring structural and functional components of a modified ecosystem towards reference conditions. Restoration alternatives that emulate natural disturbance processes, therefore, may have the best chance of succeeding in restoring characteristics representative of conditions prior to modification (i.e., reference or benchmark conditions). One such restoration alternative that has been proposed to benefit from this framework is variable-retention harvesting (Franklin et al., 2007; Palik and Zasada 2003). Briefly, variable-retention harvesting is a regeneration method that focuses on the retention of structural elements or biological legacies (e.g., trees, snags, logs) from the harvested stand for integration into the new stand to achieve various ecological objectives (Franklin et al., 2007; Mitchell and Beese, 2002).

For the most part, variable-retention harvesting has been implemented most widely in the Pacific Northwest, and its application in the northern Lake States region is in its initial stages, with most activities primarily focused on improving structural complexity in managed forests in Minnesota (Atwell et al., 2008; Peck et al., 2012; Palik and Zasada, 2003). Management objectives focused on increasing structural complexity in these managed plantation forests are often different from those of naturally regenerated mixed-pine forests where restoring historically dominant pine species and fuels reduction are critical needs. As such, a secondary goal of my dissertation was to begin to test the potential for this technique as a management tool to address restoration and fuel reduction objectives in naturally regenerated, altered mixed pine forests of eastern Upper Michigan.

Mixed-pine forest ecosystem as our model ecosystem

The stands used for all studies in this dissertation were located within the 38,542-ha Seney National Wildlife Refuge (SNWR), Schoolcraft County, eastern Upper Michigan (N46.271594◦ W86.057078◦). SNWR includes the federally designated Seney Wilderness Area, comprising about 26% of the total SNWR area (USFWS, 2009). Because extensive areas of the Seney Wilderness Area are wetland ecosystems

(Heinselman, 1965), difficulty in accessing these areas precluded logging and other anthropogenic disturbances associated with EuroAmerican settlement that occurred in the surrounding areas throughout the 19th and early 20th century (Losey, 2003). As a result, mixed-pine stands in the Seney Wilderness Area represent pre-EuroAmerican reference conditions in terms of forest structure and composition, with a relatively unaltered fire regime (a mean FRI of 32 ± 19 years for the pre-EuroAmerican settlement period) (Drobyshev et al., 2008a). The availability of a detailed fire-history, altered naturally regenerated second-growth stands that reflect the changes in historical conditions, as well as adjacent old-growth stands that represent pre-EuroAmerican reference conditions, all provide an excellent model system to explore the concepts discussed above as they relate to restoration and management of this ecosystem type.

Organization of the dissertation

To explore research questions in the mixed-pine forest ecosystem of eastern Upper Michigan, my dissertation follows a broad framework as shown in Figure 1.3. The research presented in this dissertation follows a general pattern with chapters addressing in order: 1) how legacies associated with changes to the natural disturbance regime affect current stand dynamics (Chapter 2); 2) restoration options that exist and how ecosystems respond to the implemented treatments (Chapter 3); and 3) what can be learned from post-treatment conditions to inform adaptive management strategies (Chapter 4). All these studies are heavily focused on the regeneration-layer dynamics, with the target species being red pine and eastern white pine, in large part because regeneration is an important process that can be manipulated by management to redirect stand development.

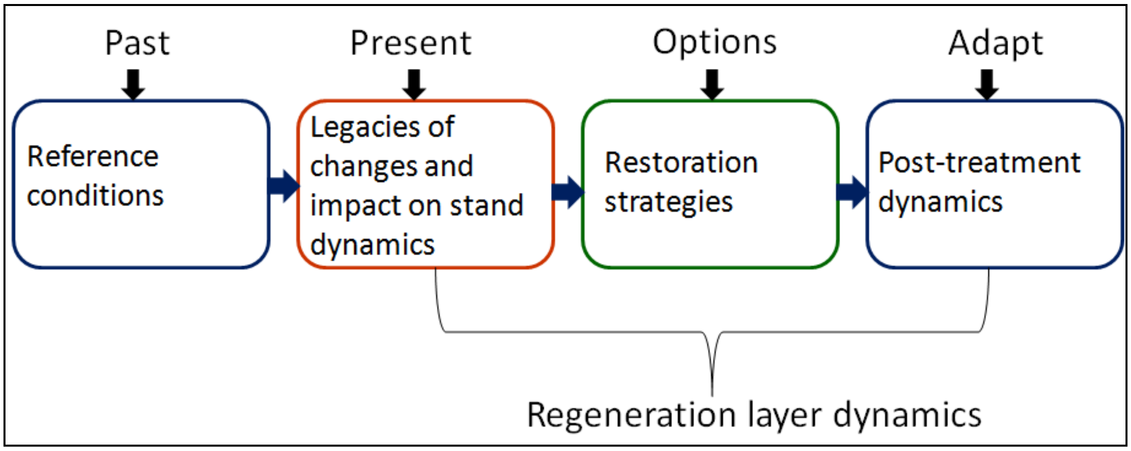

Figure 1.3 Framework for exploring research question in mixed-pine forest ecosystems of eastern Upper Michigan

Chapter 2 investigates the influence of changes in fire history, and associated changes in stand characteristics on regeneration dynamics in both reference and altered stands. Data from the original mixed-pine fire history study (Drobyshev et al., 2008a) are utilized to address the following specific question: How do fire history, fuels, and overstory characteristics influence the regeneration-layer dynamics of the mixed-pine forest ecosystems of eastern Upper Michigan? Seedling and sapling density data are related to fire history, fuel loadings and overstory characteristics to examine the influence of these three factor groups on regeneration.

Chapter 3 examines the potential of variable-retention harvesting as a restoration and fuel-reduction technique. Specifically, I examine the initial (2-year) regeneration responses of woody species (particularly red pine and eastern white pine) to treatments, the responses by understory plant communities, the potential impacts on litter decomposition as a measure of ecosystem productivity, and impacts on jack pine live fuels. The treatment consisted of retaining 30% of the initial basal area of trees by manipulating the overstory in two spatial patterns: 1) an aggregate pattern where the overstory basal area is reduced by creating gaps (~ 0.3 ha) within the residual stand; and 2) a dispersed pattern where the overstory basal area is reduced by leaving the residual trees relatively uniformly dispersed across the stand.

Chapter 4 is a case study of three stands each harvested at a different time during the last 20 years; one in 1992, a second in 2004, and a third in 2007. In this study, I investigate factors related to current stand characteristics that may be driving regeneration dynamic in these stands, with the objective of providing land managers with feedback that may be useful for adaptive management strategies and making assessments about stand development. Finally, Chapter 5 is a broader discussion of the potential management implications of findings from all these studies, with the objective of further providing feedback that land managers can then use to design appropriate treatment prescriptions for mixed-pine forests within the northern Lake States and other similar ecosystem types.

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Chapter 2: Fire history, fuels, and overstory composition effects on the regeneration layer-dynamics of mixed-pine forest ecosystems of eastern Upper Michigan, USA.

2.1 Abstract

Mixed-pine forest ecosystems of the northern Lake States were historically dominated by red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.). Extensive turn-of-the-century logging, followed by fires outside of the natural range of variability and then extended periods of fire suppression, altered the structure and composition of these forests. Prior to making decisions about appropriate restoration treatments to promote natural regeneration of target species, there is need to develop a better understanding of relationships among fire history, current stand conditions, and regeneration-layer dynamics in current naturally regenerated stands. We quantified seedling and sapling densities in reference old-growth and altered second-growth stands in eastern Upper Michigan. We then related these densities to fire history, fuel loadings, and overstory characteristics to determine their influences on regeneration patterns of red pine and eastern white pine. Our results suggest that regeneration-layer dynamics of current altered stands are influenced by complex interactions among fire history, current fuel loadings, and current overstory characteristics. Specifically, we found: 1) low densities of both red pine and eastern white pine seedlings in second-growth stands; 2) high sapling densities of these two species in both old-growth and second-growth stands; 3) red pine and eastern white pine seedling densities negatively associated with longer fire-free periods, areas with higher fire occurence over the last 142 years, all descriptors of fuel loadings, and higher importance values of deciduous species in the overstory; and 4) jack pine (*P. banksiana* Lamb.) seedlings positively associated with higher fire frequency over the last 142 years and high coarse fuel loadings. We suggest that majority of the fires that have occurred in the altered stands, especially over the last 100 years, were likely of higher

severity than those prior to the 1860s. These disturbances have instead favored regeneration of jack pine more than red pine and eastern white pine. The long-term management objective should be to reintroduce low-severity surface fires with mean return intervals determined to be characteristic of the natural regime (i.e., 32.7±19.2 years). There is, however, need for immediate restoration treatments to improve regeneration of red pine and eastern white pine, reduce down fuels, and reduce jack pine in the understory and overstory. The relatively high densities of the target species in the sapling layer suggest that opportunities exist for restoration treatments that can manipulate successional dynamics to favor red pine and eastern white pine dominance in these stands.

2.2 Introduction

Fire has shaped the structure and composition of many forest ecosystems across North America. Pine-dominated ecosystem types, including longleaf pine (*Pinus palustris* Mill.) ecosystems of the Southeast, ponderosa pine *(P. ponderosa* C. Lawson) ecosystems of the Southwest, and mixed-pine ecosystems of the northern Lake States were historically maintained by mixed-severity surface fire regimes (Covington et al., 1994; Drobyshev et al., 2008a; Ware et al., 1993). In these forest types, fire created conditions necessary for germination, seedling establishment, and dominance of pine species (Ahlgren, 1976; Bergeron and Gagnon, 1987; Romme et al., 2009), and played a major role in regulating stand density and functional processes (Fulé et al. 2009; Naficy et al., 2010). Fires within the natural range of variability also provided certain pine species with a competitive advantage during establishment by reducing competition from other vegetation, including deciduous tree species (Kershaw, 1993; Rudolf, 1990). Fire history studies in many of these ecosystem types have, however, indicated significant changes in the fire regimes (Covington and Moore, 1994; Drobyshev et al., 2008a; Frost, 1993), and, as a result, these ecosystem face a variety of similar management issues and challenges associated with the legacies of these changes (Corace et al., 2009; Fulé et al. 2009; Palik et al., 2005; Wilson et al; 2009).

Within the northern Lakes States, the legacies of altered natural fire regimes, extended fire-suppression periods, and subsequent land-use practices have been attributed to shifts in species composition, inadequate regeneration of historically dominant pine species, stands that are more simplified structurally with high stem densities, and accumulation of fuels outside of the natural range of variation, including increased snags and dead and down woody materials (Cleland et al., 2004; Corace et al., 2012; Corace et al., In Press; Drobyshev et al., 2008b; Frelich, 1995). While the extended periods of fire suppression favored increases of deciduous species such as red maple (*Acer rubrum* L.), the high severity slash fires that occurred immediately after the logging activities in many areas of the northern Lakes States likely destroyed most of the remaining pine seed trees (Barrett, 1998; Whitney, 1987). In eastern Upper Michigan, for example, mixed-pine forests historically dominated by red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.), that occupied up to 39% of the land area prior to EuroAmerican settlement, have since declined to only about 13% of the total area (Zhang et al., 2000).

Besides widespread ecoregional increases in deciduous species (Corace et al., 2012), a major management issue for land managers in current mixed-pine stands is increased abundance of both live jack pine (*P. banksiana* Lamb.) in the mid- and overstory of altered stands, and greater levels of dead jack pine material including fine fuels and snags (Corace et al., In Press; Drobyshev et al., 2008b). Following the logging era, subsequent high-severity fires and management activities (such as clearcutting) favored regeneration of jack pine, a species that had high commodity value and relatively low cost for regeneration (Rist, 2008). As a result, current mixed-pine stands contain a large and often dense component of 40-60-year old mature jack pine in the overstory that are likely limiting the successful germination and establishment of red pine and eastern white pine (Drobyshev et al., 2008b). In addition to its adaptive characteristics to regenerate efficiently following fires, the high flammability of jack pine, coupled with poor self-pruning ability, can promote higher severity fires through ladder-fuels that provide vertical fuel continuity between the surface and tree crowns (Carey 1993b; Rudolf and Laidly, 1990). Recent work on the longevity and decay class development of jack pine snags revealed high snapping rates (~ 41% within the first 2.5 years), underscoring the potential for jack pine to contribute down fuels, and likely influence fire behavior in these stands (Corace et al., 2010b; Corace et al., In Press).

While fire history and legacies of changes to the natural fire regime have been documented, little information is available from field investigations that specifically examine the effects of fire history and stand-related factors on regeneration dynamics in current mixed-pine forests of the northern Lake States. Indeed, compared with other pine-dominated ecosystems in the western and southern regions of the United States, there is little information on the effects of fire on stand development processes and a variety of ecosystem components (e.g., soils, wildlife) in pine-dominated ecosystems within the region (Miesel et al., 2012). Recent efforts to improve access to and exchange of information about fire effects and fuel issues (Kocher et al., 2012; Miesel et al., 2012), coupled with increasing public support for ecologically based management objectives (Shindler et al., 2009; Wilson et al., 2009) indicate increasing opportunities to restore these altered forest ecosystems. If land managers are going to take advantage of these opportunities to develop ecosystem-based restoration strategies, especially where objectives include restoring historically dominant species, there is a need to develop a better understanding of the important factors that drive regeneration-layer dynamics in current stands.

This study focused on exploring the following question: how do fire history, fuels, and overstory characteristics influence the regeneration-layer dynamics of the mixed-pine forest ecosystems of eastern Upper Michigan? We addressed this question by examining the seedling and sapling densities (with emphasis on red pine and eastern white pine as the target species) in both old-growth stands (reference conditions) and second-growth stands (altered conditions), and then relating these data to three primary groups of factors: 1) fire history; 2) current fuel loadings; and 3) current overstory characteristics. We focused on past fire occurrences, fuels, and overstory characteristics because these are the primary groups of factors that we anticipate are important drivers of regeneration dynamics of red pine and eastern white pine, and can be manipulated by management. We anticipate that this important baseline information about the effects of fire history and current stand characteristics on regeneration dynamics will help facilitate decision-making when selecting and implementing restoration alternatives in this and other similar ecosystem types.

2.3 Methods

Study area

The study was conducted within the 38,542-ha Seney National Wildlife Refuge (SNWR), Schoolcraft County, eastern Upper Michigan (N46.271594◦ W86.057078◦) (Figure 2.1). SNWR lies within the Seney Lake Plain ecoregion and is characterized by soils and physiographic features that resulted from postglacial erosion and soil formation processes (Albert, 1995). Two major landforms dominate the landscape: glacial outwash channels and a patterned-fen matrix interspersed by sand ridges (Heinselman, 1965). Soils range from poorly drained peats to excessively drained coarse sandy soils, on which mixed-pine stands are found. The climate is influenced by it close proximity to the Great Lakes. Temperatures vary between a minimum of -9 ^{o}C in the coldest month (January) to 30 ^{o}C in the warmest month (July), and the average annual precipitation is 78 cm, with most of the precipitation falling in the form of snow (MRCC, 2013). The length of the growing season averages 119 days, and the average daily humidity during spring and fall varies between 50 and 60%.

The Seney Wilderness Area comprises 26% (10,583 ha) of the total SNWR area (USFWS, 2009). Because extensive areas of the Seney Wilderness Area are wetland ecosystems (Heinselman, 1965), difficulty in accessing these areas precluded logging and other anthropogenic disturbances that occurred in the surrounding areas throughout the 19th and 20th century (Losey, 2003). As a result, mixed-pine stands in the Seney Wilderness Area represent reference conditions in terms of forest structure, composition and disturbance regime, with relatively unaltered fire return intervals (FRIs) (a mean FRI of 32 ± 19 years for the pre-EuroAmerican settlement) (Drobyshev et al., 2008a). The current landscape of SNWR is composed of a mosaic of upland and lowland forests and wetland vegetation (USFWS, 2009). The mixed-pine forests were historically dominated by red pine and eastern white pine, but are currently characterized by a substantial component of jack pine in the overstory (Drobyshev et al., 2008b; Corace et al., In Press). The study area thus provides a model landscape for our analyses as there are altered, naturally regenerated second-growth stands that reflect the changes in conditions characteristic of the region, as well as adjacent old-growth stands that represents reference conditions.

Vegetation sampling

Data was collected across a network of 50 mixed-pine stands that were established as part of a fire-history study (Drobyshev et al 2008a). The general criteria for selecting stands for the fire history study included the availability of fire-scarred trees, logs, and stumps to enable fire history reconstruction via destructive sampling (dendrochronology). In 2006 and 2007, a total of 85 500-m^2 (50m x 10m) sample plots were randomly established within these 50 stands, with each stand containing between one and three plots, depending on the size and configuration of the stand. In stands where more than one plot was established, the plots were randomly established 100-200 m from each other. Within each sample plot, seedlings (stems < 2.5 cm dbh) were counted by species in four 2-m^2 quadrats located at the 10, 20, 30 and 40 m along the long axis of the sample plot, while saplings (stems 2.5-10.0 cm dbh) were counted by species in a nested 300-m^2 (30m x 10m) subplot located along the long axis of the sample plot. To characterize the overstory composition associated with each sample location, the species and diameter at breast height (1.37 m above the ground) of all living trees (stems > 10.0 cm dbh) within the sample plot were recorded. The overstory consisted of trees of all crown classes (dominant, codominant, intermediate and overtopped). Taxonomic authorities followed the PLANTS database (USDA 2013).

At the center of each sample plot, we collected digital hemispherical photographs at 1 m above the ground using a fisheye lens mounted on a Nikon 8400 digital camera. We then used the WinSCANOPY digital image processing software (Regent Instruments Inc., Chemin Saint-Foy, Quebec) to estimate the proportion of the canopy that is open (percent canopy openness). Fuel data was collected by following the standard protocols adopted by the Forest Inventory and Analysis (FIA) Program of the USDA Forest Service

(Woodall and Monleon, 2007). Specifically, we recorded estimates of coarse (1000-hr fuels) and fine (consisting of 1-hr, 10-hr, and 100-hr fuels) down woody material, fuelbed depth (duff and litter) as well as live and dead shrubs and herbs using a line intercept method along three 7.3-m transects arrayed at 30 ^{o}, 150 ^{o}, and 270 ^{o} from the plot center. We then used standard calculations from Woodall and Monleon (2007) to obtain total fuel biomass. Due to the landscape matrix of the Seney Wilderness Area, availability of candidate stands was limited compared with the altered second-growth areas of the refuge. We, therefore, had fewer sample plots established in the old-growth stands (n=38) compared to the second-growth stands (n=47).

Fire history data collection and processing

In each of the 50 stands, the search criteria for trees to obtain samples from for fire scar analysis involved identifying live trees, stumps, and deadwood that had fire scars on them. From all the identified fire-scarred potential samples, those that were considered to be most informative for fire history reconstruction were selected and marked for sampling. The search for all potential sample trees in each stand was specified to cover an estimated area of up to 1 ha (or less in cases where sand ridges were < 1 ha), and a 2.5-hr maximum search time. From each marked sample tree, a wedge was extracted from the bole using the method of ‘‘wedge sampling’’ (Swetnam, 1996). A total of 97 wedge samples were collected in the old-growth stands and 151 samples in the second-growth stands. Trees that represent the oldest cohort were typically sampled to recover scars not visible from outside of the tree (overhealed scars). The majority of the samples were from red pine while only a few samples were collected from eastern white pine and jack pine. Other data recorded from each sample included species, dbh, the type of sample (living tree, stump, or deadwood), and height at which wedge was taken.

Once collected, the samples were processed in the lab to determine age and fire scars. Specifically, while mounted on wooden plates, the samples were progressively polished with up to 400-grit sandpaper to enable clear recognition of annual rings and fire scars under a binocular microscope (with up to 40x magnification). The visual cross-dating approach (Stokes and Smiley, 1968) was used to date fire scars and annual rings in all samples. Local and master 300-year-long pointer-year chronologies (Schweingruber et al., 1990) were developed for red pine using ring widths, early and latewood widths, and early and latewood densities. The pointer-year chronologies were verified using existing red pine chronologies for the region and were used to aid in fire dating. Dates of known fires, such as the Seney Fire of 1976 (Anderson, 1982), were also used to verify the cross-dating accuracy. Once the cross-dating was complete, calendar dates and seasonal information for all fire occurrences was recorded. Drobyshev et al. (2008a) provides a detailed explanation of the fire history study. We used this data to develop the following descriptors of fire history: (a) time since last fire (TLF), (b) number of fires during the last 50 years, 1956-2006 (NF_50), and (c) number of fires during the last 142-years, 1864-2006 (NF_142). The last 50-year time frame was selected because it represents recent fire history in the study area, while the 142-year time frame was selected because all stands had samples dating back to 1864, which allowed for comparisons among stands, and 1864 was also a large fire year in the study area with many of the cohorts dating back to this year (Drobyshev et al 2008a).

Statistical analyses

We examined if there were differences in the overall species composition of the seedling and sapling layers between the old-growth and second-growth stands. To accomplish this, we used a multi-response permutation procedure (MRPP) with a Sorensen (Bray-Curtis) distance measure and n/sum(n) weighting function using PC-ORD version 5.0 (MJM Software, Glenedon Beach, OR) software package. We used the Mann-Whitney test to examine the differences in mean densities of seedling and of sapling-size woody stems between the old-growth and second-growth stands. The Mann-Whitney test is a non-parametric test used to test for differences between two non-paired groups, and is robust in cases where the data comprises independent observations, but do not need to meet the normal distribution and homogeneity of variance assumptions required in parametric analyses (Zar, 2010).

To examine the influence of fire history, fuels and overstory characteristics on the seedling and sapling layers, we used partial canonical correspondence analysis (CCA) using CANOCO v. 4.5 (Braak, C. J. F. and Smilauer, Ithaca, NY, USA). CCA is a direct gradient analysis that is especially useful when there is *a priori* knowledge about major factors that might be influencing the patterns of the dependent variable in space. In this study, we constrained the occurrences of species in the seedling and sapling layers with three primary groups of factors: fire history (measured by number of fires in the last 142 years, number of fires in the last 50 years, and time since last fire), fuels loadings (measured by down coarse woody material or 1000-hr fuels, fine woody material or 1-hr, 10-hr and 100-hr fuels, fuel bed depth, and live and dead shrubs and herbs), and overstory characteristics (measured by overstory species importance values and percent canopy openness) (Table 2.1). Importance values of each species in the overstory were calculated using relative density and relative dominance. Relative density (as a percentage) was calculated by summing the total density of a species on a plot, divided by the total density of all species in the plot, and multiplying by 100. Relative dominance (as a percentage) was calculated in a similar manner, but substituting basal area for density. Importance values were then calculated by summing relative density and relative dominance, and then dividing by two

Partial CCA is useful to extract the components of the variation explained, in an effort to determine unique aspects of species occurrences explained by each group of factors or pairs of group of factors while controlling for the other group(s) of factors. As a result, during the partial CCA analyses, we decomposed the total variation in the seedling data and in the sapling data into variation explained by each group of factors, variation explained by each group of factors with the other two groups of factors as covariables, and variation explained by pairs of groups of factors with the third group of factors as a covariable. Interpretations of the relative amounts of variation explained by sets of variables in the partial CCA followed the guidelines and recommendations of Okland (1999). All CCA analyses were conducted using the default linear combination (LC) site scores, along with a Monte Carlo permutation to test the significance of the patterns observed.

Following the partial CCA ordinations of the seedlings and saplings, we examined more closely how the interaction of fire occurrence in the last 142 years and current fine fuel loadings (1-hr, 10-hr and 100-hr fuels) influence the patterns of red pine and eastern white pine seedling and sapling densities. Specifically, we classified the study plots into three groups based on number of fire occurrences over the last 142 years: 1) low (1-5); 2) moderate (6-10); and 3) high (11-15) fire occurrences. We also classified the fine fuel loadings into five classes ranging from a low of 0-10 to a high of > 40 tonnes/ha. The number of fires in the last 142 years was selected because it represented a longer time period, while fine fuels was selected because most of the measured descriptors of fine fuels exhibited negative correlations with both red pine and eastern white pine. We then developed three-dimensional surfaces relating number of fires in the last 142 years and fine fuels loadings to the seedling and sapling densities of red pine and eastern white pine.

2.4 Results

Regeneration: seedling and sapling layers

MRPP suggested there were significant differences in the overall species composition of the seedling layer between reference old-growth and altered second-growth stands ($T = -3.53$, $A = 0.02$, $P < 0.001$), largely due to significantly higher densities of eastern white pine seedlings in the old-growth stands (379 ± 469 seedlings ha^{-1}) than in second-growth stands (136 ± 254 seedlings ha^{-1}) (Table 2.2; Mann-Whitney test, w= 670, P=0.03). We found very low densities of red pine seedlings in old-growth (79 ± 269 seedlings ha^{-1}) and second-growth (64 ±138 seedlings ha^{-1}) stands, and the differences between the two stand types were not significant (Table 2.2; Mann-Whitney test, w= 916, P=0.77). Jack pine was found in low densities (60 ± 181 seedlings ha^{-1}) in the seedling layer and only in the second-growth stands (Table 2.2). Red maple and downy serviceberry (*Amelanchier arborea* (Michx. f.) Fernald) were, however, the two most common species in the seedling layer of both old-growth and second-growth stands (Table 2.2).

There were also significant differences in the overall species composition of the sapling layer between old-growth and second-growth stands (T =−3.26, A=0.02, P = 0.01). Unlike in the seedling layer, however, red pine was the most common species in both the old-growth (1805 ± 2633 saplings ha^{-1}) and second-growth (3051 ±3748 saplings ha^{-1}) stands, with no significant differences between the two stand types (Table 2.2; Mann-Whitney test, w= 779, P=0.31). Further, as opposed to the seedling layer, we observed a trend of lower densities of eastern white pine saplings in the old-growth stands (158 ± 335 saplings ha^{-1}) compared to the second-growth stands (766 ± 1739 saplings ha^{-1}), although these values were not statistically significant (Table 2.2; Mann-Whitney test, w= 952, P=0.54). We also observed significantly greater densities of jack pine saplings in second-growth stands (1404 ± 3680 saplings ha^{-1}) compared to old-growth stands (21 ± 101 saplings ha^{-1}) (Table 2.2; Mann-Whitney test, w= 1159, P < 0.001). Overall, the three pine species (red pine, eastern white pine, and jack pine) were the most common species in the sapling layer of the second-growth stands.

Influence of fire history, fuels and overstory characteristics on regeneration

CCA ordination analyses suggested significant patterns of seedling species' occurrences along gradients associated with fire history, fuels, and overstory characteristics (Monte Carlo test: F= 1.447, P = 0.05, 499 permutations). The seedling layer analyses indicated high densities of jack pine seedlings along CCA axis 1 were positively associated with number of fires in the last 142 years (NF_142), high loadings of 1000-hr (CWM) and 100-hr (FWM_100H) fuels, and high importance values for jack pine (PiBa) in the overstory (Figure 2.2). Along CCA axis 2, red pine and eastern white pine seedling densities were negatively associated with time since last fire (TLF), fuelbed depth (FBD), live (LSH) and dead (DSH) shrubs and herbs, 1-hr (FWM_1H) and 10-hr (FWM_10H) fuels, and high importance values for deciduous species in the overstory including northern red oak (QuRu) (*Quercus rubra* L.), quaking aspen (PoTr) (*Populus tremuloides* Michx.), and bigtooth aspen (PoGr) (*Populus grandidentata* Michx.) (Figure 2.2). Greater seedling densities of the two pine species along this axis were, however, positively associated with number of fires in the last 50 years (NF_50), greater canopy openness (Can_O), and high importance values for the species in the overstory (Figure

2.2). Following the partial analyses examining the unique variation explained by each group of factors or pairs of groups of factors, we found that none of the group of factors by themselves uniquely explained majority of the variation in the seedling data. Combined fire history and overstory characteristics (shared FH+O/F), however, explained the most variation (13%) in the seedling data, suggesting a stronger shared influence of these two factor groups on the seedling layer (Figure 2.3).

Ordinations also indicated significant patterns of sapling species occurrences along gradients associated with fire history, fuels, and overstory characteristics (Monte Carlo test: F= 1.603, P = 0.01, 499 permutations). CCA axis 1 was positively associated with greater jack pine sapling densities and negatively associated with greater eastern white pine sapling densities (Figure 2.4). High densities of jack pine saplings along this axis were positively associated with number of fires in the last 50 years (NF_50), 1-hr fuel loadings (FWM_1H), live (LSH) and dead (DSH) shrubs and herbs, greater canopy openness (Can_O), and high importance values for jack pine in the overstory. Further, high densities of eastern white pine along this axis was associated with time since last fire (TLF), 1000-hr (CWM) and100-hr (FWM_100H) fuels, and high importance values for eastern white pine (PiSt), northern red oak (QuRu) and bigtooth aspen (PoGr) in the overstory (Figure 2.4). Unlike the seedling layer, greater red pine sapling densities along the second CCA axis were positively associated with number of fires in the last 142 years (NF_142) and fuelbed depth (FBD) (Figure 2.4). Further, in contrast to the relatively high shared variation explained by fire history and overstory in the seedling layer, there was less shared variation explained by pairs of the groups of factors in the sapling layer. Instead, the partial analyses indicated each group of factors accounted for the total variation uniquely, with fuels accounting for most of the variation (11%) in the sapling layer (Figure 2.5).

When we examined the interactive effects of fire occurrences over the last 142 years and fine fuels on regeneration patterns, we found greater red pine seedling and sapling densities in areas that had experienced about 6-10 fires (moderate number of fires), and are currently characterized by low fine fuel loadings (Figure 2.6A and B).

Eastern white pine on the other hand, had high seedling and sapling densities in areas that had experienced both low (1-5) and moderate (6-10) fires irrespective of whether these areas were currently characterized by low or high fuel loadings (Figure 2.7A and B).

2.5 Discussion

Increased focus on ecological benefits and the need to promote safer fire management in pine-dominated ecosystems have spurred restoration efforts to improve conditions for regeneration of historically dominant pine species, enhance stand structural complexity, and reduce fuel accumulations (Corace et al., 2009; Palik et al., 2005; Palik and Zasada, 2003). There has been emphasis on developing restoration strategies that more closely emulate natural disturbance processes, especially the patterns created by fire (and wind to a lesser degree), and shifting from single-resource objectives to addressing multiple ecosystem objectives at larger spatial scales (Corace et al., 2009; 2010a; Corace et al., 2012; Franklin, 1993; Franklin and Johnson, 2012; Franklin et al., 2007). Adopting these approaches, will require an understanding of not only the natural fire regime that maintained these ecosystems, but more importantly, of the effects of changes in their characteristics (e.g., fire type, frequency, severity) on stand development processes such as regeneration.

Regeneration: seedling and sapling layers

Our results indicate inadequate regeneration of important target species in altered stands, especially in the seedling layer. For example, we observed only an average of 64 seedlings ha^{-1} of red pine and 136 seedlings ha^{-1} of eastern white pine in second-growth stands. These densities are very low compared to the 988-2224 seedlings ha^{-1} densities that are generally recommended to establish either red pine or eastern white pine plantations in the northern Lake States (Gilmore and Palik, 2006), although these guidelines do not adequately represent unmanaged stands, and often do not consider a variety of other factors (e.g., are not based on natural range of variability, and have issues related to growth rates related to different site conditions). The greater densities of other species, such as red maple, in the seedling layer suggest potential competition for resources may be negatively affecting the regeneration of red pine and eastern white pine

(Ahlgren, 1976; Carleton et al., 1996). Our results also suggest a shift in species composition with deciduous species becoming most common in the seedling layer of altered stands, and jack pine becoming increasingly common in the sapling layer, findings that are comparable to the results of other studies within the region (Corace et al., 2012; Zhang et al., 2000).

Interestingly, we found greater densities of both red pine and eastern white pine saplings in the second-growth stands, an observation that may support one or both of two conclusions: 1) sapling-sized stems are likely more able to survive the influences of fire history, fuels, and overstory characteristics better than the seedling-sized stems; and 2) stand conditions at the time of germination and early establishment of stems in the sapling layer were more favorable than they are currently (e.g., deep litter layer that may thwart regeneration). The age structure of these saplings in the old-growth stands is uneven aged, and there is strong evidence that both red pine and eastern white pine will positively respond to canopy disturbances (Rist, 2008). For land managers, the high sapling densities observed, and evidence that they will experience significant radial growth increases following canopy disturbances related to larger and presumably more severe wildfire, coupled with potential for progression of seedling-sized individuals growing into sapling-sized stems, suggest opportunities exist for restoration strategies that could facilitate stand development. Such treatments could, for example, include overstory manipulations that reduce canopy cover to allow for the recruitment of saplings into the overstory, as well as increase the establishment of seedlings.

Influence of fire history on regeneration

Fire history seems to influence the densities and distributions of the target species, especially red pine, through the effects of both longer fire-free periods, and presumed changes in the fire severity. Red pine and eastern white pine are species that have been thought to regenerate better under predominantly frequent mixed-severity surface fires that reduce competing vegetation and expose mineral soils (Carey, 1993a; Drobyshev et al., 2008a; Heinselman 1981). Drobyshev et al. (2008a) found fire return intervals for the Seney Wilderness Area (where majority of current reference stands are) was 32.7±19.2

years for pre-EuroAmerican settlement period (1707–1859). The negative relationship between both red pine and eastern white pine seedlings and time since last fire suggests that longer fire-free periods likely outside of the above range of return intervals negatively affect the regeneration-layer dynamics in these forests. This is further supported by our results indicating that most of the red pine seedlings in current stands were associated with areas that have experienced 6-10 fires over the last 142 years, which falls within the range of pre-Euro-American settlement return intervals.

We suggest that majority of the fires that have occurred in the second-growth stands over the last 142 years (especially since EuroAmerican settlement in the last 100+ years) were of relatively higher severities than the mixed-severity surface fires characteristic of the natural fire regime in this forest ecosystem type (Drobyshev et al. 2008a). If so, these fires would likely have negative effects on the survival of red pine and eastern white pine saplings and seed trees (Whitney, 1987). Although the results indicate that red pine seedlings in current stands were associated with areas that had experienced fire over the past 50 years, regeneration densities overall suggest that the fires that have occurred in the study area over the last 142 years may have had relatively little influence on the regeneration of red pine and eastern white pine. First, this observation may be associated with a time lag issue as mentioned above, where longer fire-free periods occurred between fires during the 142-year time period, resulting in little cumulative increases in regeneration of the two pine species.

Second, following fire, red pine may establish from seeds provided by seed trees that survived the fire, or seeds from nearby seed sources (Ahlgren 1976; Rudolf, 1990). Even though the thick bark of red pine is its most important adaptation to survive surface fires of low to moderate intensity (Flannigan, 1993; Van Wagner, 1971), severe fires characterized by high intensities may be detrimental to younger stems, and potentially destroy mature seed trees through crown scorching (Ahlgren, 1976; Rouse, 1988; Van Wagner, 1971). Thus, if higher-severity fires results in mortality of seed trees and high temperature resulting from such fires destroy the seeds in the seedbank, regeneration of the two pine species may be expected to be low following such severe fires. Third, potential impacts of high temperatures associated with such severe fires in altering soil chemistry maybe be another contributing factor to poor regeneration. Although little research has been conducted within the northern Lake States to examine the effects of fire on forest soils (Miesel et al., 2012), there is evidence that higher-severity fires are generally likely to negatively impact soil chemistry and soil chemical processes (Erickson and White, 2008; Neary et al., 2005). Some studies within the region have also highlighted the presence of open patches with tree stumps ("stump prairies") characterized by little to no regeneration of the two pine species in some areas within the landscape where high-severity fires following logging activities burned deep into the organic layer (Barrett, 1998). These observations provide further support for the negative impacts of these severe high intensity fires, especially in altering soil chemistry and, therefore, limiting regeneration of red pine and eastern white pine.

The fires over the last 142 years may also have limited regeneration of red pine and eastern white pine by promoting the regeneration of a competitor, jack pine. Our results indicate a strong positive association between number of fires in the last 142 years and jack pine in both the regeneration-layer and high importance values in the overstory. Increased fire activity in the non-Wilderness portion of SNWR during the settlement period (FRIs of 24.3±15.1 years for pre-EuroAmerican settlement (1707-1859), 14.1±11.2 years for the settlement period (1860-1935), and 16.1±13.5 years for the post refuge establishment (1936-2006)) likely caused shifts in species composition, favoring establishment of jack pine (Corace et al., In Press; Drobyshev et al., 2008a). Severe fires characterized by high intensities may benefit jack pine as the high temperatures associated with these fires promotes the opening of serotinous cones and the release of seeds onto the blackened soil surface (Carey, 1993b). While it is unclear whether the breaking of the resinous bond that holds jack pine cone scales together is determined by the type of fire (Alexander and Cruz, 2012) or by rates of fire spread and fuel consumption (Johnson and Gutsell, 1993), it may be possible that cone serotiny (and possibly low cone serotiny in the study area) may be another potential contributing factor promoting jack pine regeneration after these fires. More detailed investigations into these specific processes and impacts on the regeneration-layer are needed.

More broadly, our findings suggest that not all fires are equal with regard to their effects on regeneration of red pine and eastern white pine. Fire history particularly seems to influence regeneration of these target species in three ways: 1) limiting regeneration in areas that have had longer fire-free periods, 2) limiting regeneration in areas that experienced severe fires, and 3) favoring regeneration of jack pine that potentially displaces the target species. The long-term goal of restoration activities in these stands should be to reintroduce fires with characteristics (e.g., frequency, severity, seasonality) that resemble those of the natural fire regimes. Due to high fuel accumulations in current stands, however, there is need for restoration treatments that will improve stand conditions so that not only is use of fire feasible, but also that red pine and eastern white pine benefit from such fires. Land managers may need to explore treatments (e.g., mechanical treatments) that specifically reduce stand densities, create open understory structures, and reduce jack pine while improving regeneration of the target species prior to use of prescribed fire.

Influence of fuel loadings on regeneration

Our results suggest a negative influence of down fuels and fuelbed depths on the regeneration of the target species. Most descriptors of fuel loadings showed negative correlations with red pine and eastern white pine, especially in the seedling layer. While the direct influence of fuels on regeneration was not investigated in this study, both the absence of fire and occurrence of severe fires in these ecosystems may adversely affect regeneration through their impacts on accumulations of dead and down woody materials. Absence of fire may allow for accumulations of a heavy litter layer, which is likely to hamper post-germination seedling establishment (Ahlgren, 1976; Rudolf 1990), as supported by our observation of greater red pine densities in areas with low fine fuel loadings. On the other hand, higher-severity fires are likely to increase mortalities of mature woody stems, resulting in increases in coarse woody material, either as snags or as down woody materials on the forest floor. For example, the association of larger-sized fuels (1000-hr and 100-hr fuels) with areas where fire has occurred over the last 142 years (the same areas associated with high jack pine importance values in the overstory) in this study may be linked to mortalities of dominant and codominant overstory stems caused by the more severe fires, in addition to density-dependent factors and senescence.

Jack pine has become a management concern for resource managers across Upper Michigan, particularly due to its contribution of ladder fuels that could promote severe crown fires and complicate the application of prescribed fire (Corace et al., 2009). In addition to being a relatively short-lived species, jack pine snags exhibit a high snapping rate, with most falling within the first year (Corace et al., 2010b; Corace et al., In Press). Such high snapping rates suggest that jack pine will contribute significant amounts of down fuels as well, increasing the potential to complicate fire behavior. Overall, the interactions between fuel loadings and fire occurrence suggests that restoration efforts will need to also prioritize fuel reduction objectives, so as to improve conditions for germination and establishment of target species, especially for red pine that appears to be more greatly impacted by down fuels compared to eastern white pine. Treatment prescriptions will need to target species such as jack pine to minimize ladder-fuels, and reduce accumulations of fine and coarse woody materials in ways that are compatible with the potential role of these materials as wildlife habitats (Corace et al., In Press).

Influence of overstory characteristics on regeneration

Overstory characteristics, including canopy openness and species composition were also found to be important factors in the regeneration of our target species, exhibiting stronger influence on the seedling layer, together with fire history. Overstory characteristics appeared to have stronger effects on red pine, likely due to the fact that red pine is more shade intolerant compared to the mid-tolerant eastern white pine (Wendel and Smith, 1990). The higher red pine and eastern white pine seedling densities observed in stands with more open canopies suggest that their regeneration and establishment may benefit from restoration treatments that increase canopy openness. On the other hand, red pine seedling and sapling densities had negative relationships with most of the deciduous species in the overstory, most likely due to the negative effects of competition induced by these species for light and other resources. These relationships are consistent with those of other studies within the region, with some suggesting stronger overstory effects on the seedling layer (Peck and Zenner, 2009), and others suggesting stronger effects on the sapling layer (Dovciak et al., 2003). We suggest that the overstory influence on target species is primarily by inhibiting light penetration to the understory and forest floor, as well as by competing for nutrients and space.

Overall, while the measured metrics associated with each of the three primary groups of factors interact to affect regeneration dynamics, their effects are further compounded by other factors related to historical harvesting activities (Drobyshev et al., 2008b; Rist 2008; Whitney, 1987) and the conditions required for regeneration of red pine and eastern white pine. Red pine is characterized by low seed-setting ability, more exact seedbed requirements, and high sensitivity to competition, all of which make its natural regeneration greatly restricted relative to other pine species in the region (Ahlgren, 1976; Hauser, 2008). An additional confounding factor for both red pine and eastern white pine regeneration is inconsistent seed production. Good crop years will generally occur every 3-7years for red pine (Rudolf, 1990) and 3-5 years in eastern white pine (Wendel and Smith, 1990). This means that disturbances (and implemented restoration treatments for that matter) would be expected to have the most impact in improving regeneration of the two pine species when they coincide or follow immediately after good crop years.

2.6 Summary and implications for management

Our findings suggest that regeneration-layer dynamics of current second-growth stands are influenced by complex interactions among fire history, current fuel loadings, and current overstory characteristics. The results suggest that the majority of the fires that have occurred in the mixed-pine stands in eastern Upper Michigan over the last 142 years were likely outside of the range of severity that promotes regeneration of red pine and eastern white pine, and instead, favored regeneration of jack pine. The negative effects of fire history, fuels and overstory characteristics seem to have been disproportionately greater for red pine than they were for eastern white pine. We found greater densities of the target species in the sapling layer, however, indicating that opportunities exist for restoration treatments that not only improve germination of target species, but that also create conditions for seedling-sized individuals to grow into sapling-sized stems, and promote recruitment of saplings into the overstory.

The long-term objective of restoration efforts in these mixed-pine forest ecosystems should be to reintroduce surface fire with characteristics similar to that which occurred historically in these forests. Due to significant changes in species composition, stand structure, and fuel loadings, immediate use of fire as a management tool may be limited. Within the northern Lake States, this situation is further complicated by limited information on effects of fire on a variety of ecosystem components. Recently, however, there have been increased efforts to enhance access to and exchange of information on fire effects and fuel issues within the region (Kocher et al., 2012; Miesel et al., 2012). Resource management objectives have also shifted from having a single-resource focus to ecosystem approaches with emphasis on treatments that address multiple ecosystem components (Corace et al., 2009; 2010a, b; 2012). Further, recent studies indicate increasing acceptance of ecological-based management objectives and strategies (Shindler et al., 2009; Wilson et al., 2009).

Our study contributes to these efforts by providing important baseline information on multiple factors influencing regeneration dynamics in mixed-pine forests of eastern Upper Michigan. This information is needed to facilitate decision making, inform the design of restoration prescriptions, and advance our understanding of fire and fuel issues within these forests. Our results suggest there is need to explore restoration strategies to enhance regeneration of red pine and eastern white pine. Such restoration strategies may include opening the canopy, and reducing, in both the overstory and understory, the current densities of jack pine, red maple and other species that may have gained a competitive advantage over red pine and eastern white pine in these stands. Being a poor self-pruner, jack pine is likely to contribute to increasing risk of crown fires, and therefore, restoration efforts will need to include fuel reduction treatments to minimize the potential for severe fires that may be destructive and difficult to control (Corace, et al., 2010b). Where immediate use of fires as a restoration tool is limited, alternative silvicultural practices have been suggested to achieve objectives such as fuel reduction and restoration of desired species (Franklin et al., 2007). Future research that evaluates the response of red pine and eastern white pine regeneration to implemented restoration and fuel reduction treatments would be useful in taking the information from this study further in the efforts to restore this forest ecosystem type and help it persist across the landscape.

2.7 Acknowledgements

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Table 2.1 Species (in seedling and sapling layers) and factor groups, with associated codes used in the canonical correspondence analysis. Nomenclature: http://plants.usda.gov/

Species		Code	Factors groups (with measured variables)	Code
Red pine	*Pinus resinosa Ait.*	PIRE	**Fire history**	
Eastern white pine	*Pinus strobus L.*	PIST	Number of fires in the last 142 years	NF_142
Jack pine	*Pinus banksiana Lamb.*	PIBA	Number of fires in the last 50 years	NF_50
Red maple	*Acer rubrum L.*	ACRU	Time since last fire (years)	TLF
Downey serviceberry	*Amelanchier arborea* (Michx. f.) Fernald	AMAR		
Northern red oak	*Quercus rubra* L.	QURU	**Fuels**	
Paper birch	*Betula papyrifera* Marsh.	BEPA	Coarse woody material (1000-hr fuels; tonnes/ha)	CWM
Black spruce	*Picea mariana* (Mill.) BSP	PIMA	1-hr fine woody material (tonnes/ha)	FWM_1H
Bigtooth aspen	*Populus grandidentata* Michx.	POGR	10-hr fine woody material (tonnes/ha)	FWM_10H
Quaking aspen	*Populus tremuloides* Michx.	POTR	100-hr fine woody material (tonnes/ha)	FWM_100H
Balsam fir	*Abies balsamea* (L.) Mill	ABBA	Live shrubs and herbs (tonnes/ha)	LSH
Black cherry	*Prunus serotina* Ehrh.	PRSE	Dead shrubs and herbs (tonnes/ha)	DSH
Speckled alder	*Alnus rugosa* (Du Roi) R.T. Clausen	ALRU	Fuelbed depth (litter + duff; cm)	FBD
Nannyberry	*Viburnum lentago* L.	VILE		
Sugar maple	*Acer saccharum* Marsh.	ACSA	**Overstory characteristics**	
			Canopy openness (%)	Can_O
			Red pine (IV)	PiRe
			Eastern white pine (IV)	PiSt
			Jack pine (IV)	PiBa
			Northern red oak (IV)	QuRu
			Bigtooth aspen (IV)	PoGr
			Quaking aspen (IV)	PoTr

Table 2.2 Mean (±1 SD) seedling and sapling densities (stems ha^{-1}) in old-growth and second-growth stands in mixed-pine forest ecosystems at Seney National Wildlife Refuge. Mann-Whitney tests were used to test for differences in mean densities between stand types.

	SEEDLINGS			SAPLINGS		
Species	**Second-growth**	**Old-growth**	**P-value**	**Second-growth**	**Old-growth**	**P-value**
Red pine	64 ± 138	79 ± 269	0.98	3051 ± 3748	1805 ± 2633	0.52
Eastern white pine	136 ± 254	379 ± 469	0.03	766 ± 1739	158 ± 335	0.42
Jack pine	60 ± 181	0 ± 0	0.02	1404 ± 3680	21 ± 101	0.0008
Red maple	1344 ± 2944	1678 ± 2433	0.02	328 ± 2100	442 ± 1131	0.007
Downy serviceberry	757 ± 1122	547 ± 752	0.17	17 ± 70	310 ± 643	0.001
Northern red oak	166 ± 409	142 ± 502	0.77	0 ± 0	0 ± 0	0.38
Paper birch	4 ± 29	37 ± 112	0.02	34 ± 113	195 ± 508	0.05
Black spruce	64 ± 325	47 ± 188	0.84	140 ± 341	78 ± 200	0.92
Bigtooth aspen	9 ± 41	11 ± 45	0.93	102 ± 273	95 ± 311	0.46
Quaking aspen	0 ± 0	63 ± 390	0.08	89 ± 395	100 ± 254	0.09

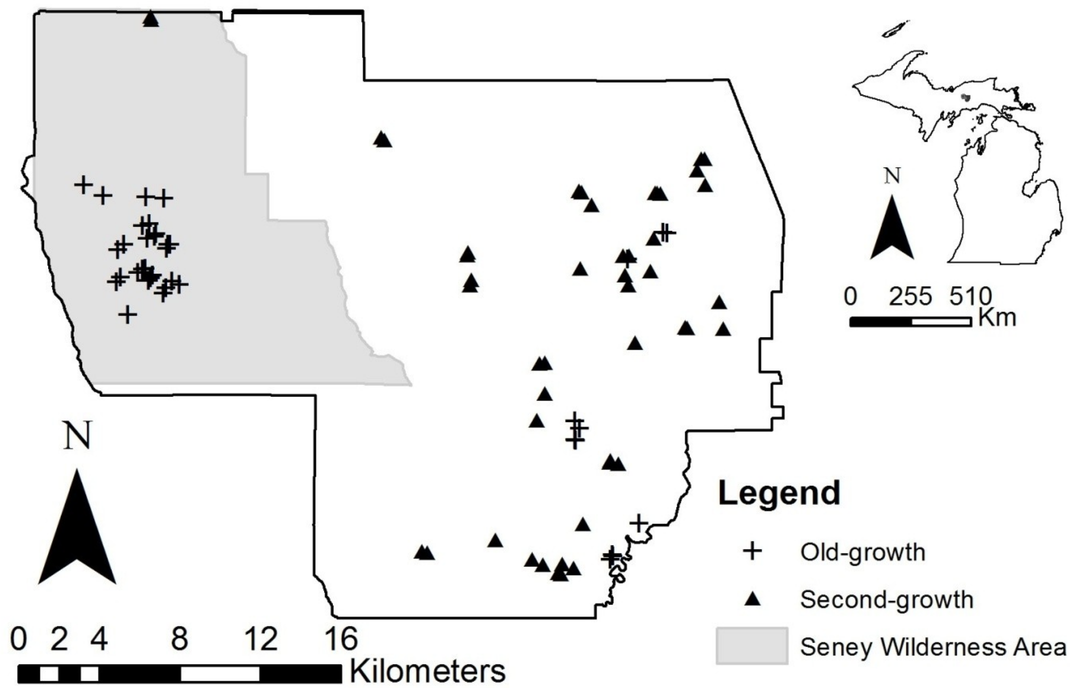

Figure 2.1 Study area at Seney National Wildlife Refuge showing study plot locations in old-growth and second-growth stands.

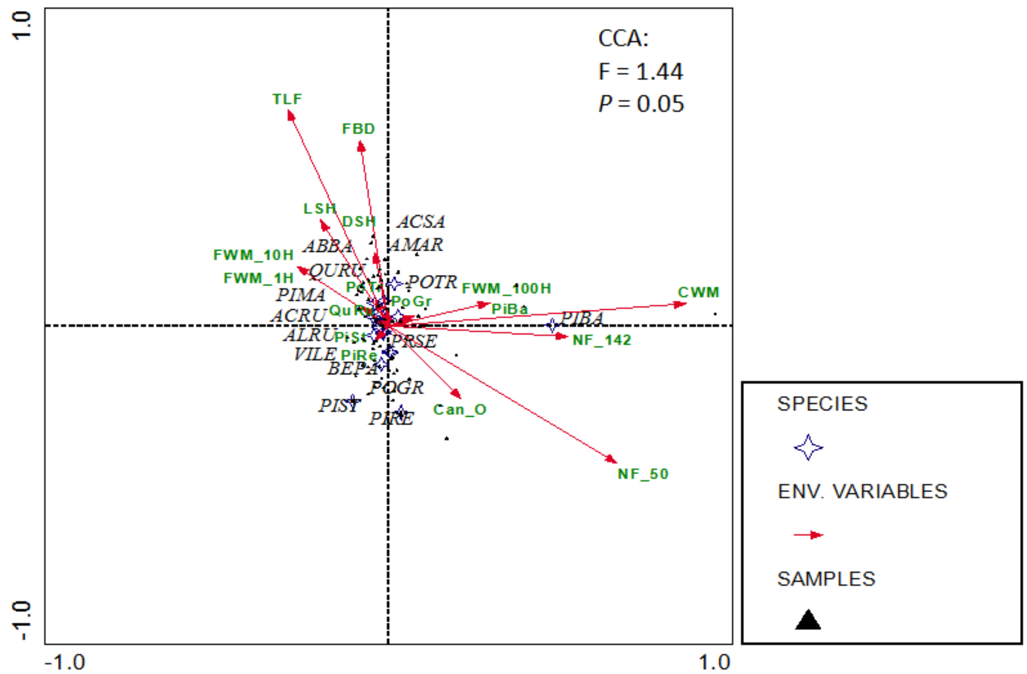

Figure 2.2 Canonical correspondence analysis relating species' seedling densities to fire history, fuels and overstory characteristics in mixed-pine forest ecosystems at Seney National Wildlife Refuge. See Table 1 for description of codes used in the graph.

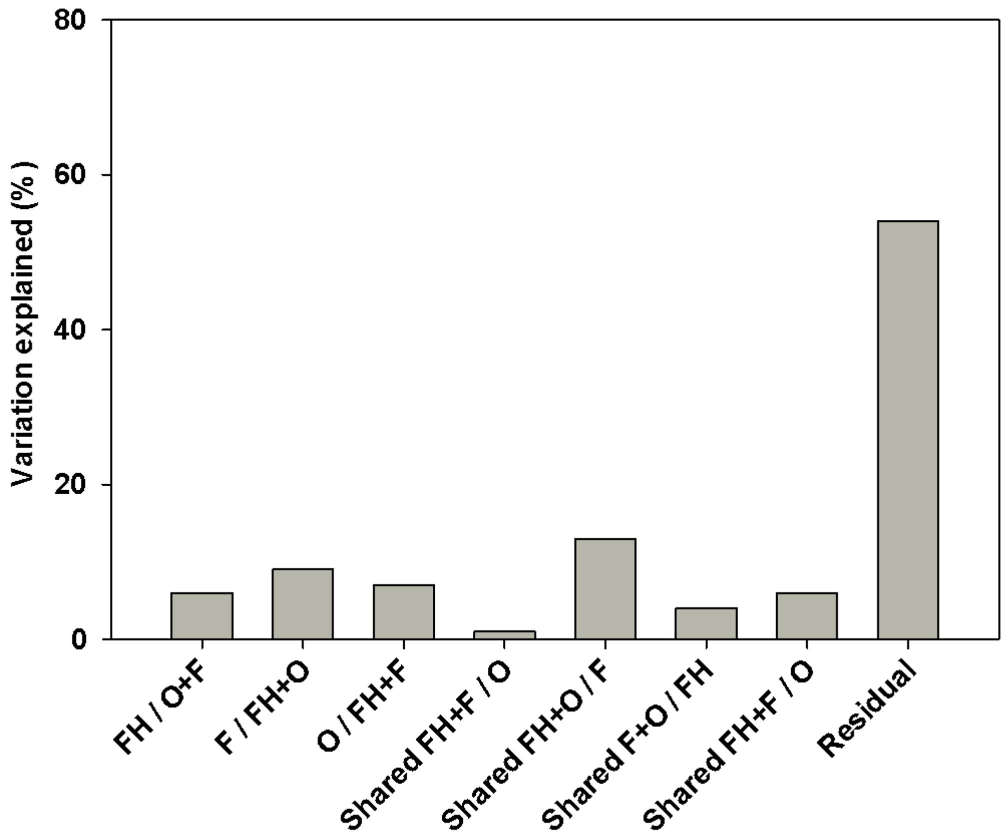

Figure 2.3 Partial canonical correspondence analysis showing percent individual and shared variance explained by fire history, fuels and overstory characteristics in seedling data in mixed-pine forest ecosystems at Seney National Wildlife Refuge. FH=fire history, F=fuels and O=overstory characteristics. Slash (/) sign means given the influence of the variable (s) to the right.

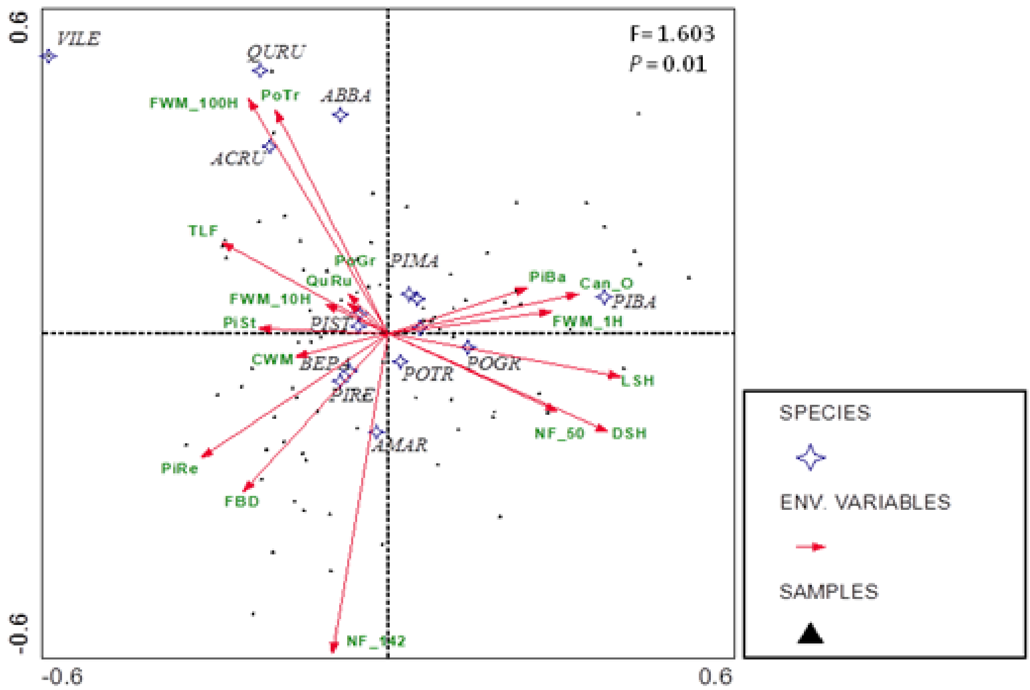

Figure 2.4 Canonical correspondence analysis relating species' sapling densities to fire history, fuels and overstory characteristics in mixed-pine forest ecosystems at Seney National Wildlife Refuge. See Table 1 for description of codes used in the graph.

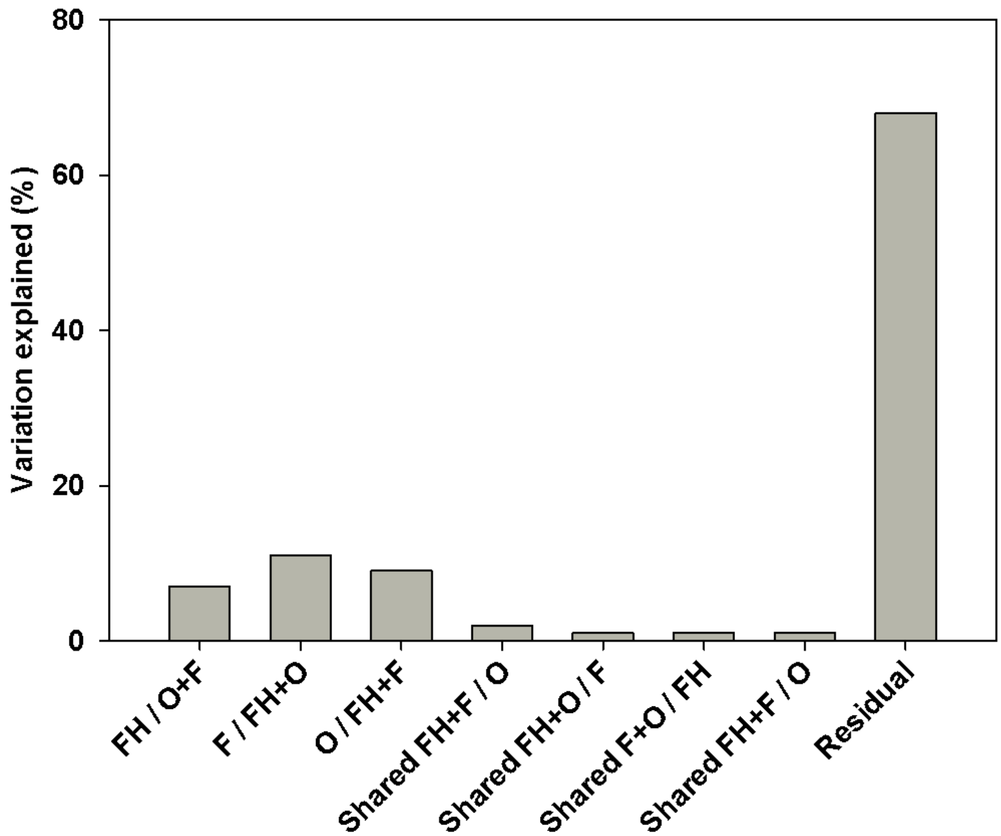

Figure 2.5 Partial canonical correspondence analysis showing percent individual and shared variance explained by fire history, fuels and overstory characteristics in sapling data in mixed-pine forest ecosystems at Seney National Wildlife Refuge. FH=fire history, F=fuels and O=overstory characteristics. Slash (/) sign means given the influence of the variable (s) to the right.

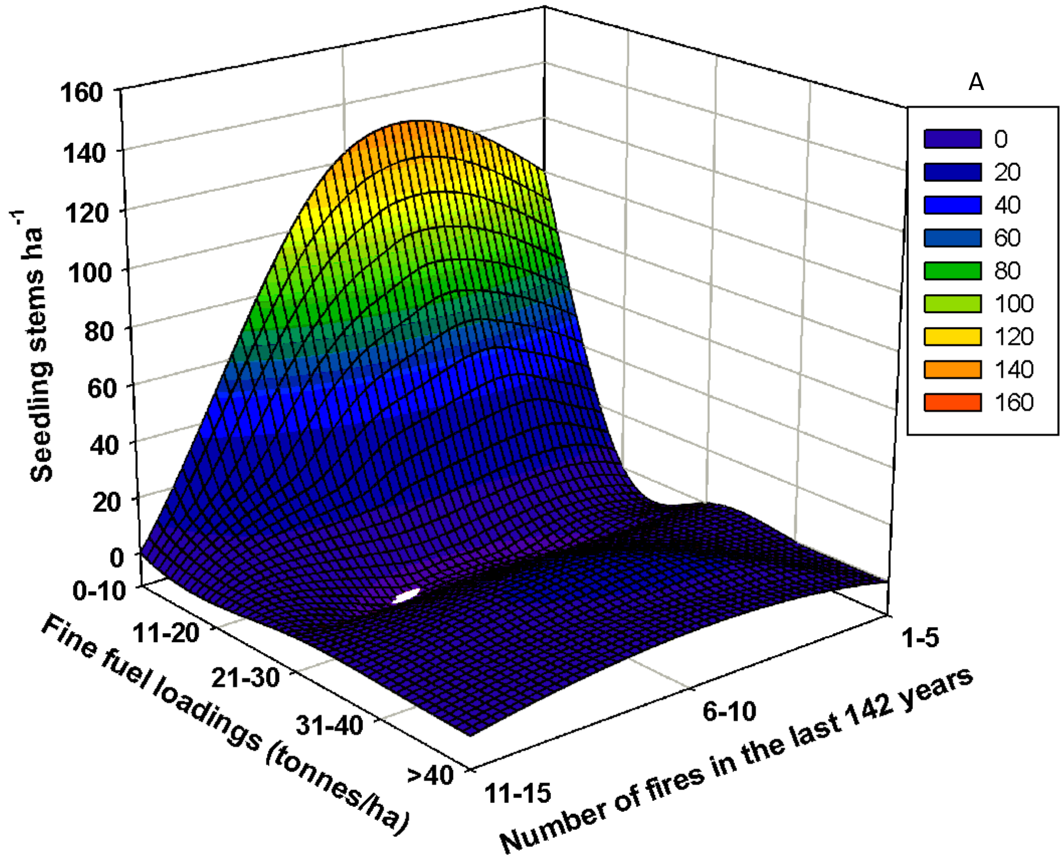

Figure 2.6 Three-dimensional surfaces relating red pine seedling (A), and sapling (B) densities to number of fires in the last 142 years and fine fuels at Seney National Wildlife Refuge. Fine fuels comprises the 1, 10, 100-hr fuels.

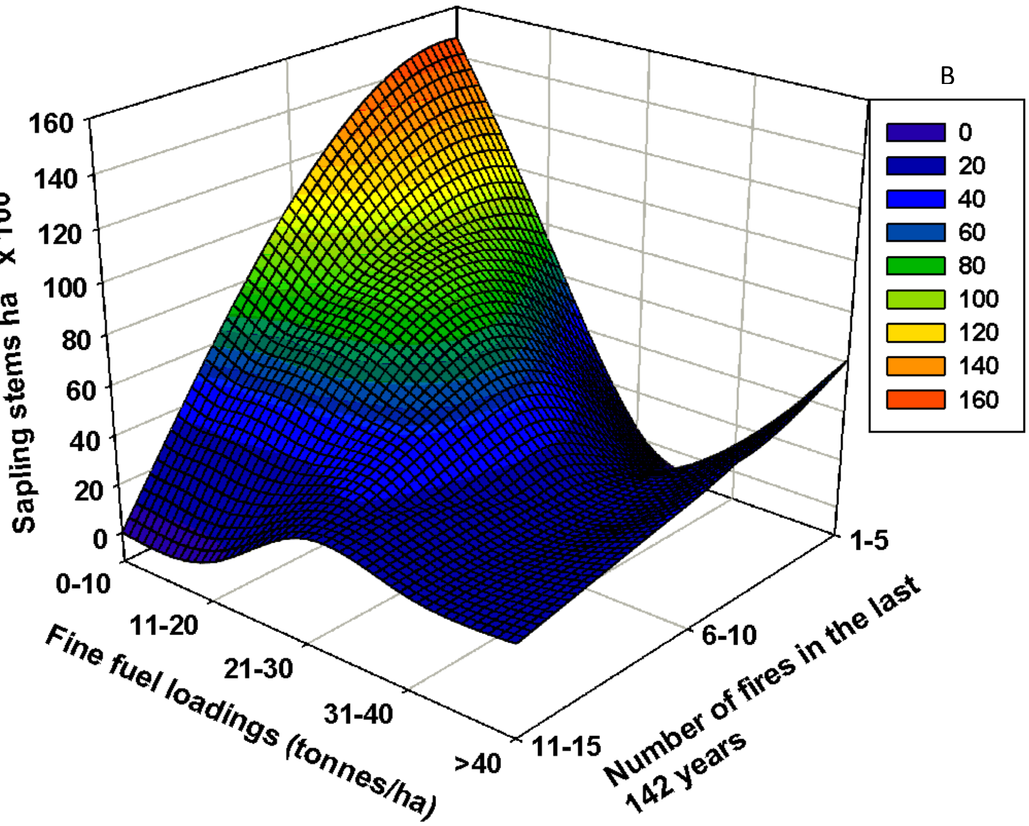

Figure 2.6 continued

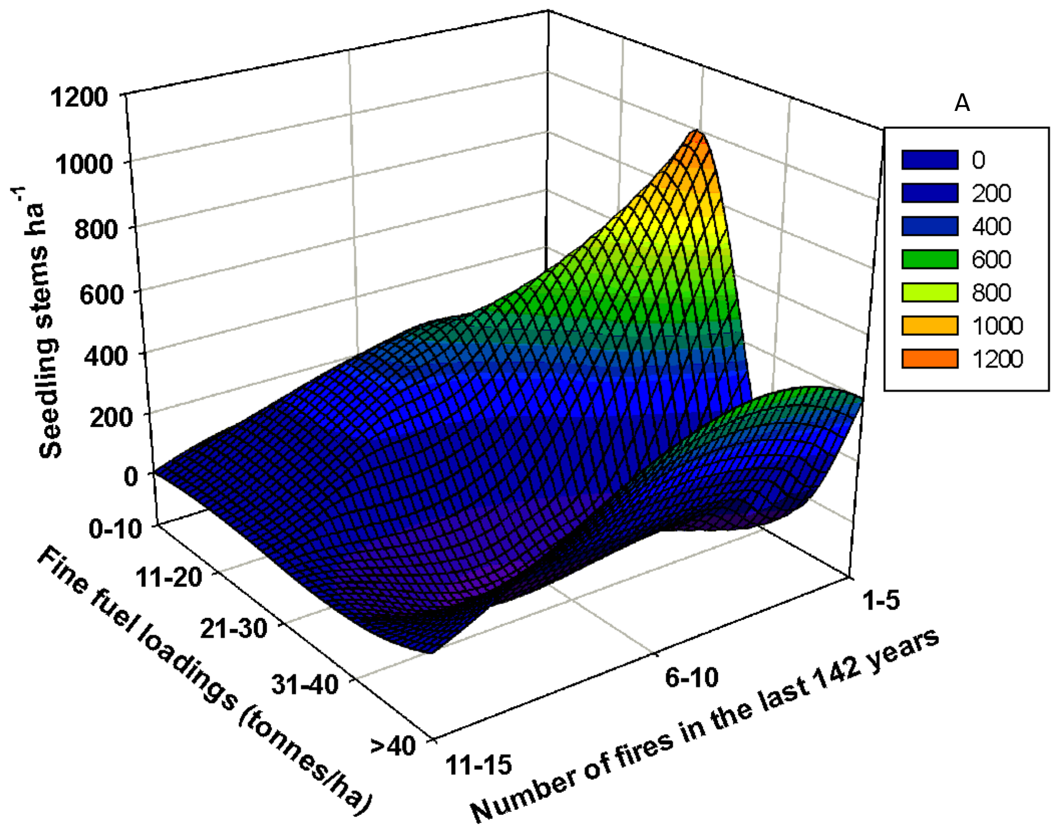

Figure 2.7 Three-dimensional surfaces relating eastern white pine seedling (A), and sapling (B) densities to number of fires in the last 142 years and fine fuels at Seney National Wildlife Refuge. Fine fuels comprises the 1, 10, 100-hr fuels.

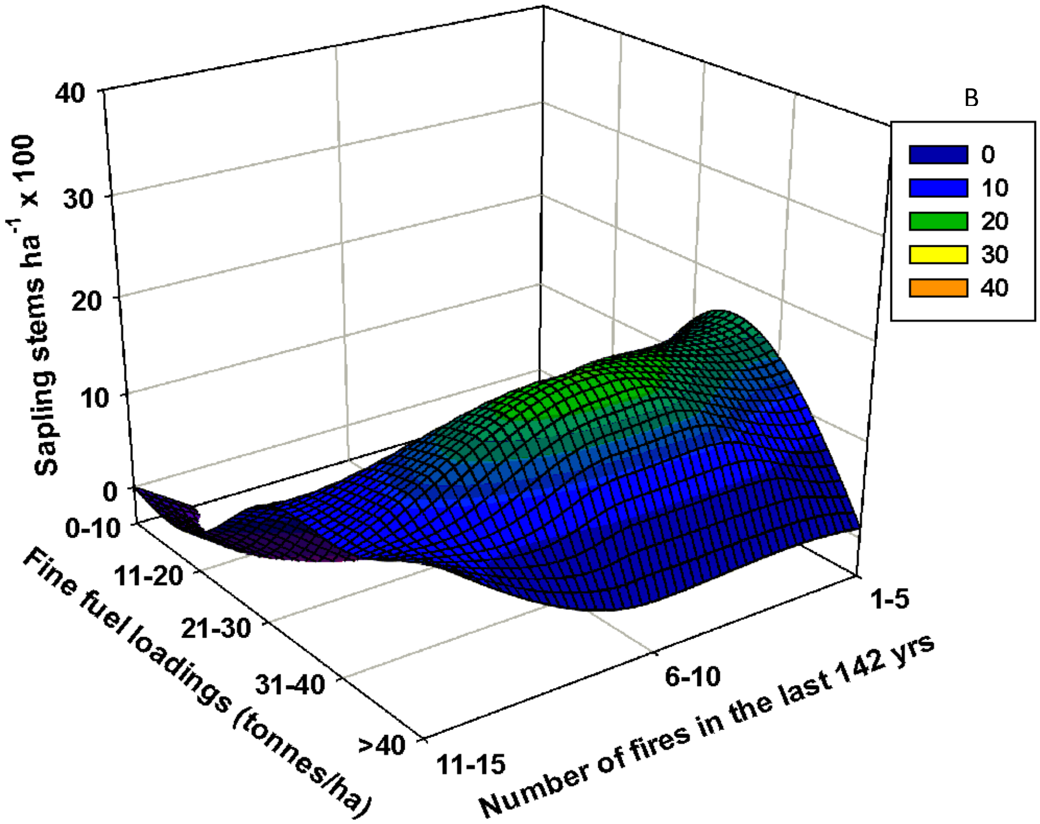

Figure 2.7 continued

Chapter 3: Initial regeneration and litter decomposition following variable-retention harvesting in a mixed-pine forest ecosystem of eastern Upper Michigan

3.1 Abstract

The structure and composition of mixed-pine forest ecosystems across the Lake States region have been significantly altered due to changes in the natural fire regime and current and past land uses. In an effort to restore these forests, scientists and land managers have focused on developing ecosystem-based restoration strategies that more closely emulate natural disturbance patterns and processes. Variable-retention harvesting is one such technique that has been proposed to help achieve a variety of restoration and management objectives by manipulating the overstory in two spatial patterns (each of which emulates patterns created by natural disturbance processes) while retaining important structural elements and biological legacies. In the northern Lake States, however, this approach has been primarily applied in plantations to improve structural complexity, with no implementation in naturally regenerated forests where restoring historically dominant pine species and fuel reduction are important management objectives. To address the potential of this technique as a tool for restoring ecosystem conditions and reducing fuel loadings, we implemented a variable-retention harvest in a mixed-pine forest ecosystem in eastern Upper Michigan, with the dual objective of restoring red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.), and reducing live jack pine *(P. banksiana* Lamb.) fuels. The treatment involved retaining 30% of the initial overstory basal area in a stand by opening the overstory in two spatial patterns: 1) an aggregate pattern where gaps (~ 0.3 ha) were created within the residual stand; and 2) a dispersed pattern where the residual overstory was relatively uniformly dispersed across the stand. Initial (2-yr) results indicate: 1) greater eastern white pine seedling densities in treated compared to unharvested control stands, but no significant differences in red pine seedling densities between treated and control stands; 2) negative

influence of down woody fuels and overstory characteristics on the density of red pine seedlings; 3) significant reduction in jack pine live fuels; 4) no significant treatment effects on ground-flora (herbs and shrubs) cover when compared to the control; 5) no significant treatment effects on litter decomposition over a one-year period; and 6) no significant differences in measured responses between aggregate and dispersed spatial retention patterns. Our results suggest that overall, variable-retention harvesting may be a viable technique that offers opportunities to restore historically dominant pine species (especially eastern white pine) and address live fuel reduction objectives. Additional treatments during or after harvesting (e.g., creating exposed seedbeds or use of prescribed fire post-harvest), however, may be needed to facilitate red pine regeneration. Treatment prescriptions may need to be tailored to better suit the specific ecosystem and management objectives. Further, longer-term comparisons of ecosystem structure and function between treated and untreated stands will be needed as these stands develop to better understand the long-term efficacy of variable-retention harvesting.

3.2 Introduction

The significant changes in natural fire regimes associated with fire suppression policies and other changes to land use in many fire-dependent forest ecosystem types across North America are well documented (Covington and Moore, 1994; Drobyshev et al., 2008a; Stephens and Ruth, 2005). Within the northern Lakes States, altered fire regimes, coupled with subsequent land-use practices (e.g., clearcutting and land conversion to agriculture) have led to changes in species composition, declines in regeneration of historically dominant species, structurally simplified stands with increased stand densities, and accumulation of both live and down fuels outside of the natural range of variability, increasing the risk of severe fires (Cleland et al., 2004; Corace et al., 2012; Drobyshev et al., 2008b; Rist, 2008; Thompson et al., 2006). As a result, restoration efforts to address stand structure, regeneration of historically dominant species, and fuel concerns have become increasingly important in these pine-dominated ecosystems (Bebber et al., 2005; Corace et al., In Press; D’Amato et al., 2012; Peck et al., 2012).

Ecosystem-based restoration techniques that address multiple resource objectives and more closely emulate patterns created by natural disturbances have been recommended for many altered forest ecosystem types (Corace et al., 2009; 2012; Hunter 2005; Franklin and Johnson; 2012). Specifically, modified silvicultural practices that are designed based on an understanding of the characteristics of natural disturbance events specific to a given ecosystem type, and subsequent stand development processes, have been proposed to better address multiple and often competing management objectives (Franklin et al. 2007; Fries et al., 1997; Seymour et al., 2002). The use of such modified silvicultural practices stems from the recognition that traditional silvicultural approaches are not always good analogs for natural disturbance events and stand development processes, and may not adequately address a variety of ecosystem management objectives (Bauhus et al., 2009; Bergeron et al., 2002; Coates and Burton, 1997; Lindenmayer and McCarthy, 2002; Pedlar et al., 2002; Seymour et al., 2002; Spies and Franklin, 1989). For example, traditional silvicultural systems, (including uneven-aged regeneration methods), have often overtly or inadvertently led to homogeneity and simplification of stand structure and composition, contributing to lack of spatial heterogeneity across the landscape (Palik and Levy, 2004; Palik and Zasada, 2003). As such, there is a need to modify these techniques and reorient management practices to better align with the natural dynamics of forest ecosystems and emulate natural disturbances that shape forest patterns and structure.

The theoretical framework upon which the design and application of the proposed modified silvicultural strategies is built involves two concepts: 1) successional trajectories that lead to reference conditions characterized by the natural range of variability that is reflective of pre-disturbance conditions; and 2) biological legacies and patterns associated with natural disturbance events (Dobson et al. 1997; Franklin et al. 2007). Ecological restoration provides an opportunity to move an altered structurally simplified ecosystem along an often non-linear ecological trajectory towards more structurally complex reference conditions, by enhancing both structure and function (Allen et al., 2002, Landres et al., 1999; SER, 2004). On the other hand, each ecosystem type was maintained by a specific natural disturbance regime that in addition to maintaining stand structure and the dominant tree species, created specific patterns and biological legacies (such as declining trees and snags) that influenced recovery processes in the post-disturbance ecosystem (Foster et al., 1998; Franklin et al., 2007). Where conditions allow for their reintroduction, natural disturbance processes characteristic of a given ecosystem type are thus believed to be the best alternative to restore modified ecosystems (Dobson et al., 1997). Restoration alternatives that emulate natural disturbance processes, therefore, provide better opportunities to achieve ecological restoration objectives specific to a given ecosystem type (Dobson et al., 1997).

Variable-retention harvesting is one such modified silvicultural practice that is based upon this framework, and has been proposed to help achieve various management objectives (Franklin et al., 2007; Mitchell and Beese, 2002; Palik and Zasada, 2003). Within the United States and Canada, variable-retention harvesting has been implemented in pine-dominated forest ecosystems of the South (Battaglia et al., 2002; Palik et al., 2003), West (Aubrey et al., 2009; Halpern et al., 1999) and Great Lakes (Atwell et al., 2008; Bebber et al, 2005; Peck et al., 2012) regions. Variable-retention harvesting has been described as, "…an approach to harvesting based on the retention of structural elements or biological legacies (trees, snags, logs, etc.) from the harvested stand for integration into the new stand to achieve various ecological objectives" (Helms, 1998). Other names such as green-tree retention or structured retention harvest have been used synonymously with variable-retention harvesting in the silvicultural and forest management literature (Bebber et al., 2005; Craig and Macdonald, 2009; Halpern et al., 1999). The three key characteristics of variable-retention harvesting are: 1) what is retained (species targeted for retention); 2) how much is retained (level of reduction of initial stand basal area); and 3) the spatial pattern of retention (spatial distribution of retained trees; aggregate or dispersed) (Franklin et al., 2007).

In variable-retention harvests that utilize an aggregate retention pattern, the overstory basal area is reduced by creating gaps of a defined size within the residual stand, while in dispersed retention, the overstory basal area is reduced by opening the overstory such that retained trees are relatively uniformly dispersed across the stand

(Aubry et al., 2009; Franklin et al. 2007; Mitchell and Beese, 2002; Palik and Zasada, 2003). The two retention patterns are used to emulate the structural patterns created by natural disturbance events typical of that forest type (e.g., a mosaic of burned patches and unburned residual stand area following fire), and because each of them can be used to meet different management objectives (Franklin et al., 2007). As such, the decisions regarding what is retained, how much is retained, and the spatial pattern of retention is heavily determined by initial existing conditions of the stand and specific management objectives (Bauhus et al., 2009; Coates and Burton, 1997). While only a single level of initial basal area reduction and spatial patterns of retention may be implemented at the stand-level (depending on size of stand), at the landscape level, variable-retention harvesting may consist of varying the retention prescriptions from stand to stand, and possibly combining the two spatial patterns, depending on management objectives to be achieved and the size of the stand (Mitchell and Beese, 2002).

While it has been applied extensively in the western United States and other regions (Aubry et al., 2009; Mitchell and Beese, 2002; Palik et al., 2003; Sullivan et al., 2001), variable-retention harvesting has not been used widely within the northern Lake States, and has primarily been implemented in managed forests or plantations to increase structural complexity (Atwell et al., 2008; Peck et al., 2012; Palik and Zasada, 2003). Management objectives focused on increasing structural complexity in managed plantation forests are often different from those of naturally regenerated forests where ecological management and fuels reduction objectives take precedence. Further, we are aware of no studies that have examined the viability of variable-retention harvesting as technique to address restoration of target species and/or fuel reduction in naturally regenerated mixed-pine forests within the northern Lake States.

In the fall of 2010, we initiated an experiment using variable-retention harvesting to evaluate its effectiveness as a restoration and fuel-reduction treatment in naturally regenerated mixed-pine forest ecosystems of eastern Upper Michigan. Specifically, we quantified the initial (2-year) response to the harvest treatment by examining: 1) regeneration of target species (red pine and eastern white pine) with respect to other woody species; 2) reductions in overstory jack pine basal area (representing significant live fuels); 3) the development of the ground-flora (herb and shrub cover); and 4) ecosystem productivity as measured by leaf/needle litter decomposition. We hypothesized that: 1) regeneration of red pine and eastern white pine would be greater following harvesting compared to the controls, and greater under the aggregate retention pattern as greater changes in understory microclimate may favor the two target species; 2) harvesting would result in significant reduction in overstory jack pine basal area; and 3) litter decomposition would be higher under treatments and differ among retention patterns as changes in understory environmental conditions may be expected to influence decomposition in treated stands. While this study only addresses the initial two-year response, it will provide valuable information regarding the viability of variable-retention harvesting as a technique to achieve dual objectives of restoring historically dominant species and reducing live fuels. It will also provide a basis for the application of adaptive management principles for forest ecosystem restoration activities that utilize variable-retention harvesting.

3.3 Methods

Study area

The study was conducted within the 38,542-ha Seney National Wildlife Refuge (SNWR) (N46.271594◦ W86.057078◦), Schoolcraft County, Michigan, U.S.A. SNWR lies within the Seney Lake Plain ecoregion and is characterized by soils and physiographic features that resulted from postglacial erosion and soil formation processes (Albert, 1995). Two major landforms dominate the landscape: glacial outwash channels and a patterned fen matrix interspersed by sand ridges (Heinselman, 1965). The soils range from poorly drained peats to excessively drained coarse, sandy soils, on which mixed-pine stands are found. The climate is influenced by it close proximity to the Great Lakes. Temperatures vary between a minimum of -9 ^{o}C in the coldest month (January) to 30 ^{o}C in the warmest month (July), and the average annual precipitation is 78 cm, with most of the precipitation falling in the form of snow (MRCC, 2013). The length of the growing season averages 119 days, and the average daily humidity during spring and fall varies between 50 and 60%.

The landscape of SNWR is composed of a mosaic of upland and lowland forests, and wetland vegetation (USFWS, 2009). The mixed-pine forests where historically dominated by red pine and eastern white pine (Drobyshev et al., 2008b: Zhang et al., 2000). Regeneration of red pine and eastern white pine have been negatively affected by greater time lags between fires, as well as by occasional severe fires and management practices (e.g., clearcutting) that are thought to have favored regeneration of jack pine over the other two pine species (Drobyshev et al., 2008b; Rist 2008). Consequently, besides increases in fire-sensitive deciduous species, there is a significant component of 40-60 year old mature jack pines in the overstory of most of the current stands, which through both live and down fuels, may contribute to the potential risk of severe fires (Corace et al., 2009; Corace et al., In Press). The study area thus provides a model landscape to test new restoration strategies, as there is altered, naturally regenerated second-growth stands that reflect the changes in historical conditions characteristic of the region as well as adjacent old-growth stands that represent reference conditions.

Experimental design and harvest treatments

We implemented a variable-retention harvest in September-October of 2010. Six stands classified as the *Pinus-Vaccinium-Epigaea* habitat type (Burger and Kotar, 2003), and ranging in size from 3.2 ha to 6.4 ha were selected (Table 3.1). Reconnaissance and inventory of all stands prior to harvesting indicated that they were relatively similar in stand structure and overstory basal area. Additionally, because treatments would be defined by proportional reduction in initial basal area, the reconnaissance was helpful in estimating stand densities and marking stems to be either removed or retained.

Following the pre-treatment assessments, each stand was randomly assigned to one of two retention patterns: 1) an aggregate pattern where the overstory basal area was reduced by creating gaps (~ 0.3 ha) within the residual stand (Figure 3.1A); and 2) a dispersed pattern where the overstory basal area was reduced by leaving the residual trees relatively uniformly dispersed across the stand (Figure 3.1B). The two retention patterns were implemented as part of efforts to emulate patterns created by natural disturbances;

for example the aggregate retention emulates the patchy mosaic pattern created by natural wildfire. Both harvest patterns targeted a 30% reduction of the initial overstory basal area. This retention level was selected to provide a balance between higher retention levels that may not achieve adequate modification of understory environmental conditions, and lower retention levels that may result in extreme changes in understory microclimatic conditions that do not favor target species (Aubry et al., 2009). Three nearby unharvested control stands of similar composition and structure that approximated the pre-harvest conditions were additionally selected (see description of stands in Table 3.1).

During harvesting, jack pine was a priority target for removal, followed by deciduous species (e.g., red maple, *Acer rubrum* L.). In some instances, red pine and eastern white pine stems were also removed to reach the 30% retention level. Additionally, older red pine and eastern white pine trees that presumably predated the logging era were left uncut for their old-growth characteristics and as seed sources, as were the advanced regeneration of the two species. Snags were also left in place for their potential wildlife habitat functions (Corace et al., In Press). Harvested trees were de-limbed on site, merchantable logs removed, and the smaller branches, twigs and other slash were distributed as evenly as possible across each site.

Within each stand, we established a network of six 25-m^2 (5 m by 5 m) permanent sample plots to collect regeneration, ground-flora, and fuels data. For the dispersed retention treatment and control stands, we used a grid system to identify the location of sample plots. Using ArcGIS (ArcGIS 9.3, 2008), we overlaid a 50m by 50m grid on the stand boundaries, sequentially numbered the grid intersections, and randomly selected six grid intersections as locations for the sample plots. In the aggregate retention treatment, plots were established by randomly assigning three plots in the harvested patches (gaps) and three plots in the residual areas of the stand. The plots were distributed in this manner because the aggregate retention treatment as a whole comprises both the harvested open patches and the unharvested residual patches, so that average measured response from both areas can be compared to those in the dispersed retention pattern (similar plot location approach as Palik et al., 2003). Effort was made to ensure the plots in the gaps were located as close to the center of the gap as possible to minimize edge influence (Peck et al., 2012). In total, we established 54 sample plots in the treated and control stands, with six replications at the plot level and three replications at the stand level.

Determining seedling age

Because we did not have the opportunity to collect pre-treatment regeneration-layer data, it was necessary to determine the age of all woody seedlings post harvest. To determine seedling age, we counted the number of whorls for pine species or number of terminal bud scars for deciduous species so as to discriminate new seedlings that were recruited following treatment application (used in the analysis of the current study) from advance regeneration (similar technique used by Clark and Hallgren, 2004; Palik and Pregitzer, 1995; Peck and Zenner, 2008). As part of this effort, we developed regression models that predict the age of each pine seedling stem as a function of diameter, height, or the number of whorls. We identified three adjacent mixed-pine stands with similar soils, species composition, structure and habitat type (Burger and Kotar, 2003), representing similar growing conditions. Within these stands, we randomly identified and destructively sampled 50 seedlings each for red pine, white pine, and jack pine with heights ranging from 5 cm to 300 cm.

Prior to collecting stem-sections at the base of each seedling, we measured the basal diameter, height (cm) and number of whorls on each individual. We collected sections as close to the base of the stem (root collar) as possible so as to reduce potential errors in age estimation (Fraver et al., 2011, Gutsell and Johnson, 2002: Palik and Pregitzer, 1995). Care was also taken to cut stems right at the ground level to avoid potential swellings or other malformations around the root collar that may cause distorted ring patterns. In the laboratory, cross-sections were air-dried and sanded to a smooth polish with up to 400 grit sandpaper to enable clear recognition of annual rings. Samples were then scanned at 600 dpi, and the age (based on number of annual rings) of each sample was obtained using the WinDendro image analysis system and software (Regent Instruments Inc., Chemin Sainte-Foy, Quebec).

Vegetation and fuels sampling procedures

Within each 25-m^2 regeneration-layer sample plot, four 4-m^2 (2 m by 2 m) quadrats were used to quantify woody seedlings and estimates of ground-flora (vascular plants defined as a herb or shrub by PLANTS database (USDA 2013) and < 1 m tall, excluding tree seedlings) cover, allowing for a 1-m buffer through the plot center in each cardinal direction to minimize trampling vegetation within the quadrats during sampling. Within each quadrat, seedling counts of all woody seedlings (stems < 2.5 cm dbh and no height limits) were recorded, including the basal diameter (measured at the root collar), height, number of whorls for pine species, and number of terminal bud scars for deciduous species. Among deciduous species such as red maple that exhibited sprouting, each individual sprout was counted separately. Stems in the sapling layer (stems > 2.5 cm dbh up to10cm dbh) were not sampled as the responses of the regeneration-layer to the treatments were measured by response of the seedling layer in the current study.

Within each quadrat, we also visually estimated the percent cover of ground-flora species (herbs and shrubs) using the following cover classes: 1), < 1%; 2), 1-5%; 3), 6-10%; 4), 11-20%; 5), 21-40%; 6), 41-600%; 7), 61-80%; and 8), 81-100%. All plants that were rooted outside but whose cover extended into the quadrats were included in the cover estimates. To characterize the overstory composition associated with each sample location, the species and diameter at breast height (1.37 m above the ground) of all living trees (stems > 10.0 cm dbh) within the sample plot were recorded within a 400-m^2 circular plot established from the center of the sample plot. The overstory consisted of trees of all crown classes (dominant, codominant, intermediate and overtopped). All plants encountered in sample plots were identified, and taxonomic authorities followed the PLANTS database (USDA 2013).

In addition to the vegetation sampling, we collected digital hemispherical photographs at 1 m above the ground using a fisheye-lens mounted on a Nikon 8400 digital camera stationed at the center of the regeneration-layer sample plot. We then used the WinSCANOPY digital image processing software (Regent Instruments Inc., Chemin Saint-Foy, Quebec) to estimate the proportion of the canopy that is open (i.e., percent canopy openness). Fuel data was collected by following the standard protocols adopted by the Forest Inventory and Analysis (FIA) Program of the USDA Forest Service (Woodall and Monleon, 2007). Specifically, we recorded estimates of coarse (1000-hr fuels) and fine (consisting of 1-hr, 10-hr and 100-hr fuels) down woody material, fuelbed depth (duff and litter), and live and dead herb and shrub cover using a line intercept method along three 7.3-m transects arrayed at 30^{o}, 150^{o}, and 270^{o} from the plot center. We then used standard calculations from Woodall and Monleon (2007) to obtain total fuel biomass.

Litter decomposition field procedures

In September 2011, we collected freshly fallen red pine needles and mixed-hardwood leaves on fabric tarps in adjacent unharvested mixed-pine stands, to examine potential effects of the retention harvest treatments (over a 1-year period) on litter decomposition. The study was conducted using the litter bag technique as described in Karberg et al., (2008), and used as a proxy for ecosystem productivity. Two types of litter were used to represent the main types of tree litter in the ecosystem, and also because decomposition of leaves may differ from those of needles (Kim et al., 1996; Polyakova and Billor, 2007; Prescott et al. 2000). After collection, litter was sun-dried for 10 days to remove as much moisture as possible. Following drying, 10 g of each litter type was weighed and placed in a 30 cm by 30 cm mesh bag (mesh size of 0.5 cm by 0.5 cm). Four litter bags of each litter type were placed on the ground surface in each sample plot, secured with a metal pins and retrieved from the plots at the designated time intervals (1 (serving as a control), 30, 230 and 365 days). Litter samples were placed at each regeneration-layer plot, resulting in a total of 108 samples for each time period (54 pine samples and 54 hardwood samples), and achieving replication at both the plot and stand levels.

Following each retrieval, litter bags were stored at approximately 4^{o} C until transported to the laboratory where they were placed in drying ovens set at 50^{o} C for 10 days, reweighed and the amount of mass loss calculated. From these samples, we randomly selected six samples of each litter type from each treatment (aggregate, dispersed, control) for a total of 36 samples for each time period. These dried litter samples were ground and chemical analysis of carbon and nitrogen conducted using a Leco TruSpec C and N analyzer (Leco Corporation, St. Joseph, MI). Both biomass loss and C:N ratios were used to quantify litter decomposition from two perspectives: while changes in weight of biomass provide an indication of the organic matter breakdown during decomposition, the dynamics of carbon and nitrogen during decomposition makes C:N ratio a good indicator of the quality of litter, and therefore, a good indicator of decomposition (Edmonds, 1991). To measure temperature and relative humidity as factors that potentially influence litter decomposition, we placed Hobo loggers (U23 Pro v2 Temp/Relative Humidity Data Logger, Onset Computer Corporation, Bourne, MA) in four plots in the aggregate (two loggers in gaps, two in the residual stand), dispersed, and control treatments in the summer of 2012. The loggers were placed at the center of each plot by securing it onto a wooden stick at 30 cm above the ground, and set to record temperature and relative humidity at hourly intervals for a period of approximately two months (June 17 to August 15, 2012).

Statistical Analyses

To discriminate seedlings of the target species (red pine and eastern white pine) recruited following treatment implementation from advance regeneration, we developed regression models relating measured tree characteristics (basal diameter, height, and number of whorls) to the number of annual rings. Examination of residual plots of all predictor variables (diameter, height, and number of whorls) indicated distributional assumptions were met. From these models, we developed regression equations that predict age (inferred from number of annual rings) given the basal diameter, height, or number of whorls. The equations relating number of rings to basal diameter of seedlings were then applied to all red pine and eastern white pine seedlings (stems < 2.5 cm dbh) inventoried in the regeneration-layer plots. Although height and number of whorls were also good predictors of age (Appendix A), we selected the model using basal diameter as a predictor variable based upon suggestions that basal diameter is likely to have better correlation with age compared to variables such as height that are can sometimes be poorly related to age (Johnson et al., 1994, Ranius et al., 2009). The models developed for pine species, along with counted bud scars for deciduous species were also useful in obtaining the ages of all sampled seedlings (stems < 2.5 cm dbh) for all woody species in the regeneration-layer for purposes of examining the age-structure of the seedling layer. We also used a Weibull Distribution probability density function with the method of moments to determine the shape of the age distributions of seedlings in the regeneration-layer plots. All regressions analyses were performed using SigmaPlot 11.0 (SPSS, Evanston, Illinois, USA).

Prior to analysis, tree seedling densities as well as ground-flora (herbs and shrubs) cover for each species was summarized by plot and seedling densities expressed on a per hectare basis. Litter biomass loss was calculated from the difference between the dry weights of the control (initial 10-g sample minus loss during transportation and placement), and the dry weights after sample retrieval at the designated time intervals, while the results of the chemical analysis of carbon and nitrogen were used to calculate C:N ratios. Treatment effects on both regeneration, ground-flora and litter decomposition were examined using Analysis of Variance (ANOVA) (proc GLM in SAS v. 9.2). This analysis was carried out in two ways: comparing treatment (average of aggregate and dispersed) with the control, and comparing among individual retention patterns (aggregate and dispersed) and the control. Where significant treatment effects were found, a Tukey's HSD post-hoc test was used to test for significant differences between pairs of means at the 0.05 level. To examine if there were differences in the composition of ground-flora between retention patterns, we used a multi-response permutation procedure (MRPP) with a Sorensen (Bray-Curtis) distance measure and n/sum(n) weighting function using PC-ORD version 5.0 (MJM Software, Glenedon Beach, OR) software package.

To investigate whether harvest treatment effects on litter decomposition were mediated through its effects on understory microclimatic conditions (temperature and moisture), the mean temperature and relative humidity for each treatment was used as covariates of the dependent variable in Analysis of Covariance (ANCOVA). Following assessments of the assumptions of constant variance and normality, an arcsine square-root transformation was performed on all percentage data. Calculations of mean seedlings densities, biomass loss, and fuels for each treatment were, however, performed on untransformed data. Standard specified FIA procedures and equations were used to obtain fuel biomass for each treatment (Woodall and Monleon, 2007).

To examine if there were additional stand-related factors in addition to treatment effects that may be influencing regeneration dynamics, we used canonical correspondence analysis (CCA) using CANOCO v. 4.5 (Braak, C. J. F. and Smilauer, Ithaca, NY, USA) to examine relationships among species' seedling densities, fuel loadings and overstory characteristics. CCA is a direct gradient analysis that is especially useful when there is *a priori* knowledge about major factors that might be influencing the patterns of the dependent variable in space. In this case, and based upon trends documented by Drobyshev et al. (2008b), we anticipated that two primary groups of factors, fuels and overstory characteristics, would likely influence the composition of the regeneration-layer, particularly red pine and eastern white pine. The measured variables for fuel loadings included coarse (CWM) and fine (F-1H, F-10, F_100H) woody materials, litter (LT), duff depth (DD), live herbs and shrubs (LHS) and dead herbs and shrubs (DHS) (Table 3.2). The measured variables for overstory characteristics included percent canopy openness (Can_open) and importance values for each tree species in the overstory (Table 3.2). Importance values for each species in the overstory (stems >10cm dbh) were calculated using relative density and relative dominance. Relative density (as a percentage) was calculated by summing the total density of a species on a plot, divided by the total density of all species in the plot, and multiplying by 100. Relative dominance (as a percentage) was calculated in a similar manner, but substituting basal area for density. Importance values were then calculated by summing relative density and relative dominance, then dividing by two. All CCA analyses were performed using CANOCO v. 4.5, and the default linear combination (LC) site scores were used, along with a Monte Carlo permutation to test the significance of the patterns observed.

3.4 Results

Age of seedlings

The regression models relating measured tree characteristics (basal diameter, height, and number of whorls) to the number of annual rings indicated significant correlations (Figure 3.2, Appendix A), suggesting these metrics were good predictors of age. For red pine, basal diameter was significantly correlated with number of annual rings (F= 48.65, P = <0.001 R^2 = 0.51), while a similar relationship was observed for eastern white pine (F= 38.88, P = <0.001 R^2 = 0.46) (Figure 3.2). Using these equations for pine species and by counting terminal bud scars in broad-leaved species, we successfully estimated the age of each seedling, and were able to discriminate among those seedlings that established both prior to and after the harvest treatments (i.e., those 1or 2 years old are assumed to have established post-treatment). The age distributions for the three stands tended to be unimodal in shape and slighly skewed to the right (Figure 3.3). The age range was relatively narrow in all stands (aggregate, dispersed and control), ranging from 1 to 5 years, with most seedling having established within the last 1-3 years. The age distributions of red maple particularly indicated substatial recruitment in the treated stands (especially in the aggregate retention treatment) (Figure 3.3, Table 3.3).

Treatment effects on the regeneration-layer species

Two years following the harvest treatment, we found significantly higher eastern white pine seedling densities in the treated stands (aggregate and dispersed) compared to the controls (F = 12.1, P = 0.01) (Figure 3.4). Based on the successful discrimination of newly recruited seedlings from advance regeneration using the age determination models (see above), these seedlings represent an increase in newly established seedlings associated with the effects of variable-retention harvesting. Eastern white pine seedling densities were also significantly higher in both aggregate (F = 4.09, P = 0.04) and dispersed (F = 6.91, P = 0.01) retention patterns compared to the control, but there was no significant difference between the two spatial patterns of retention (aggregate vs dispersed) (Figure 3.4). Overall, there was little red pine establishment, with no significant difference between treated and control stands for red pine (F = 1.856, P = 0.1); all red pine seedlings were only found in the dispersed retention treatment (Figure

3.4). Between the two target species, eastern white pine establishment showed the greatest response to the harvest treatment, with a mean (±1SD) seedling density of 659 ± 786 seedling ha^{-1} in the aggregate retention, and 764 ± 972 seedling ha^{-1} in the dispersed retention, compared to only 104 ± 321 seedling ha^{-1} of red pine in the dispersed retention. Among other tree species inventoried within the sample plots, red maple had the highest seedling density, especially in the aggregate retention treatment. We found a mean (±1SD) red maple seedling density of 6840 ± 8042 seedling ha^{-1} in the aggregate retention treatment (Table 3.3), which is approximately 31% of the total density of all tree seedlings recorded in all stands. Northern red oak (*Quercus rubra* L.) was commonly observed, with its highest density (1631 ± 1591 seedling ha^{-1}) in the aggregate retention treatment as well. Other tree species observed with high densities in treated stands include quaking aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*Populus grandidentata* Michx.) (Table 3.3).

From the CCA, we found overall significant patterns of species occurrences along gradients inferred to be closely associated with fuel loadings and overstory characteristics, suggesting strong influences of these two groups of factors on red pine and eastern white pine regeneration (Monte Carlo test: F = 1.765, P = 0.01, 499 permutations). All four canonical axes accounted for 50% of the variation in the species composition data, with the first and second axes together accounting for 25% of this variation (axis 1 = 15%, axis 2 = 10%). Greater red pine seedling densities in particular were negatively associated with all descriptors of both fuel loadings and overstory characteristics, suggesting a negative influence of the two groups of factors on red pine regeneration (Figure 3.5). Red pine in the regeneration-layer was not associated more strongly with high importance values of mature red pine in the overstory or areas associated with greater canopy openness. These areas that had greater canopy openness, however, also tended to have higher amounts of fine fuels (F_1H, F_10H, F_100H), which may suggest a negative influence of these fine fuels. Compared to red pine, eastern white pine appeared to be more correlated with higher fuel loadings and tended to be associated with areas that had greater canopy openness and high overstory eastern white pine importance values (Figure 3.5).

Treatment effects on live fuels

Jack pine was targeted for removal during harvesting as part of a live fuel reduction strategy, and we found significantly lower live jack pine basal area in both aggregate (F = 12.1, $P < 0.001$) and dispersed (F = 11.2, $P = 0.009$) treatment stands compared to the control (Figure 3.6). The treatment achieved an overall 92% reduction in initial jack pine overstory basal area with residual basal areas of $14 m^2/ha$ and $16 m^2/ha$ in the aggregate and dispersed retention treatments, respectively. There were no significant differences in overstory basal area between the two retention patterns.

Treatment effects on ground-flora species

Overall, we did not find significant differences in percent cover of ground-flora species between treated and control stands (F = 1.07, $P = 0.3$ for herbs, F = 0.55, $P = 0.47$ for shrubs,) (Figure 3.7). We did, however, observe significantly lower herbaceous plant cover in the dispersed retention pattern compared to the aggregate retention (F = 6.98, $P = 0.01$) and to the control (F = 4.01, $P = 0.04$) (Figure 3.7). The most common species in the herbaceous layer was bracken fern (*Pteridium aquilinum* (L.) Kuhn), while the most common species in the shrub layer were the lowbush blueberry (*Vaccinium angustifolium* Aiton) and velvet-leaf (*Vaccinium myrtilloides* Michx) blueberry (Table 3.4). A Multi-Response Permutation Procedure (MRPP) test for differences in species composition among treatments showed no significant differences for herbs ($T = -0.98$, A=0.02, $P = 0.15$) and for shrubs ($T = -0.35$, A=0.003, $P = 0.31$).

Treatment effects on litter decomposition

Our results indicated no significant differences in litter biomass loss between treated and control stands over the 1-year duration of the study (Figure 3.8). On average, approximately 26% of the initial red pine needle biomass was lost in treated stands compared to 30% in the control stands after one year, while about 45% of the initial hardwood leaf biomass was lost in treated stands compared to 46% in the control stands (Figure 3.8). Comparing between retention patterns and among retention patterns and control, there were also no significant differences in percent biomass loss for both needles and leaves (Figure 3.8). Similar responses were observed with regard to C:N ratio for both needles and leaves when C:N ratios were compared between treated and control stands and among retention patterns and control (Figure 3.9). We observed a general increasing trend in biomass loss, as well a general declining trend in C:N ratio over time for both needles and leaves (Table 3.5).

We recorded mean (±1SD) temperatures of 21.1 ± 8.7 ^{o}C in the aggregate retention treatment, 21.4 ± 9.2 ^{o}C in the dispersed retention treatment and 20.3 ± 6.9 ^{o}C in the control stands over the two-month period in the summer of 2012. The corresponding mean relative humidity (as a percentage) recorded were 76.7 ± 22.9 in the aggregate retention treatment, 75.4 ± 24.6 in the dispersed retention treatment, and 80.4 ± 20.1 in the control stands. The results of the analysis of covariance to test whether the harvest treatment effects on litter decomposition were moderated through its influence on temperature and relative humidity were also not significant for temperature (F = 2.52, P = 0.11) and for relative humidity (F = 1.12, P = 0.29). Further, mean recorded temperatures and relative humidity values were not significantly different between the retention patterns or among the retention patterns and control.

3.5 Discussion

Regeneration of target species

Two years following harvesting, our analyses suggest that the initial establishment of the regeneration-layer is mixed for target restoration species, and only supported our hypothesis of greater regeneration under treatments compared to controls for eastern white pine. The significantly higher eastern white pine seedling densities in both the aggregate and dispersed retention treatments (representing an increase in newly recruited seedlings after harvesting, based on age determinations) compared to the unharvested controls suggest that the harvest treatments likely improved regeneration of eastern white pine. These findings compare with those of studies in other pine-dominated forest ecosystems that have suggested high regeneration of target pine species in harvested stands compared to unharvested controls (Battaglia et al., 2002; Bebber et al., 2005; MacGuire et al., 2001; Palik et al., 2003, Palik et al., 2005; Peck et al., 2012). A number of reasons may help explain the observed regeneration response of the target species, supported by our data and other variable-retention harvesting studies within and outside of the northern Lake States.

Compared to eastern white pine, red pine more often has relatively poor seed-setting ability, more restrictive seedbed requirements, and great sensitivity to moderate levels of competition, all of which result in infrequent occurrence of optimum conditions required for establishment of red pine (Ahlgren, 1976; Hauser, 2008; Rudolf, 1990). Eastern white pine on the other hand is an intermediate shade tolerant species that responds well to partial harvests techniques (including shelterwood regeneration methods) in terms of germination rates, and recruitment of established individuals (Carey, 1993; Wendel and Smith, 1990). One of the factors we suspect may have contributed to the low response of red pine is competition for resources with other tree species. Our results indicate high densities of red maple and northern red oak that were recruited in the treated stands post-harvest, more than in the unharvested controls. Given their ability to regenerate from both seedlings and sprouts, both red maple and northern red oak are likely to exert significant competitive pressure for resources placing red pine at a competitive disadvantage. It has also been suggested that harvesting that involves moderate levels of overstory retention may sometimes result in reduced regeneration of pine species that are particularly very intolerant of shade, in large part due to competition induced by the residual trees as well as other regenerating tree species (Palik et al., 1997; Palik et al., 2003).

The optimum seedbed conditions required by red pine for successful establishment are very restrictive (Ahlgren, 1976). Red pine germinates better in nearly-exposed mineral soils seedbed, with thin layers of litter and organic depth, and very little competition from other vegetation (Ahlgren, 1976; Hauser, 2008; Rudolf, 1990). Because of this, establishment following harvesting may also be a function of the extent of disturbances on the forest floor surface during the harvest operation, as has been suggested in other studies (D’Amato et al., 2012). Our multivariate analysis suggests that even with mature red pine in the overstory as potential seed tree, red pine establishment did not seem to have greatly increased from these seed trees, at least in terms of an initial response to overstory basal area reduction by 70%. It is possible that seedbed characteristics may have been too restrictive for the germination and establishment of red pine, probably more that it was for eastern white pine. The inconsistent seed production of red pine is an additional confounding factor that may limit natural regeneration of red pine (Bielecki, et al., 2006). Good crop years in red pine occur only at intervals of about 3-7 years (Rudolf, 1990), during which time heavy seed production is expected to result in greater germination compared to non-crop years. Because of these inconsistencies, when disturbances such as harvesting (or surface fires for that matter) do not necessarily precede a good crop year, establishment may not increase significantly over the following year.

Related to characteristics of the seedbed required for germination and establishment, CCA revealed that down woody fuels had a negative relationship with red pine seedling densities. Accumulations of fine fuels on the forest floor in particular can contribute to increases in the thickness of the litter layer and duff depth, potentially hampering red pine seedling germination and establishment (Ahlgren, 1976; Rudolf, 1990; Wendel and Smith, 1990). Similar interactions between fuel loadings and seedling germination and establishment have been suggested for longleaf pine (*P. palustris* Mill.) (Mitchell et al., 2009). An analysis of the effects of litter on germination and establishment of different plant species in a variety of ecosystem types also highlight these inhibitory effects especially in the early stages of plant establishment, with recommendations to implement treatments that help reduce the litter layer (Xiong and Nilsson, 1999).

Overall, while the use of variable-retention harvesting provides an opportunity to improve regeneration of target species, a species such as red pine that has specific life history-requirements not met by the initial harvest may need additional treatments to address important barriers to successful germination and establishment. In the case of red pine, these treatments would need to address creating a more favorable seedbed and eliminating competing vegetation. D'Amato et al. (2012) suggested that harvesting that mainly impacts the aboveground vegetation with little impact on exposing mineral soil are likely to leave red pine at a disadvantage compared to other species, especially those that readily reproduce vegetatively. Efforts to reduce the litter layer and expose the mineral seedbed, for example, by scarifying the seedbed or through the use of prescribed burning following the harvesting may be warranted.

Reduction of live fuels

Relative to other fire-dependent ecosystems across the United States, little information is available from field investigations that specifically examines the effects of fire on a variety of ecosystem components (e.g., wildlife, soils) in mixed-pine forests of the northern Lake States (Miesel et al., 2012). Recently, however, there have been concerted efforts to enhance exchange of information about fire and fuel issues within the region (Kocher et al., 2012; Miesel et al., 2012) to not only inform the design and implementation of fuel reduction treatments, but to also facilitate the adoption of emerging techniques such as variable-retention harvesting. Across mixed-pine forests of eastern Upper Michigan, increased jack pine dominance in the overstory of former mixed-pine forest ecosystems has become a concern for land managers, especially due to its contribution of both live and dead fuels, and vertical continuity through ladder fuels that could promote severe crown fires (Corace et al., 2010b; Rudolf and Laidly, 1990). Although snags are important structural component of wildlife habitat within these forests (Corace et al., In Press), high snapping rates of jack pine snags (up to 41%) especially within the first two years have been reported (Corace et al., 2010b), highlighting the potential for jack pine to contribute to fuel loadings and increasing the risk of high severity fires.

Consequently, in addition to restoring the historically dominant pine species, fuel reduction has become an increasingly important management objective for land managers of these ecosystem types. Our data suggests that targeting removal of jack pine in the overstory during harvesting as a live fuel reduction strategy is successful as our treatments reduced jack pine in the overstory by over 92%. While the current study mainly focused on reducing live jack pine, where opportunities arise, complementary studies that examine the effects of live fuel reduction on fire severity may be needed, in addition to exploring other ways to specifically address reduction of dead fuels on the floor. Mastication treatments that involve shredding, chopping or chipping of the logging debris into small pieces as a way to reduce crown-fire risk (Sharik et al., 2010) may be potential techniques to explore. While methods such as mastication are commonplace in fire-dependent conifer forests of the western United States (Glitzenstein et al., 2006; Reiner et al., 2009), their application to the northern Lake States has been limited.

Treatment effects on ground-flora species

Our study suggests no significant treatment effects on ground-flora species cover two years following treatment. Although we did not find comparisons within our study region, these results compare with those found by Sullivan et al. (2001) in mixed-conifer forests of British Columbia, but contrast with those of Aubry et al. (2009) in the Pacific Northwest who found treatment effects on the shrub layer but no differences in responses between spatial patterns of retention. The ground-flora communities and potential impacts of the implemented treatments warrant consideration, especially given their potential to compete for resources with target tree seedlings (George and Bazzaz, 1999). Activities that manipulate stand density and reduce overstory canopy cover could have significant impacts on the abundance and distribution of ground-flora species. This is especially important because in the initial stages following treatment, most of the understory responses are likely to be driven by patterns created by the disturbance both in the overstory and on the forest floor, and corresponding resource availability. These results suggest that the implemented treatments may not be a major driver of post-harvest dynamics of the ground-flora in the current stands, but instead, other factors such as competitive interactions among the individual plant species may be more important. Where improving conditions for regeneration of species such as red pine is a management priority, our observation of no treatments effects on the ground-flora may be beneficial because it suggests that the treatments did not increase competition for resources by ground-flora species.

Treatment effects on litter decomposition

Plant litter decomposition is an important process within forest ecosystems as it serves as a major source of nutrients to the ecosystem through the breakdown of the organically bound nutrients in the litter, which are then released and gradually made available for plant uptake. Given the key role that litter decomposition plays in nutrient cycling, understanding the influences of management practices on this process is crucial to maintaining or improving ecosystem productivity. As a biological process, litter decompositions can be influenced by factors such as chemical composition of the litter or litter quality (Aerts, 1997; Cornelissen, 1996), environmental factors such as temperature, moisture, or acidity (Couteaux et al., 1995; Murphy et al., 1998) and biotic factors largely driven by micro-organisms that make up the decomposer community (Edmonds, 1991). Because of the potential influence on understory environmental conditions (including temperature and moisture), harvest treatments that manipulate the overstory may be expected to result in contrasts in the rates of decomposition between harvested and unharvested stands.

Results from our one-year study of litter decomposition did not support our hypothesis of greater decomposition rates in the treated stands compared to the unharvested controls, or even among treated stands with different spatial patterns of retention. Our finding of no treatment effects on decomposition compare with those found in studies examining canopy cover effects on litter mass loss and nutrient dynamics in oak and red pine stands in northern Lower Michigan (Kim et al., 1996), and effects of clearcutting and alternative silvicultural systems on litter decomposition in montane forests of British Columbia (Prescott, 1997). While limited temporally, we also did not find significant differences in temperature and relative humidity at the ground-level between treated and control stands, possibly due to the narrow window in which we monitored the microclimatic conditions. A number of potential ecological explanations can be suggested for the low litter decomposition response to treatments in this study, including: 1) microclimate such as temperature or relative humidity may not be the main factors regulating litter decomposition rates in these mixed-pine ecosystems, the decomposer community may be more important (Edmonds, 1991; Kim et al., 1996); 2) possible ameliorative effects of ground-flora layer and/or the harvest debris accumulations on the forest floor on microclimate at the ground level; and 3) the observed increasing trend in biomass loss and decreasing trend in C:N ratios suggest limitations imposed by duration of study, and that the lack of significant treatment effects may be a function of time rather than treatments per se. Longer periods for litter decomposition studies maybe warranted.

Effectiveness of different spatial retention patterns

The spatial pattern of overstory retention is a key characteristic of variable retention harvesting as it provides the land manager with an opportunity to emulate spatial patterns and stand structures left on the landscape after natural disturbances (Franklin et al., 2007). The two most common spatial patterns that characterize variable-retention harvesting (aggregate and dispersed) have been suggested to differ in their effects on post-harvest stand structure and, therefore, some ecological objectives may be best met by dispersing retained structures and others by aggregating them (see Table 5 in Franklin et al., 2007). For example, it has been suggested that eastern white pine might do well in both dispersed and aggregate retention treatments, while red pine might do better in an aggregate retention treatment (Palik and Zasada, 2003). This suggestion is based upon the hypothesis that there is a greater potential for significant changes in competitive environments in gaps created by aggregate treatments, leading to better regeneration conditions for intolerant pine species (Battaglia et al. 2002; Palik et al. 1997; Palik and Zasada, 2003).

Our results did not support our hypothesis that establishment would differ between the two retention patterns, findings that compare with other studies in conifer forests in the Pacific Northwest where pattern of retention was found to have limited effect on measured responses (Aubry et al., 2009), but contrast with others where responses differed between patterns of retention (Battaglia et al. 2002; Peck et al., 2012; Palik et al., 2003). It is important to highlight that unlike studies in longleaf pine ecosystems in the South (e.g., Palik et al., 2003) and red pine dominated forests in Minnesota (e.g., Peck et al., 2012) that involved underplanting of the target pine species as well as removal of understory species, our study relied on natural regeneration of red pine and eastern white pine following the harvest, with no pretreatment site preparation. As discussed above regarding the regeneration requirements of red pine and eastern white pine, natural regeneration responses following harvest treatments overall may not be the same as in cases where the target species are planted, and in some instances, advance regeneration of the two species could potentially benefit more as treatments that manipulate the overstory may release these established individuals.

More broadly, however, the land manager's decision on the use of different spatial retention patterns will be heavily determined by specific management objectives and site conditions. In mixed-pine forest ecosystems, we suggest that the relative similarity in initial response of different ecosystem components between retention patterns may provide managers with the flexibility to accommodate multiple management objectives, especially where such objectives are complimentary (for example in cases where restoration treatments also create diverse wildlife habitats). Further, Mitchell and Beese (2002) suggest that depending on the scale of treatment, there may be flexibility to implement both patterns within a stand or at the landscape level, especially where improving structural and spatial heterogeneity is desired.

3.6 Implications for management

Due to significant changes in species composition and stand structure, and high fuel accumulations in unmanaged, fire-dependent pine-dominated forest ecosystems across North America, the use of prescribed fire as a management tool may be limited. Within the northern Lake States, this situation is further complicated by limited information on fire effects for a variety of ecosystem components (Miesel et al., 2012). As restoration efforts within the region become increasingly focused on ecosystem management approaches (Corace et al., 2009; 2012), and the desire for and acceptance of ecological-based management objectives and strategies increases (Shindler et al., 2009; Wilson et al., 2009), emerging restoration techniques such as variable-retention harvesting provide opportunities to address a variety of restoration and management objectives.

Our study suggests that variable-retention harvesting may be a viable technique that offers opportunities to restore historically dominant pine species and address fire and fuel concerns in mixed-pine forests. It also offers opportunities to manage for wildlife habitat (for example by leaving snags during harvest) and manage for age-class and stand structure complexity (through a matrix of newly established seedlings in harvested gaps as well as residual trees). The implementation of variable-retention harvesting to achieve ecological management objectives, however, can benefit from a solid understanding of the natural disturbance regimes that historically shaped the dynamics of the specific ecosystem type, the silvics of species targeted for restoration and those targeted for removal, as well as stand development processes. Within the northern Lake States, application of variable-retention harvesting is in its initial phases. As a result, experimental studies will be critical to advancing our understanding of the viability of variable-retention harvesting to achieve both short-term and long-term management goals, especially in areas with large public forests that provide opportunities for implementation of treatments at larger spatial scales (Corace et al., 2012). This information will also be useful to land managers as they make decisions about appropriate techniques to implement so as to meet specific management objectives in specific areas, and potential trade-offs that may be warranted.

While our study contributes to understanding of initial regeneration-layer and ecosystem response to treatments, monitoring and continued assessment of the regeneration-layer dynamics and stand development over time would be useful. Longer-term monitoring will also facilitate assessments of the successional trajectories of the stands as they develop, especially as shifts occur between responses being strongly driven by the disturbance immediately post-treatment, and overstory effects becoming important as stands develop. Additional studies that examine impacts of treatment on different wildlife species and habitats, potential impacts on mortality of residual trees and soil disturbance, and continued monitoring of both live and down fuels within these stands will be needed. While variable-retention harvesting provides a management tool whose underlying concepts make it applicable to many altered forest ecosystems, its implementation will depend on specific management goals and objectives, and the expected ecological responses may vary depending on the characteristics of target species, as well as local variations in initial condition of the ecosystem. For example, while pine-dominated forest ecosystems within the Lake States are likely to have a number of similar characteristics, there may be a few differences in ecological or biological factors that influence stand dynamics at a local scale. This means that while the general guiding concepts may be similar and hence replicable in similar ecosystem types in other regions, treatments may be most effective when tailored to better suit the specific ecosystem type and the specific management objectives.

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Table 3.1 Characteristics of the stands used in the variable-retention harvesting study in mixed-pine forest ecosystems at Seney National Wildlife Refuge.

Treatment	Stand	Area (ha)	Area in gaps (ha)	% of stand in gaps
Aggregate	1	3.2	1.9	63.1
Aggregate	2	6.2	3.8	61.1
Aggregate	3	5.1	3.6	71.2
Dispersed	1	6.4	--	--
Dispersed	2	5.5	--	--
Dispersed	3	6.1	--	--
Control	1	5.7	--	--
Control	2	5.7	--	--
Control	3	5.7	--	--

Table 3.2 Species and factor groups used in the canonical correspondence analysis (CCA) ordination triplots. Nomenclature: http://plants.usda.gov/

Species		**Code**	**Factor groups (with measured variables)**	**Code**
Red pine	*Pinus resinosa* Ait.	PIRE	**Fuels**	
Eastern white pine	*Pinus strobus L.*	PIST	Coarse woody material (1000-hr fuels;tonnes/ha	CWM
Red maple	*Acer rubrum* L.	ACRU	1-hr fine woody material (tonnes/ha)	F_1H
Northern red oak	*Quercus rubra* L.	QURU	10-hr fine woody material (tonnes/ha)	F_10H
Quaking aspen	*Populus tremuloides* Michx.	POTR	100-hr fine woody material (tonnes/ha)	F_100H
Bigtooth aspen	*Populus grandidentata* Michx.	POGR	Litter (cm)	LT
Balsam fir	*Abies balsamea* (L.) Mill	ABBA	Duff depth (cm)	DD
			Live herbs and shrubs (tonnes/ha)	LHS
			Dead herbs and shrubs (tonnes/ha)	DHS
			Overstory characteristics	
			Canopy openness (%)	Can_open
			Red pine (IV)	PiRe
			Eastern white pine (IV)	PiSt
			Jack pine (IV)	PiBa
			Red maple (IV)	AcRu
			Northern red oak (IV)	QuRu

Table 3.3 Mean (±1SD) seedling densities (seedlings ha^{-1}) by treatment type of other tree species inventoried in study plots at Seney National Wildlife Refuge.

Species	**Aggregate**	**Dispersed**	**Control**
Red maple	6840 ± 8042	2395 ± 1783	1979 ± 2188
Northern red oak	1076 ± 977	1631 ± 1591	659 ± 1163
Quaking aspen	694 ± 1436	1041 ± 2923	--
Bigtooth aspen	520 ± 964	2673 ± 3566	69 ± 294
Balsam fir	243 ± 887	--	486 ± 1912
Black spruce	--	--	381 ± 861

Table 3.4 Mean (±1SD) percent cover by treatment of ground-flora species (herb and shrub) species inventoried in study plots ($16 m^2$ plots) at Seney National Wildlife Refuge.

Species (herbs)		**Aggregate**	**Dispersed**	**Control**
Bracken fern	*Pteridium aquilinum* (L.) Kuhn	39.3 ± 15.4	27.8 ± 16	39 ± 19
Bunchberry	*Cornus canadensis* L.	1.5 ± 3.7	0 ± 0	0.2 ± 0.5
Starflower	*Trientalis borealis* Raf.	0.9 ± 1.4	0.2 ± 0.3	0.1 ± 0.3
Canada mayflower	*Maianthemum canadense* Desf.	0.3 ± 0.9	0 ± 0	0.1 ± 0.2
Cowwheat	*Melampyrum lineare* Desr.	0.2 ± 0.5	0.3 ± 0.7	0.1 ± 0.2
Sheep sorrel	*Rumex acetosella* L.	0 ± 0	0.3 ± 1.2	0 ± 0
Species (shrubs)				
Lowbush blueberry	*Vaccinium angustifolium* Aiton	15.8 ± 12.5	25.9 ± 20	17.9 ± 11.4
Velvet-leaf blueberry	*Vaccinium myrtilloides* Michx.	9.2 ± 13.5	6.7 ± 13.5	10.2 ± 11.1
Wintergreen	*Gaultheria procumbens* L.	4.8 ± 5.5	3.0 ± 2.1	4.2 ± 3.9
Black huckleberry	*Gaylussacia baccata* (Wangenh.) K. Koch	2.6 ± 6.6	3.7 ± 8.8	0 ± 0
Sand cherry	*Prunus pumila* L.	0.6 ± 1.1	0.3 ± 0.4	0.3 ± 0.8
Sweetfern	*Comptonia peregrina* (L.) J.M. Coult.	0.7 ± 2.1	0 ± 0	0.2 ± 0.9
Bush honeysuckle	*Diervilla lonicera* Mill.	0 ± 0	0 ± 0	0.6 ± 2.4
Trailing arbutus	*Epigaea repens* L.	0.1 ± 0.3	0 ± 0	0.4 ± 1.2
Running serviceberry	*Amelanchier stolonifera* Wiegand	0 ± 0	0.1 ± 0.2	0.1 ± 0.1
Downy serviceberry	*Amelanchier arborea* (Michx. f.) Fernald	0.1 ± 0.3	0.1 ± 0.3	0 ± 0
Labrador tea	*Ledum groenlandicum* Oeder	0 ± 0	0 ± 0	3.1 ± 9.2
Leatherleaf	*Chamaedaphne calyculata* (L.) Moench	0 ± 0	0 ± 0	0.4 ± 1.1

Table 3.5 Mean (±1SD) litter biomass loss and C:N ratio by treatment for red pine needles and mixed-hardwood leaves for each deployment interval (days) at Seney National Wildlife Refuge.

	Percent biomass loss (Needles)			**Percent biomass loss (Leaves)**		
Duration (days)	**Aggregate**	**Dispersed**	**Control**	**Aggregate**	**Dispersed**	**Control**
30	9.6 ± 4.4	12.4 ± 5.5	14.2 ± 3.8	19.3 ± 5.6	20.9 ± 3.7	20.9 ± 5.8
230	21.9 ± 12.1	22.7 ± 10.3	20.9 ± 9.6	33.1 ± 6.7	32.1 ± 2.9	32.1 ± 6.1
300	25.5 ± 8.8	20.2 ± 10.1	26.9 ± 7.9	41.6 ± 7.7	47.5 ± 6.9	38.9 ± 7.1
365	28.4 ± 8.1	24.5 ± 8.9	28.9 ± 8.6	42.2 ± 7.8	46.8 ± 9.4	45.5 ± 10.2
	C:N ratio (Needles)			**C:N ratio (Leaves)**		
30	46.7 ± 0.7	45.6 ± 0.7	46.0 ± 0.4	57.8 ± 7.2	58.8 ± 4.1	49.9 ± 10.2
230	41.9 ± 2.62	22.7 ± 10.3	40.4 ± 0.5	42.7 ± 3.5	45.1 ± 2.7	43.9 ± 1.6
300	39.9 ± 1.8	20.2 ± 10.1	38.2 ± 0.8	39.4 ± 3.2	38.3 ± 3.3	41.6 ± 1.4
365	38.9 ± 2.0	24.5 ± 8.9	36.9 ± 0.8	39.9 ± 4.7	38.4 ± 3.4	40.3 ± 1.8

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Figure 3.1 Ground-level view of the aggregate retention harvest treatment showing the gaps created within the residual stand (A), and dispersed retention harvest treatment showing the uniform distribution of retained trees (B) in mixed-pine forests at Seney National Wildlife Refuge.

Figure 3.1 continued

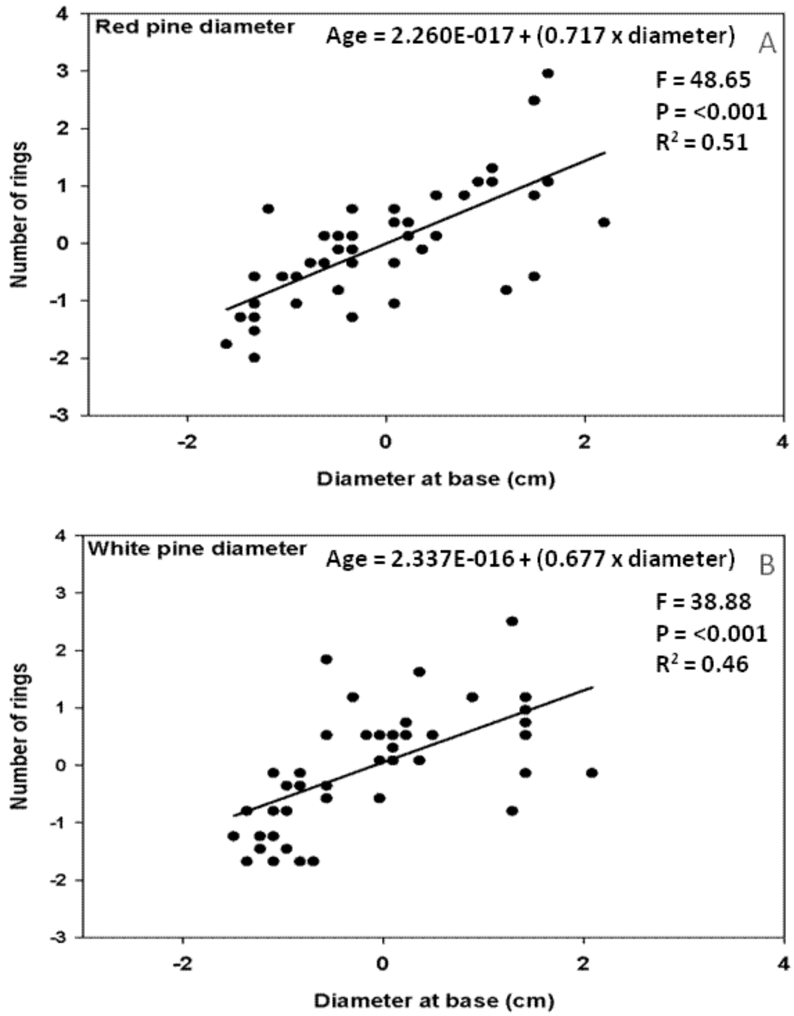


Figure 3.2 Regression models and equations relating diameter at the base to age for red pine (A) and eastern white pine (B) at Seney National Wildlife Refuge.

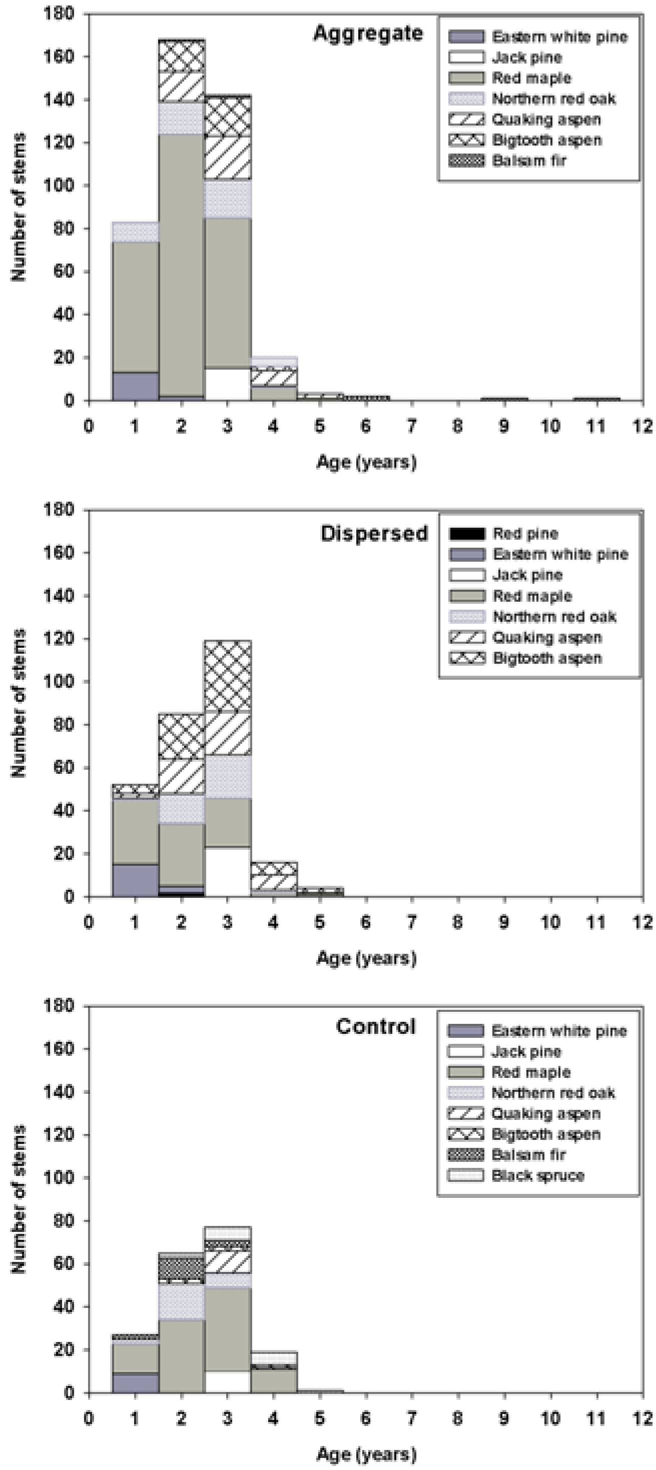


Figure 3.3 Age distribution of all seedlings (stems < 2.5cm dbh) for each tree species inventoried in the aggregate, dispersed and control stands at Seney National Wildlife Refuge.

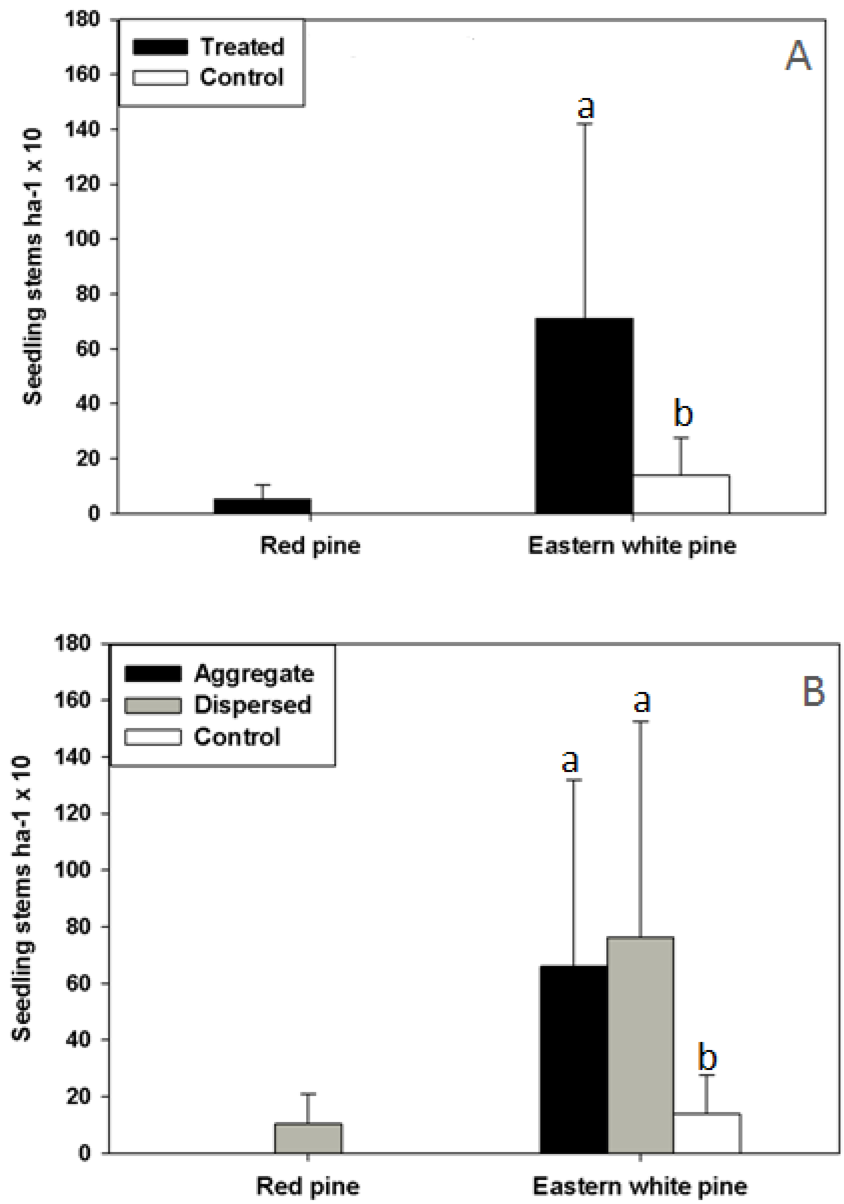


Figure 3.4 Seedling densities (seedlings ha^{-1}) of target species (red pine and eastern white pine between treated and control (A), and among spatial patterns and control (B). Similar letters within each group of bars indicate no significant difference ($P > 0.05$) between individual bars within the group.

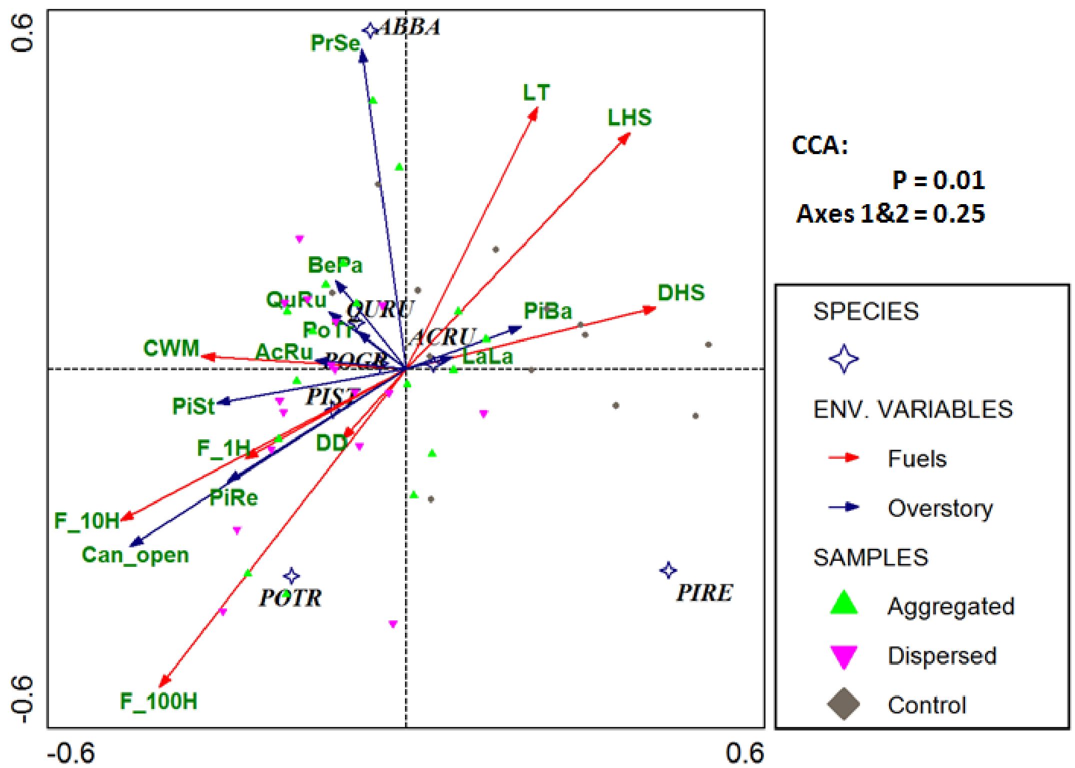


Figure 3.5 Canonical correspondence ordination of the relationship between seedlings (species coded in capital and *italicized*), overstory characteristics (species coded in mixed lower and upper case letters and canopy openness), and fuels (CWM, F_1H, F_10H, F_100H, LT, DD, LSH, DSH). The variables and codes used in the graph are described in Table 3.2.

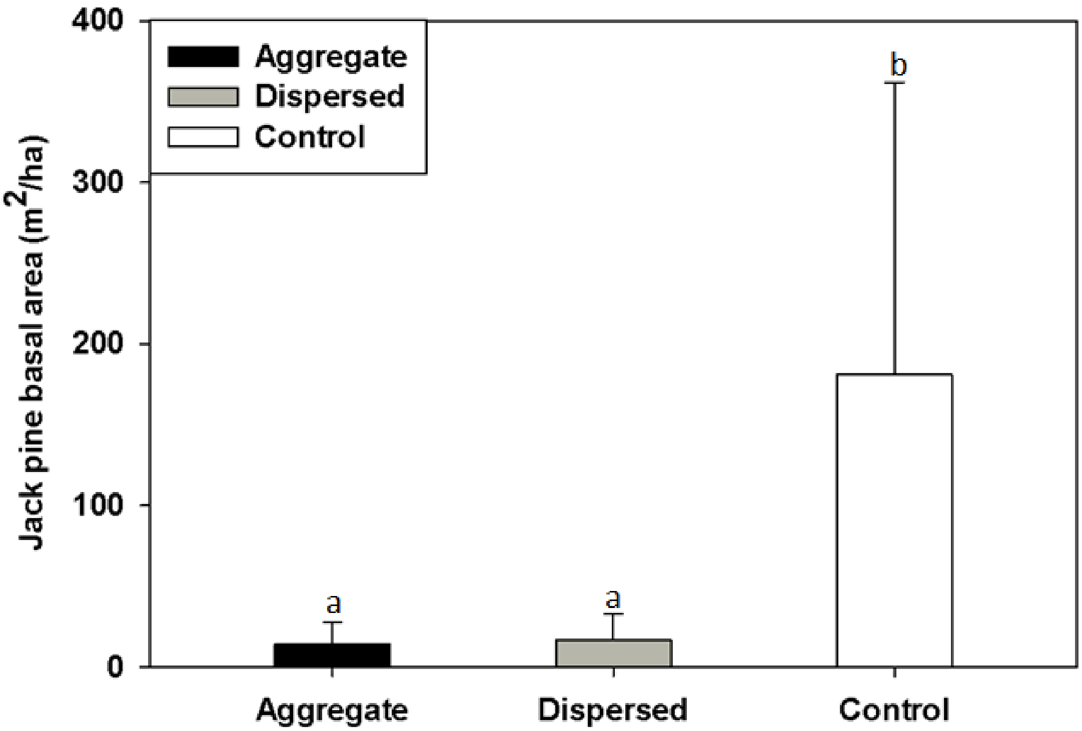
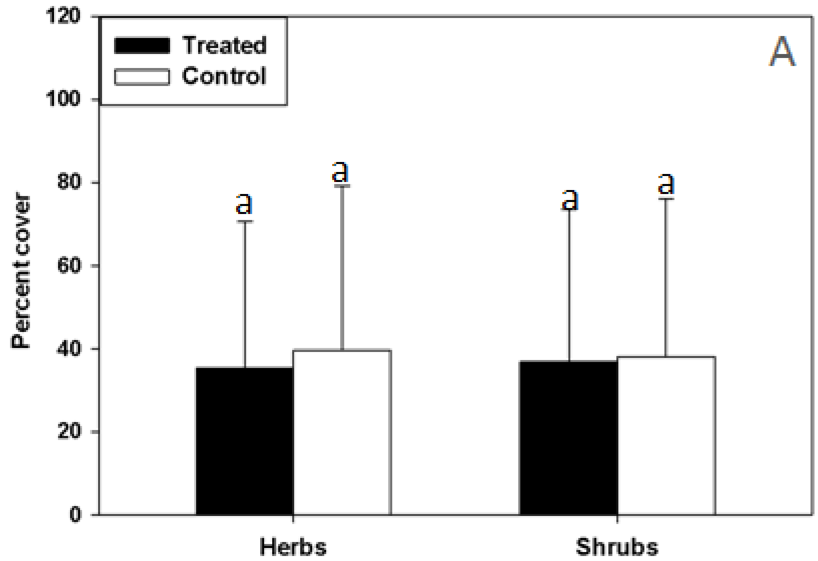


Figure 3.6 Live jack pine overstory basal area ($m^2\ ha^{-1}$) in harvested (aggregate and dispersed retention patterns) and control stands. Similar letters within each group of bars indicate no significant difference ($P > 0.05$) between individual bars within the group.



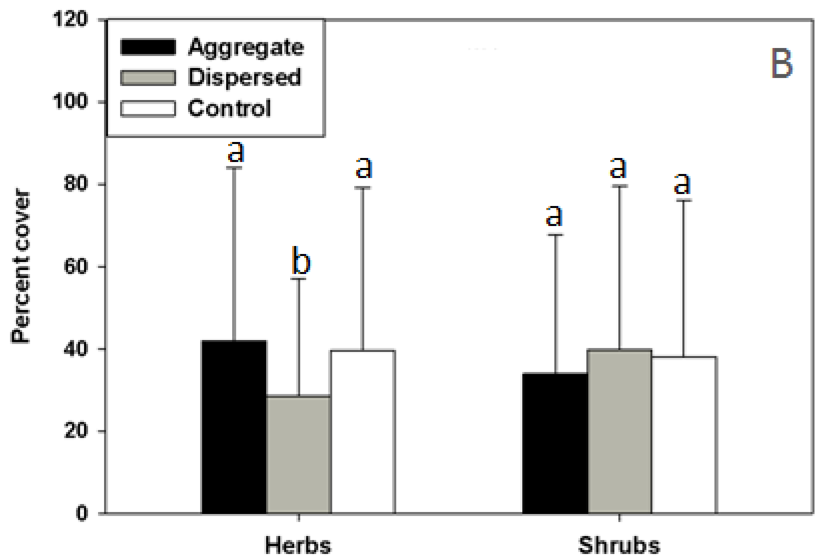


Figure 3.7 Estimated percent cover of ground-flora between treated and control (A), and among spatial patterns and control (B). Similar letters within each group of bars indicate no significant difference ($P > 0.05$) between individual bars within the group.

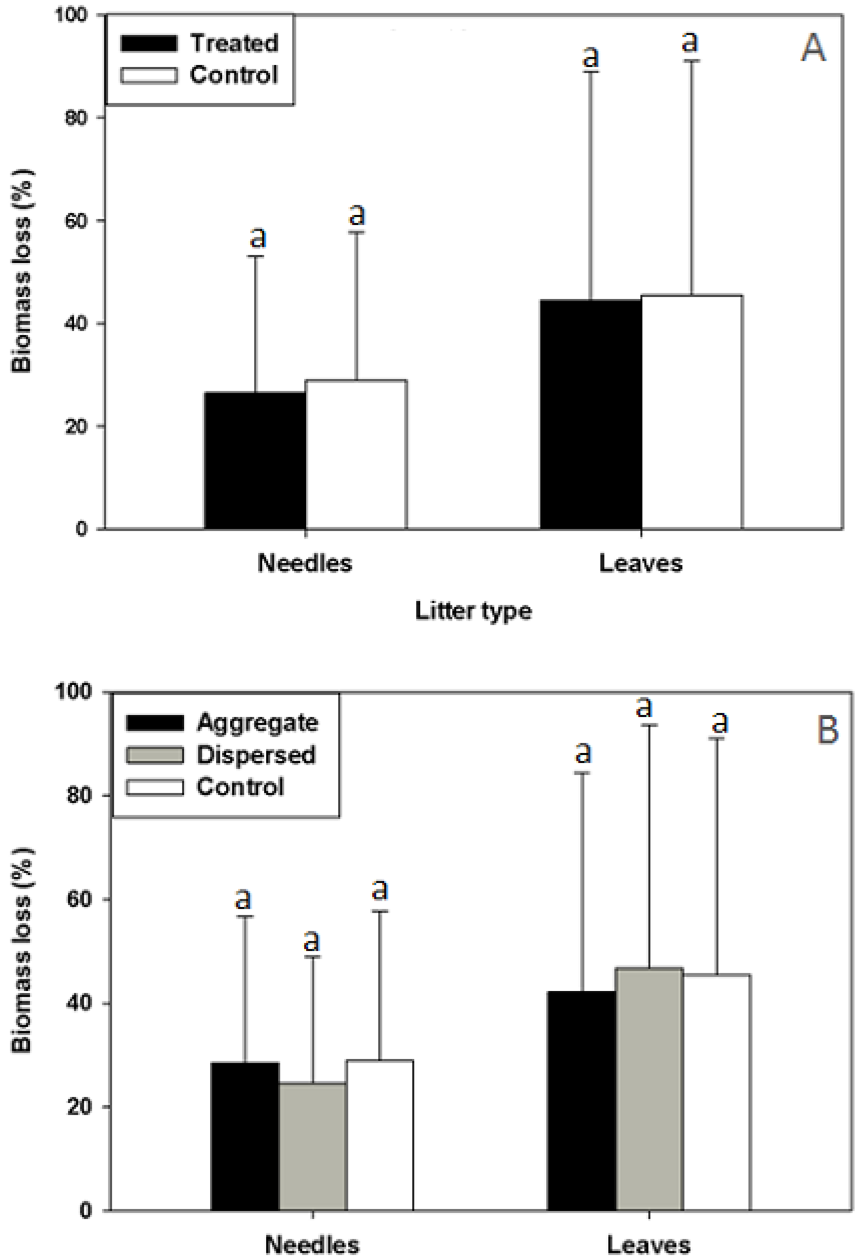


Figure 3.8 Percent biomass loss between treated and control (A), and among spatial patterns and control (B). Similar letters within each group of bars indicate no significant difference ($P > 0.05$) between individual bars within the group.

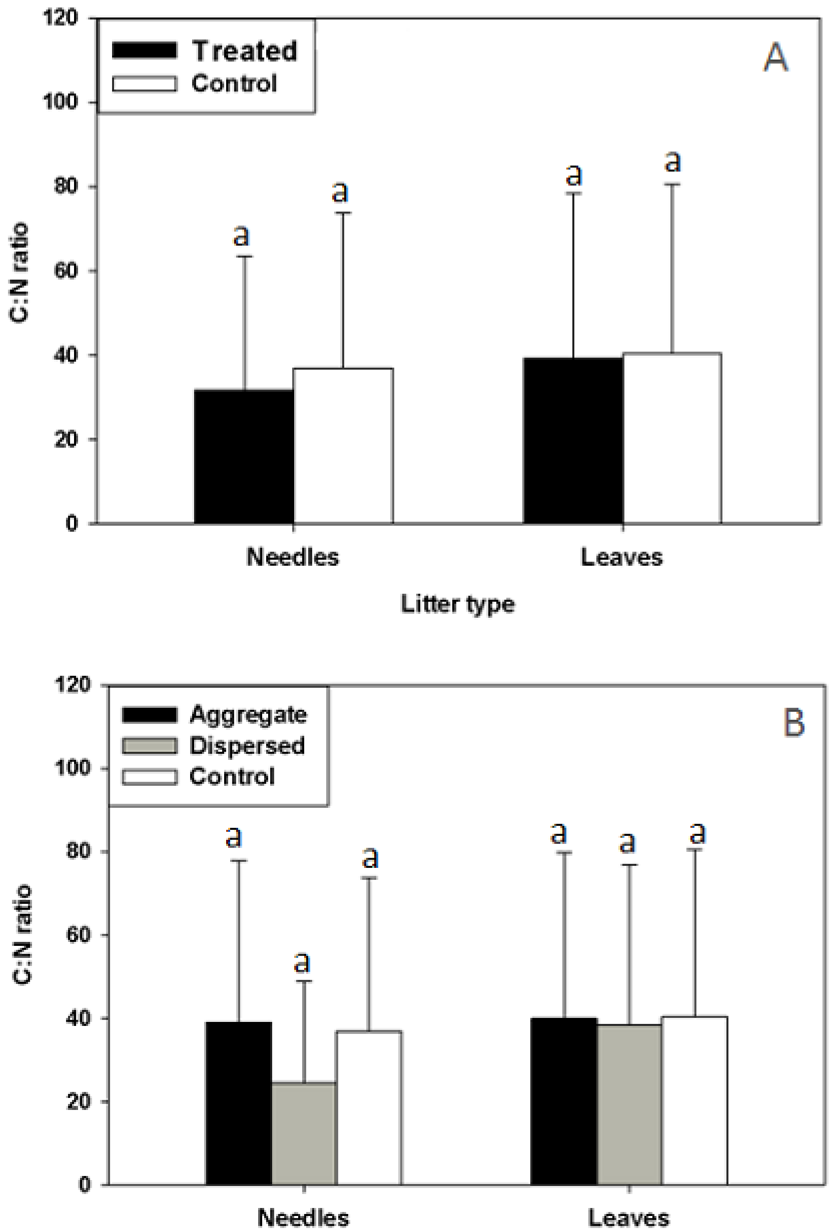


Figure 3.9 C:N ratio between treated and control (A), and among spatial patterns and control (B). Similar letters within each group of bars indicate no significant difference ($P > 0.05$) between individual bars within the group.

Chapter 4: Factors influencing regeneration dynamics along an age gradient following harvest treatments in mixed-pine forest ecosystems of eastern Upper Michigan.

4.1 Abstract

Poor natural regeneration of red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.) in mixed-pine forest ecosystems across the northern Lake States has become a major concern for land managers. Besides changes to the natural fire regime, factors related to current stand conditions, including seed source limitations, overstory influences and competition from other woody species and the ground-flora have been attributed to the poor regeneration of these historically dominant pine species. Although restoration efforts are underway to improve natural regeneration of the target species (red pine and eastern white pine) in these ecosystems, additional efforts to examine factors affecting regeneration dynamics post-treatment as part of adaptive management strategies are needed. To better understand how these different factors influence regeneration-layer dynamics following harvest treatments, we examined three mixed-pine stands harvested in 1992, 2004 and 2007 respectively at Seney National Wildlife Refuge in eastern Upper Michigan. Specifically, we addressed the following questions: Are greater red pine and eastern white pine seedling and sapling densities associated with 1) areas close to potential seed trees? 2) areas with lower overstory density and overstory basal area, and low importance values of species other than red pine and eastern white pine? 3) areas with greater canopy openness? 4) areas characterized by greater harvest volumes and larger gap sizes, and 5) areas with less cover of ground-flora (herbs and shrubs)? Although we found most red pine and eastern white pine seedlings between 6-10 m from potential seed tree, we did not find significant patterns of increasing seedling densities with decreasing distances to potential seed tree. Overstory characteristics indicated a stronger influence on regeneration in all three stands, with decreasing seedling and sapling densities in areas with greater overstory density and basal area, and greater

dominance of other species other than the red pine and eastern white pine in the overstory. Seedling and sapling densities exhibited a negative relationship with canopy openness overall, and we only found high sapling densities in areas with greater canopy openness in the 2004 stand. Similarly, we observed high sapling densities of the target species in areas with greater harvest volumes in the 2004 and 1992 stands, while the seedling densities indicated a negative relationship with harvest volumes in all the three stands, findings we attribute to potential negative influence of slash on the seedbed. Regeneration of target species also did not increase with harvested patch size, but we found support for increasing seedling and sapling densities with less herb and shrub cover, suggesting that the ground-flora may have gained a competitive advantage in the harvested patches. Our findings and suggested management implications provide important feedback information to land managers that may be useful for adaptive management and making assessments about stand development at a given temporal scale post-treatment.

4.2 Introduction

Prior to EuroAmerican settlement, red pine and eastern white pine were the dominant tree species in the mixed-pine forest ecosystems of the northern Lake States (Drobyshev et al., 2008b; Gilmore and Palik, 2006; Whitney, 1987). In eastern Upper Michigan, this forest type was maintained by frequent mixed-severity, late season surface fires with a mean fire return interval (FRI) of 32.7±19.2 years (Drobyshev et al., 2008a). It is believed that this fire regime promoted natural regeneration of red pine and eastern white pine by exposing mineral seedbeds and reducing competition from other vegetation (Ahlgren, 1976; Carey, 1993; Heinselman, 1981). However, the large-scale logging operations that occurred from 1860 to 1910 favored removal of red pine and eastern white pine for sawtimber and, reduced the dominance of the two species (Drobyshev et al., 2008b; Losey, 2003; Rist, 2008; Schmidt, 2002; Stearns, 1997). The slash left behind from the harvesting contributed to high fuel loads that facilitated severe fires in many areas, significantly altering the soil chemistry in some areas with possible adverse implications for future regeneration of these pine species (Barrett, 1998; Heinselman, 1973; Losey, 2003; Whitney, 1987). Changes to the natural fire regime, including fire suppression, likely favored regeneration of fire-sensitive deciduous species such as red maple (*Acer rubrum* L.). Subsequent management activities (e.g., clearcutting) likely promoted fire-adapted short-lived species such as jack pine (*P. banksiana* Lamb) which now dominate many of these sites (Corace et al., In Press; Drobyshev et al., 2008b; Rist, 2008).

In response to the subsequent changes in structure and composition of mixed-pine forest ecosystems in the northern Lake States, land managers are increasingly focusing on ecologically-based restoration efforts designed to improve conditions for regeneration of red pine and eastern white pine, among other objectives (Corace et al., 2009; Palik et al., 2005). While the reintroduction of fire with characteristics that resemble those of the historical regime may be the long-term management objective (Neumann and Dickmann, 2001: Wilson et al., 2009), significant fuel accumulations in these ecosystems present challenges to immediate use of fire as a restoration tool (Corace et al., 2009; Corace et al., In Press). Other restoration techniques that emulate natural disturbance processes have, therefore, been proposed to improve not just the regeneration of target species, but also the structure and composition of these stands (Corace et al., 2009; Franklin et al., 2007; Palik and Zasada, 2003). Among the objectives of such efforts are to ensure that the target species are in a position to benefit when fire is reintroduced, in addition to enhancing the adaptive capacity and resilience of the ecosystem to disturbance events (Gunderson, 2000). Many of these techniques involve harvesting treatments that aim to improve regeneration of target species, reduce fuel loadings, improve stand structural complexity, and enhance forest functional processes such as provision of wildlife habitat (Atwell et al., 2008; Bebber et al., 2004, 2005; Palik et al., 2005; Peck et al., 2012).

In order to achieve specific harvest treatment objectives, land managers need a better understanding of how both disturbances and stand-related factors potentially drive the regeneration dynamics of target species, and how these factors can be manipulated by management practices. For red pine and eastern white pine, this means more information on factors related to fire history as well as current stand characteristics (see Chapter 2), particularly those factors that may be directly influencing regeneration processes of the two species at the stand level. Although logging era activities led to severe declines in mature red pine and eastern white pine that could have served as seed trees (Whitney, 1987), there is evidence that remnant pine trees, as well as mature trees left following more recent harvesting activities, can play an important role in natural regeneration of red pine and eastern white pine (Ahlgren, 1976; Palik and Pregitzer, 1994). It has, however, been suggested that the distance from the seed sources may impact the successful regeneration of these species in the stand (Peck and Zenner, 2009; Weyenberg et al., 2004), and would be an important consideration for land managers when making harvesting prescriptions. Species composition and structural characteristics of the overstory might also influence not just the germination and early establishment of red pine and eastern white pine, but also the recruitment of saplings into the overstory (Dovciak et al., 2003; Peck and Zenner, 2009). Additional factors that may also affect the regeneration-layer dynamics include competition from other plants in the understory community (Ahlgren, 1976; Weyenberg et al., 2004), light availability (Rudolf, 1990), and characteristics of the gaps to be colonized (Peck et al., 2012; Powers et al., 2008).

Examining these factors as potential drivers of the regeneration dynamics and spatial patterns of target species is critical to advancing the knowledge needed to design and implement restoration strategies that best address specified management objectives. Going a step further, however, and examining potential roles of the same factors in stands that have experienced such harvest treatments is additionally key to providing feedback to land managers that may be useful for adaptive management and making assessments about stand development at a given temporal scale post-treatment. In this study, we explore the role of a number of factors related to current stand characteristics on the natural regeneration and spatial patterns of red pine and eastern white pine seedlings and saplings to elucidate the important factors driving the regeneration dynamics in three previously harvested mixed-pine stands. We suggest that seed source limitations, overstory influences, characteristics related to amount of material harvested and resulting gap sizes, and competition from ground-flora may be important factors driving the regeneration of red pine and eastern white pine in these previously harvested mixed-pine forests.

Specifically, we hypothesize that greater regeneration of red pine and eastern white pine will be associated with 1) areas close to potential seed trees, 2) areas with lower overstory density and overstory basal area, and low importance values for species other than red pine and eastern white pine, 3) areas with greater canopy openness, 4) areas that had higher harvest volumes and larger gap sizes, and 5) areas with less cover of ground-flora (herbs and shrubs). To test these hypotheses, we, examined the influence of current stand characteristics on the regeneration-layer (seedlings and sapling) dynamics in three stands harvested at different times in the past 20 years: one harvested in 1992; one in 2004; and a third in 2007 (Table 4.1; Figures 4.1 A, B, and C). Specifically, we quantified seedling and sapling densities in each stand, and then related these densities to potential correlates to regeneration, including 1) distance from observed seedling to nearest potential seed tree, 2) overstory basal area, 3) overstory density, 4) importance values of species in the overstory 5) percent canopy openness, 6) volume of material harvested, 7) gap size following harvesting, and 8) percent ground-flora (herb and shrub) cover.

4.3 Methods

Study area

This study was conducted within the 38,542-ha Seney National Wildlife Refuge (SNWR) (N46.271594◦ W86.057078◦), Schoolcraft County, Michigan, U.S.A. SNWR lies within the Seney Lake Plain ecoregion and characterized by soils and physiographic features that resulted from postglacial erosion and soil formation processes (Albert, 1995). Two major landforms dominate the landscape: glacial outwash channels and a patterned fen matrix interspersed by sand ridges (Heinselman, 1965). The soils range from poorly drained peats to excessively drained coarse, sandy soils, on which mixed-pine stands are found. The climate is influenced by it close proximity to the Great Lakes. Temperatures vary between a minimum of -9 ^{o}C in the coldest month (January) to 30 ^{o}C in the warmest month (July), and the average annual precipitation is 78 cm, with most of the precipitation falling in the form of snow (MRCC, 2013). The length of the growing season averages 119 days, and the average daily humidity during spring and fall varies between 50 and 60%.

The landscape of SNWR is composed of a mosaic of upland and lowland forests, and wetland vegetation (USFWS, 2009). The mixed-pine forests where historically dominated by red pine and eastern white pine (Drobyshev et al., 2008b: Zhang et al., 2000). Regeneration of red pine and eastern white pine have been negatively affected by greater time lags between fires, as well as by occasional severe fires and management practices (e.g., clearcutting) that are thought to have favored regeneration of jack pine over the other two pine species (Drobyshev et al., 2008b; Rist 2008). Consequently, in addition to increases in fire-sensitive deciduous species, there is a significant component of 40-60 year old mature jack pines in the overstory of most of the current stands, which through both live and down fuels, may contribute to the potential risk of severe fires (Corace et al 2009; Corace et al., In Press).

Description of stands

As part of ecosystem management activities at SNWR (USFWS, 2009), harvesting treatments have been implemented in some of these stands for a variety of objectives, including restoration. Forest management at SNWR in the last 10 years or so has been more ecologically based with greater focus on ecosystem management approaches (Corace et al., 2009). Consequently, restoration treatments were implemented in a 173-ha stand in 2007 (hereafter referred to as 2007 stand; Figure 4.1A, Appendix B) and in a 114.5-ha stand in 2004 (hereafter referred to as 2004 stand; Figure 4.1B, Appendix C), both with the objectives of reducing live fuels, promoting safer fire management, and creating favorable conditions for regeneration of red pine and eastern white pine (Table 4.1). Both harvests were regeneration methods, targeting retention of red pine and eastern white pine seed trees, but with an additional fuel reduction component where jack pine was specifically targeted for removal during harvesting. Earlier forest management strategies, however, were more focused on managing forests for single wildlife species, and harvesting types were designed to help meet these single-focus management objectives (Rist, 2008). One such harvest treatment was initiated in 1992, specifically a seed tree harvesting of a 16 ha stand (hereafter referred to as 1992 stand; Figure 4.1C, Appendix D) to improve regeneration and release of northern red oak (*Quercus rubra* L.) and improve acorn production, with the objective of expanding the winter food base for a variety of wildlife species (unpublished report; Table 4.1). Overall, the harvesting objectives in the three stands were different and so were the species targeted for retention or removal. In the 2004 and 2007 stands, species (e.g., jack pine, black spruce (*Picea mariana* (Mill.) BSP, and red maple) were prioritized for harvest, while all mature red pine and eastern white pine were retained. In the 1992 stand on the other hand, species other than northern red oak (e.g., red pine, eastern white pine, and jack pine) were prioritized for removal.

Experimental design

In order to determine the harvested areas of each stand, we used aerial images dated as close to the harvest year of each stand as possible. Specifically, we used a 2009 aerial image for the 2007 and 2004 stands, and a 1996 aerial image for the 1992 stand. Using ArcGIS (ArcGIS 9.3, 2008), we delineated the harvest boundaries to produce polygons of harvest areas from each of the three stands (Appendix B, C, D). We then overlaid a 100m by 100m grid over the harvest area polygons from the 2007 and 2004 stands, and a 50m by 50m grid over the harvest area polygon from the 1992 stand (because the 1992 stand was relatively smaller in size, Table 4.1). Grid intersections were numbered sequentially as potential sample plot locations, and then further stratified in GIS by habitat type using Burger and Kotar (2003) habitat type classification. In order to minimize potential environmental variation in each stand, we randomly selected a total of 15 points in each stand that were classified as having similar landform type, soils and *Pinus-Vaccinium-Epigaea* (PVE) plant association (Burger and Kotar, 2003). At each selected point, we established a 25-m^2 (5 m by 5 m) permanent sample plots to collect regeneration-layer and ground-flora data, for a total of 15 plots in each stand (Appendix B, C, D).

Vegetation sampling

Within each 25-m^2 sample plot, four 4-m^2 (2 m by 2 m) quadrats were used to quantify woody seedlings and estimates of ground-flora (vascular plants defined as a herb or shrub by PLANTS database (USDA 2013) and < 1 m tall, excluding tree seedlings) cover, allowing for a 1-m buffer through the plot center in each cardinal direction to minimize trampling vegetation within the quadrats during sampling. Within each quadrat, seedling counts of all woody seedlings (stems < 2.5 cm dbh and no height limits) were recorded, including the basal diameter (measured at the root collar), height, number of whorls for pine species, and number of terminal bud scars for deciduous species (we used these metrics, along with regression models developed in Chapter 3 to determine the age of seedlings and saplings). For deciduous species that exhibited sprouting such as red maple, each individual sprout was counted separately. Within each quadrat, we also visually estimated the percent cover of ground-flora species (herbs and shrubs) using the following cover classes: 1), < 1%; 2), 1-5%; 3), 6-10%; 4), 11-20%; 5), 21-40%; 6), 41-600%; 7), 61-80%; and 8), 81-100%. All plants that were rooted outside but whose cover extended into the quadrats were included in the cover estimates. Additionally, from the center of each sample plot, we established a 400m^2 circular plot within which we recorded counts of saplings (stems 2.5-10.0 cm dbh) of all tree species. To characterize the overstory composition associated with each sample location, the species and diameter at breast height (1.37 m above the ground) of all living trees (stems > 10.0 cm dbh) within the sample plot were recorded within a 400-m^2 circular plot established from the center of the sample plot. The overstory consisted of trees of all crown classes (dominant, codominant, intermediate and overtopped). All plants encountered in sample plots were identified, and taxonomic authorities followed the PLANTS database (USDA 2013).

Field procedures for correlates to regeneration

To obtain distance to the nearest potential seed tree, we measured the distance from where each red pine and eastern white pine seedling was observed within the sample plot to the nearest seed tree that that may have served as a seed source. Red pine begins to produce viable seeds at about 12-15 years of age (Rudolf, 1990) and eastern white pine at 5-10 years (Wendel and Smith, 1990). Thus, we determined potential seed trees by counting the number of whorls in the identified seed tree, to ensure that it was within these age ranges at the time of harvest of each of the stands. Seedlings were selected for the distance analysis because it has been suggested that the correlation between distances to seed tree with seedling densities may be stronger than that with older regeneration such as saplings (Palik and Pregitzer, 1994). At the center of each sample plot, we collected digital hemispherical photographs at 1 m above the ground using a fisheye lens mounted on a Nikon 8400 digital camera. We then used the WinSCANOPY digital image processing software (Regent Instruments Inc., Chemin Saint-Foy, Quebec) to estimate the proportion of the canopy that is open (percent canopy openness)

To determine how much material was removed during harvesting, we reconstructed the total volume by using cut stumps observed around each sample plot, and presumed to be those from harvesting. Specifically, we established a 1000-m^2 circular plot from the center of each regeneration-layer sample plot, and recorded the species and diameter at 30 cm above the ground of each stump within the plot. We then used established volume calculations equations to determine the volume of material harvested around each of the regeneration-layer sample plots. Additionally, unlike in the 2007 and 1992 stands where the harvesting pattern was more dispersed, the harvesting pattern in the 2004 stand followed a more of an aggregate removal pattern, which allowed for identification of distinct harvested patches around the location of each sample plot (Figure 4.1B). As a result, in the 2004 stand, we measured the size of each gap around each plot location by holding a hand-held GPS device from a start point at the edge of the patch, and recording the area of the gap while walking its perimeter.

Statistical analyses

To determine whether seedlings and saplings originated prior to or after the harvest treatment, we determined the age of each seedling and sapling using equations developed in Chapter 3 for pine species, and by counting the terminal bud scars for deciduous species. As a result, all seedlings and saplings used in the current analyses are those that were determined to have been recruited post-harvest in each of the three stands.

Tree seedling and sapling densities as well as ground-flora (herbs and shrubs) cover for each species was summarized by plot and densities expressed on a per hectare basis.

To determine the volume of material removed, we used a stepwise process using published equations to obtain, the dbh of the cut tree from measured stump diameters at 30 cm from the ground, then height, and finally volume. Specifically, measured diameters were used to calculate dbh (dbh converted from cm to in) using equations from Wharton (1984; Tables 2 and 3):

$$Y = a + bx \qquad \text{(Eq1)}$$

where Y=tree diameter at breast height in inches, x=stump diameter in inches at 30cm above ground, and *a* and *b* are coefficients from Tables 2 and 3.

Next, we obtained tree height using the following equation from Hahn (1984; Equation 2 and Table 1):

$$Height= 4.5 + b_1 (1-e^{(-b2D)})^{b3} \, x \, S^{b4} \, x \, T^{b5} \, xB^{b6} \qquad \text{(Eq 2.)}$$

Where:

Height = tree height (total height from base of stem to crown top)

D = diameter breast height (in; from Eq 1 above)

E = base of natural logarithm

S = site index (species specific)

T = (1.00001, for total height)

B = stand basal area

b_1-b_6 = coefficients from Table 1

Finally, we calculated volume using the following equation from Hahn (1984 Equation 1 and Table 2)

$$V = b_0 + b_1 D^2 H \qquad \text{(Eq 3)}$$

where:

D =diameter breast height (from Eq 1 above), H= height (from Eq 2 above), and b_1 and b_2 are coefficient from Table 2 in Hahn (1984).

Importance values of each tree species in the overstory were calculated using relative density and relative dominance. Relative density (as a percentage) was calculated by summing the total density of a species on a plot, divided by the total density of all species in the plot, and multiplying by 100. Relative dominance (as a percentage) was calculated in a similar manner, but substituting basal area for density. Importance values were then calculated by summing relative density and relative dominance, and then dividing by two

To explore patterns in seedling and sapling species composition, we related red pine and eastern white pine seedling and sapling densities with measured stand characteristics using principal component analysis (PCA) in a similar fashion as Palik and Pregitzer (1994). Limitations imposed by the number of predictor variables (12 in this case) relative to the number of samples (15 for each stand), and susceptibility to multicollinearity precluded the use of multiple linear regression. PCA is a multivariate statistical technique that reduces the dimensionality of a dataset by reducing a large set of predictor variables into a smaller set that accounts for most of the patterns observed in the response variable (Quinn and Keough, 2002). From the large initial set of predictor variables, the process generates fewer uncorrelated orthogonal variables called principal components (PCs), each of which is associated with a single or linear combinations of the original predictor variables. A predictor variable is associated with a PC through factor loadings, the amount of variation accounted for by the predictor variable along that PC. As a result, the higher the factor loading of a predictor variable along a PC, the more associated the variable is with that PC (Table 4.1). PCA is a robust technique in cases where there may be collinearity between the original predictor variables, making it necessary to reduce the variables to a few linear combinations that explain most variation along a given component. Additionally, only subsequent regression with selected PCs assumes a multivariate normality.

We performed PCA analyses on correlation matrices of untransformed stand characteristics variables to examine their association with each PC. The stand characteristics variables used as predictor variables in the PCA were: 1) overstory basal area, 2) overstory density, 3) importance values of species in the overstory, 4) percent canopy openness, 5) volume harvested, 6) harvested gap size (for the 2004 harvest), and 7) ground-flora (herb and shrub) cover. Because up to eight PCs were generated, the decision on the number of PCs to retain for interpretation was based on the recommendations by Norman and Streiner (1994), i.e., only PCs with an eigenvalue greater than 1.0 retained. The retained PCs were then used in a regression model as predictor variables to predict red pine and eastern white pine seedling and sapling densities and spatial distributions. The correlations between the selected PCs with the response variables were used to make inferences about the associations between the stand characteristics and seedling and sapling densities. Pearson's correlation coefficients (r) were used to assess the strength and direction of association between PC and seedling or sapling densities. The strength of correlation were described as follows based on the values of the correlation coefficient: $r < 0.25$ as weak; r between 0.25-0.35 as moderate; and $r > 0.35$ as strong.

Due to the difference in number of observations for the variable distance to seed tree (where zero observation means no data) compared to other predictor variables (where zero observation means zero), we used a simple linear regression to examine the relationship between distance from seed tree and seedling densities. Further, it has been suggested there may be an effective distance from seed tree to the germination site that is likely to be optimal for regeneration of red pine (Rudolf, 1990). As a result, to investigate the distributional patterns of seedling occurrences with distances from seed trees, we classified the number of red pine and eastern white pine seedlings into distance classes. All analyses were conducted in R (R version 2.10.).

4.4 Results

The 2007 stand

Although there are no optimum densities recommended for naturally regenerating unmanaged mixed-pine stands that we know of within the northern Lake States, seedling densities of 988-2224 seedlings ha^{-1} have generally been recommended to establish plantations in the northern Lake States (Gilmore and Palik, 2006). We use these guidelines as references in this study, although these guidelines do not adequately represent unmanaged stands, and often do not consider a variety of other factors (e.g., are not based on natural range of variability, and have issues related to growth rates related to different site conditions). That being said, we observed low densities (mean (±1SD) seedling ha^{-1}) of red pine in both the seedling (41 ± 161), and sapling (208 ± 385) layers (Table 4.2). We, however, observed high densities of eastern white pine seedlings and saplings. High densities of jack pine were also observed in both the seedling and sapling layers. Additionally, high densities of red maple and northern red oak were observed in the seedling layer (Table 4.2). The most common ground-flora species were lowbush blueberry (*Vaccinium angustifolium* Aiton), velvetleaf blueberry (*Vaccinium myrtilloides* Michx.*)*, Wintergreens (*Gaultheria procumbens* L.), and black huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch) in the shrub layer, and mostly bracken fern (*Pteridium aquilinum* L.) in the herbaceous layer (Table 4.3). Northern red oak had the highest basal area in the overstory with a mean (±1SD) of 6.4 ± 3.5 m^2/ha, followed by red pine with 4.3 ± 3.8 m^2/ha (Table 4.4). Jack pine was surprisingly dominant in the overstory with an importance value (as a percentage) of 52± 48 followed by red pine with 29 ± 38 (Table 4.4).

Principal component analysis of stand characteristics variables

The PCA using the correlation matrix of stand characteristics indicated that the first four principal components (PCs) accounted for 80% of the total variation among plots. Based on the factor loadings contributed by stand variables (Table 4.5), PC1 was positively associated with overstory basal area, overstory density and high importance values for red maple, and negatively associated with shrub and herbaceous cover, suggesting that plots associated with this axis were mainly influenced by species in the overstory and understory. PC2 showed a positive association with high importance values for jack pine, herbaceous cover and canopy openness, and a negative association with high importance values for northern red oak, suggesting that plots associated with this axis were influenced by canopy openness in addition to the influence of overstory composition and the herbaceous layer. PC3 was negatively associated with high importance values for red pine and eastern white pine, but showed a positive association with high importance values for northern red oak and red maple, suggesting that plots associated with this axis were primarily influenced by overstory species composition. PC4 was positively associated with volume harvested.

Correlation between stand characteristics and regeneration densities

Red pine seedling density showed a moderate negative correlation with PC4 (r = -0.34), but a weak positive correlation with PC1 (r = -0.22), and weak negative correlation with PC2 (r = -0.22; Table 4.5), suggesting that red pine seedling densities were lower where greater volume had been harvested. Red pine saplings, however, indicated a strong negative correlation with PC3 (r = -0.71), suggesting that sapling densities increased with greater dominance of red pine and eastern white pine in the overstory, and less dominance of deciduous species. Eastern white pine seedling densities showed a moderate positive correlation with PC1 (r = -0.31; Table 4.5), suggesting that overstory basal area, overstory density and red maple in the overstory did not significantly impact eastern white pine in the seedling layer, although higher densities tended to be associated with less herbaceous and shrub cover. Eastern white pine sapling densities showed a strong negative correlation with PC3 (r = -0.42), indicating greater sapling densities in areas dominated by red pine and eastern white pine, but a moderate negative correlation with PC2 (r = -0.33), suggesting lower sapling densities in areas with greater jack pine dominance, high herbaceous cover and greater canopy openness.

The linear regression relating seedling densities with distance to seed tree was not significant for red pine (F = 3.11, P = 0.06) and eastern white pine (F = 4.91, P = 0.07). Examining the distribution of stems from potential seed tree, however, all red pine seedlings and majority of eastern white pine seedlings were found in the 6.0-10.9 m distance category, although eastern white pine showed a larger range of up to 21 m from the potential seed tree (Figure 4.2). While we were able to determine the relationships between the PCs and species regeneration densities, and hence the inferred relationships between stand characteristics and regeneration, we unfortunately did not find statistical significance between the PCs and seedling or sapling densities for either species in this stand (Table 4.5) and the other two stands.

The 2004 stand

As was with the 2007 stand, there was overall low densities (mean (±1SD) seedlings/saplings ha^{-1}) of red pine in both the seedling (291 ± 399) and sapling (125 ± 258) layers (Table 4.2). Eastern white had high densities in the sapling layer. High densities of jack pine were also observed especially in the sapling layer. Deciduous species with high densities in this stand included red maple and quaking aspen (*Populus tremuloides* Michx.) in both seedling and sapling layers (Table 4.2). The most common ground-flora species were lowbush blueberry (*Vaccinium angustifolium* Aiton), velvetleaf blueberry (*Vaccinium myrtilloides* Michx.), Blue Ridge blueberry (*Vaccinium vacillans* Kalm ex Torr), wintergreen (*Gaultheria procumbens* L.), and sweet fern (*Comptonia peregrina* (L.) J.M. Coult.) in the shrub layer, and mainly bracken fern (*Pteridium aquilinum* L.) in the herbaceous layer (Table 4.3). The two species with the highest basal area in the overstory were red pine with a mean (±1SD) of 6.1 ± 5m^2/ha and quaking aspen (*Populus tremuloides* Michx.) with 5.4 ± 4.2 m^2/ha (Table 4.6). The two species were also dominant in the overstory with importance values (as a percentage) of 31 ± 30 for red pine and 26 ± 46 for quaking aspen (Table 4.6).

Principal component analysis of stand characteristics variables

The PCA using the correlation matrix of stand characteristics indicated that the first four principal components (PCs) accounted for 78% of the total variation among plots. Based on the factor loadings contributed by stand variables (Table 4.7), PC1 was positively associated with overstory basal area and overstory density, but negatively associated with shrub cover, suggesting a stronger influence of overstory characteristics and the shrub layer on plots associated with this axis. PC2 indicated a positive association with gap size, herbaceous and shrub cover and high importance values for eastern white pine, suggesting that plots associated with this axis are mainly influenced by gap size, overstory composition and the ground-flora. PC3 showed a positive association with high importance values for jack pine and red maple, but showed a negative association with high importance values for red pine, suggesting overstory species composition primarily influenced plots associated with this axis. PC4 was positively associated with volume harvested and canopy openness, but negatively associated with high importance values for red maple, suggesting that amount of material harvested, the canopy openness as well as red maple dominance in the overstory all influenced the plots associated with this axis.

Correlation between stand characteristics and regeneration densities

Red pine seedling density exhibited a strong negative correlation with PC1 (r = -0.42), and a strong positive correlation with PC3 (r = 0.48;Table 4.7), suggesting that red pine seedling densities decreased with increasing overstory basal area and density, but were also found in areas with higher jack pine and red maple importance values. Red pine saplings showed a similar pattern, indicating a moderate negative correlation with PC1 (r = -0.32) and PC3 (r = -0.34), but a positive correlation with PC4 (r = 0.3). This suggests that sapling densities decreased with greater overstory basal area and density, were higher in areas with greater dominance of red pine in the overstory, and increased with greater volume harvested and canopy openness. Eastern white pine seedling densities showed a moderate negative correlation with PC2 (r = -0.32;Table 4.7), suggesting that seedling densities decreased with increasing gap sizes, ground-flora cover as well as with dominance of eastern white pine. Eastern white pine saplings showed a strong positive correlation with PC4 (r = -0.42), indicating greater sapling densities with higher harvest volume and greater canopy openness, but decreasing densities in areas with greater red maple dominance.

Linear regression relating seedling densities with distance to potential seed tree was not significant for both red pine (F = 1.17, P = 0.38) and eastern white pine (F = 0.94, P = 0.36). The distribution of seedlings by distance from seed tree indicated most of the red pine seedlings were in the 6.0-10.9 m distance category, with little distribution after 15.9 m, while majority of the eastern white pine seedlings occurred in the 1.0-5.0-m category, and the distribution indicating a range up to 21 m from the potential seed tree (Figure 4.2).

The 1992 stand

In this stand, higher densities (mean (±1SD) seedlings/saplings ha^{-1}) of red pine were observed in the sapling layer (1750 ± 2007) compared to the seedling layer (208 ± 510) (Table 4.2). We also observed high densities of eastern white pine in both the seedling and sapling layers following treatment. As was the case with the 2007 stand, we observed high densities of jack pine in the sapling layer with none in the seedling layer. We also observed high densities of red maple in both the seedling and sapling layers, northern red oak in the seedling layer, and bigtooth aspen (*Populus grandidentata* Michx.) in the sapling layer (Table 4.2). The most common ground-flora species were lowbush blueberry (*Vaccinium angustifolium* Aiton), velvetleaf blueberry (*Vaccinium myrtilloides* Michx.*)*, Blue Ridge blueberry (*Vaccinium vacillans* Kalm ex Torr), and black huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch) in the shrub layer, with mainly bracken fern (*Pteridium aquilinum* L.) in the herbaceous layer (Table 4.3). As we had expected due to the harvest treatment implemented in this stand, northern red oak had the highest basal area in the overstory with a mean (±1SD) of 9.6 ± 6.3 m^2/ha (Table 4.8). Corresponding to this basal area, northern red oak was also the dominant species in the overstory with an importance value (as a percentage) of 82 ± 68, although eastern white pine was also common in this stand, with an importance value of 37 ± 31 (Table 4.8).

Principal component analysis of stand characteristics variables

The PCA using the correlation matrix of stand characteristics indicated that the first four principal components (PCs) accounted for 80% of the total variation among plots. Based on the factor loadings contributed by stand variables (Table 4.9), PC1 showed a positive association with high importance values for red maple and jack pine, and a negative association with high importance value for northern red oak, overstory basal area and canopy openness, suggesting that characteristics of the overstory was the main factor influencing plots associated with this axis. PC2 was positively associated with volume harvested, canopy openness, and herbaceous and shrub cover, suggesting that amount of material harvested, canopy openness and the ground-flora were the main influences on plots associated with this axis. PC3 showed a positive association with high importance values for red pine and eastern white pine, and a negative association with high importance value for northern red oak and higher shrub cover, suggesting overstory composition and the shrub layer were the main factors influencing plots associated with this axis. PC4 was positively associated with overstory density and basal area suggesting overstory characteristics as the major influence on plots associated with this axis.

Correlation between stand characteristics and regeneration densities

Red pine seedling density showed a moderate negative correlation with PC3 (r = -0.32), which suggests decreasing red pine seedling densities with higher red pine and eastern white pine importance values, but are found in areas with high importance value for northern red oak as well as greater shrub cover (Table 4.9). Red pine sapling density, however, showed weak correlations with all of the PCs suggesting little influence of the stand characteristics on red pine sapling densities in this stand. Eastern white pine seedling densities showed a strong negative correlation with PC2 (r = -0.48; Table 4.9) and PC4 (r = -0.47, which suggests that seedling densities decreased with greater volume harvested, greater canopy openness, high ground-flora cover, as well as high overstory basal area density. Eastern white pine saplings showed a strong negative correlation with PC2 (r = -0.48) and a strong positive correlation with PC4 (r = -0.47), suggesting that sapling densities decreased with greater volume harvested, greater canopy openness, and high ground-flora cover, but increased with greater overstory basal area and density.

Linear regression relating seedling densities with distance to potential seed tree was not significant for red pine (F = 2.47, P = 0.11) and eastern white pine (F = 0.86, P = 0.37). The distribution of observed seedling stems from potential seed tree indicated most red pine seedlings occurred from 6.0 to15.9 m. The majority of eastern white pine seedlings were, however, found between the distances of 1.0 to 10.9 m from the seed tree (Figure 4.2).

4.5 Discussion

Seed source availability and distance to seed trees

Overall, we found little support for our first hypothesis that regeneration would decrease with increasing distance from seed tree for both red pine and eastern white. These results contrast with findings from other studies within the region that have suggested that eastern white pine seedling and sapling densities decrease with increasing distance from the seed source (Palik and Pregitzer, 1994; Peck and Zenner, 2009; Weyenberg et al.; 2004). We suggest a number of possible explanations for this observation in the current study. First, it may be possible that the overstory composition and structure of these stands affect patterns of red pine and eastern white pine seed distribution, for example by trees in the overstory influencing seed dispersal and where seeds land, hence no clear pattern of decreasing seedling densities with increasing distance from potential seed tree. If true, this finding may have important implications for prescription of harvest treatments, as it suggests that a heterogeneous arrangement of mature trees affects regeneration patterns. Second, low seed availability and supply may be another potential reason for the lack of clear relationship between seedling densities and distance to potential seed tree. It may be possible that the seed trees retained during harvest in these stands are of low quality and may not be producing adequate seeds for dispersal across sites. The issue of seed supply may be exacerbated by lack of a nearby seed source, or if the nearby seed sources are not supplying adequate amounts of seeds (Ahlgren, 1976), contrasting with the study by Peck and Zenner, (2009) where besides the stands being dominated by red pine and eastern white pine, there was a nearby seed source that supplied adequate seeds to the harvested area. Weyenberg et al. (2004) also highlight that the patterns of seedling spatial distribution in relation to seed trees are likely to be influenced by the interaction between seed supply and the quality of microsite and seedbed conditions of the site to be occupied.

Third, issues related to the seedbed may be an important factor, especially in the case of red pine. If the seedbed condition are not consistently optimal within the general area to be colonized, patterns of seedling distribution from the seed tree may not be consistent as well. And finally, the relatively smaller sample size in this study may be a limiting factor in the regression analysis. Larger sample sizes would possibly further elucidate seedling distribution patterns from potential seed trees in analyses where linear regressions are used. We, however, found that most of the red pine and eastern white pine seedling stems were found within the distance range of 6.0-10.9 m from the seed tree, although some eastern white pine seedlings were found up to 21 m from potential seed tree in the 2007 and 2004 stands. Our findings support the suggestion that although dispersal range is generally within a radius equal to the height of the seed tree, the effective dispersal range averages about 12 m, especially for red pine (Rudolf, 1990; Stiell 1978).

More broadly, availability of seed source is critical to the natural regeneration of red pine and eastern white pine and greatly influences the successional development of a stand (Ahlgren, 1976; Palik and Pregitzer, 1994). For a species such as red pine, additional factors such as restrictive requirements for seed germination and establishment, inconsistent seed production and poor seed-setting ability may be imposing limitations on natural regeneration (Ahlgren, 1976; Benzie, 1977; Chapeskie et al., 1989; Hauser, 2008). Our findings suggest that: 1) harvest prescriptions designed to improve regeneration of red pine and eastern white pine should provide for retention of sufficient seed trees to act as seed sources for the site; 2) the distribution of these seed sources is critical and should allow for effective reach to the new sites to be colonized; and 3) distance from potential seed tree as a factor that potentially influences regeneration of target species in these stands may be best addressed in concert with other stand-related factors such as overstory composition and stand density. Restoration harvests such as variable-retention harvests (see Chapter 3) where residual trees are spatially distributed in a manner that emulates outcomes of natural disturbance may be one way land managers can achieve these objectives.

Influence of overstory characteristics on regeneration

There was strong support for our second hypothesis that greater regeneration densities of red pine and eastern white pine would be expected in areas with lower overstory basal area and overstory density, and importance values of species other than red pine and eastern white pine, especially in the 2007 and 2004 stands. The seedling and sapling densities of both red pine and eastern white pine were generally greater in areas dominated by red pine and eastern white pine in the overstory, and decreased with greater overstory basal area and overstory density, and higher importance value for jack pine and deciduous species in the overstory. These findings suggest that factors related to overstory density and species composition remained important with regard to regeneration of red pine and eastern white pine in these stands, even after harvest treatments were implemented. Our findings compare with those of other studies, with some suggesting that the effects of overstory would be more pronounced on the seedling layer (Peck and Zenner, 2009), and others suggesting greater effects on the sapling layer (Dovciak et al., 2003).

Overstory trees may negatively influence regeneration of target pine species through competition for space, water, and nutrients, as well as through shading effects (Ahlgren, 1976; Elliot and White, 1993; Puettmann and Reich, 1995). Although some shading may be beneficial during germination as it reduces the likelihood of desiccation, shading inhibits subsequent survival and growth of the germinated red pine and eastern white pine (OMNR, 1998; Rudolf, 1990; Zenner and Krueger, 2006). The mixed results regarding influence of overstory basal area, density and species composition found in the 1992 stand, however, may be a function of the harvest treatment implemented in this particular stand, where the harvesting strategy involved preferential removal of species including red pine and eastern white pine.

Our findings regarding the influence of canopy openness on regeneration densities were mixed among stands. Only in the sapling layer of the 2004 stand did we find an increase in red pine sapling densities with greater canopy openness as we had hypothesized, while the relationship was negative in the 2007 and 1992 stands. A measure of percent canopy openness was used as a proxy for amount of light that is reaching the understory, and greater light penetration into the understory was expected to favor the regeneration of the red pine and eastern white pine. According to the gap partition theory, larger canopy gaps result in greater light penetration into the understory and warmer soil temperatures, conditions likely conducive for shade intolerant species to outcompete tolerant species (Denslow, 1980). It is possible, however that the negative effects of the overstory including basal area, density and species composition may be stronger than potential positive effects of percent canopy openness on regeneration in these stands (Kern, 2012). The areas characterized by greater canopy openness were also mostly associated with high herb and shrub cover, suggesting that ground-flora species may have benefitted from modified conditions in the created gaps, inducing additional competition against target species. Additionally, the current average canopy openness were 46% in the 2007 stand, 44% in the 2004 stand, and 37% in the 1992 stand (see Tables 4.4, 4.6, and 4.8 respectively), which may not be adequate to allow for understory conditions that favor regeneration of red pine and eastern white pine (although these values may have been higher one or two years post-harvest).

In terms of management, these results provide important information for land managers to make decisions about additional treatments, such as additional manipulation of the overstory to favor regeneration of red pine and eastern white pine. Eastern white pine responds well to release (Krueger et al., 2007; Zenner and Krueger, 2006), and so additional overstory and understory manipulations may be adequate to facilitate recruitment of the high densities of saplings observed in this study into the overstory. Such treatments also need to target the harvest of jack pine that currently make a large component of the overstory and are a legacy of past management practices such as clearcutting (Drobyshev et al., 2008; Rist, 2008). For red pine, site preparation treatments that reduce competition and significantly disturb the soil to expose mineral soil (D'Amato et al., 2012), proper timing of harvesting to follow immediately after a good crop year, and a post-harvest prescribed burning where conditions allow, may be some suggested options to improve regeneration.

Factors related to volume harvested and gap sizes

We found support for our hypothesis that greater red pine and eastern white pine regeneration would be associated with higher harvest volume, but only for the sapling layers of the 2004 and the 1992 stands. Greater volume removal tended to have the exact opposite effect on seedlings in the 2007 and 1992 stands. We suggest that high harvest intensities may sometimes result in large amounts of slash on the forest floor. If this slash is not removed from the forest floor, it may contribute to increases in depths of the duff and the litter layers, causing unfavorable conditions on the surface that may limit the germination and establishment of red pine and eastern white pine (Ahlgren, 1976; Rudolf, 1990; Wendel and Smith, 1990) These inhibitory effects may override the potential positive effects of higher canopy openness or reduced competition associated with high harvest volumes. Additionally, the high densities of saplings of both species could suggest a window of opportunity for these treatments, i.e., the favorable understory conditions created by greater harvest volume may only last for a number of years (within which seedlings were established) and potentially decline as stands develop.

We, however, did not find support for our hypothesis of greater red pine and eastern white pine regeneration with larger gap sizes in the 2004 stand. This finding may be attributed to a number of factors already discussed above. First, the gaps created by the harvest may have been readily occupied by ground-flora species that then exerted their own influence on regeneration regardless of the size of the gap. Second, although seed dispersal maybe favored in larger open areas (Dovciak et al., 2005), lack of an adequate nearby seed source to supply seeds to these sites can potentially limit recruitment in these gaps. Third, potential for significant initial seedling mortalities of species such as red pine due to extreme microclimatic changes (desiccation) in a gap, coupled with species such as jack pine that may be competitively superior in such conditions, may also be contributing factors (Peck et al. 2012; Powers, 2008). In terms of management, Bradshaw (1992) suggests that no particular gap size may be appropriate to meet all silvicultural objectives, and land managers using gap size as a guideline are likely to run into challenges of separating between even-aged and uneven-aged harvest treatments. As such, depending on species targeted for regeneration, harvest treatments that involve creation of gaps within the residual stand may need to address a variety of factors, including balancing between selecting a gap size that allows for amelioration of potential extreme microclimatic conditions within the gap, while managing edge-effects, and controlling competing vegetation.

Influence of the ground-flora

Overall, decreases in both seedling and sapling densities with increases in estimated herbaceous and shrub cover were found in all three stands, supporting our hypothesis of greater regeneration densities in areas with less cover ground-flora species. These results are consistent with other studies that have also found negative relationships between regeneration and herbaceous and shrub cover, with the relationship largely explained by competition for resources (Corbett 1994; Cornett et al., 1998; Saunders and Puettmann, 1999; Weyenberg et al., 2004). The understory of the three stands used in this study are mainly dominated by blueberries in the shrub layer and bracken fern in the herbaceous layer, and competition induced by understory species is likely to negatively impact species such as red pine. Techniques such as mowing and herbicides have been used with harvest treatments as part of efforts to control understory vegetation and improve conditions for regeneration of red pine (D'Amato et al., 2012; Peck et al., 2012).

General stand conditions

Overall, red pine regeneration in the current stands appears to be more limited compared to eastern white pine, observations that support those made in chapters two and three of this dissertation. In addition to influences related to the overstory, seed supply, seedbed conditions, and ground-flora species discussed above, we observed high densities of jack pine in the sapling layer of all three stands, as well as high densities of red maple and northern red oak in both the seedling and sapling layers. It is likely that these species may be negatively influencing regeneration, especially with respect to red pine, through competition and displacement. These findings suggest that the current treatments may not have had significant impact on limiting regeneration of these competing species and opportunities exist for land managers to implement additional treatments that more specifically target species such as jack pine and red maple. Such treatments may focus on limiting the resprouting of species such as red maple, as well as use of prescribed fires in areas where stand condition can accommodate safe use of fire.

The overall trend of red pine and eastern white pine sapling densities in all three stands suggest potential for progressive stand development, where seedling-size individuals that survived the influence of the factors described in this study grew into the sapling layer, and where additional treatments can target further reduction of canopy cover in order to facilitate their recruitment into the overstory. The higher densities of red pine and eastern white pine in the sapling layer of the 1992 stand may also suggest that past conditions in this stand had been better for the regeneration of the target pine species, but also that time for recovery may be an important factor for land managers to consider (Franklin et al., 2007). These high sapling densities may suggest that while efforts to improve seedbed conditions and establishment of new seedlings should be ongoing, individuals that make it to the sapling stage may be able to better survive current stand conditions, and that additional treatments should provide for their release and recruitment into the overstory. Further, the high densities of saplings could suggest that the effectiveness of these treatments potentially decline as stands develop, hence land managers need to make assessments about possible additional treatments within an adaptive management framework.

4.6 Conclusions

Restoring characteristics that resemble those of pre-EuroAmerican settlement forests, and enhancing the structural and functional capacity of current mixed-pine stands to withstand expected disturbance events associated with changing environmental conditions will require successful restoration of the historically dominant red pine and eastern white pine. In the absence of the natural fire regime, and with limitations imposed by high fuel loadings in current stands, harvesting techniques have become a major agent of disturbance that can be manipulated to achieve specific management goals, such as improving natural regeneration of red pine and eastern white pine. Our study provides useful information on stand-related factors that affect natural regeneration of these two species in current mixed-pine stands following harvest treatments. Even though planting red pine and eastern white pine may be a restoration option, natural regeneration is less costly to land managers, especially when managing at large spatial scales, as it does not require purchase of seedlings or costs for labor and equipment.

Where management objectives are to improve natural regeneration of red pine and eastern white pine, the availability of a seed source and seed dispersal throughout the stand should also be important considerations with regard to the design and implementation of silvicultural prescriptions. As our findings suggest the manipulation of the overstory, especially through careful choice of which species to retain and their densities and spatial distribution will be critical to achieving management objectives targeted at improving conditions for regeneration of red pine and eastern white pine.

Where emerging multi-objective silvicultural techniques such as variable-retention harvesting encourages creation of gaps within a matrix of aggregately retained trees (Palik et al., 1997, Palik and Zasada, 2003; Peck et al., 2012), decisions regarding the basal area of trees to be retained and characteristics of the created gaps will need to be made based on the species targeted for regeneration, potential for competing species to establish in the gaps and influences associated with forest edge. We have examined the effects of factors related to fire history and fuels on the regeneration layer dynamics of current stands (see Chapter 2), and initial regeneration and ecosystem productivity response to implemented restoration variable-retention harvesting (see Chapter 3). This study allows us to take an additional step and advance our knowledge by examining natural regeneration dynamics as stands develop in order to provide knowledge that will facilitate adaptive management decisions by land managers.

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Table 4.1 Characteristics of three stands harvested in 2007, 2004, and 1992 respectively in mixed-pine forest ecosystems at Seney National Wildlife Refuge. Habitat classification by Burger and Kotar (2003)

Stand name	Year harvested	Size (ha)	Habitat type	Harvest objective	Goal
2007	2007 (Late summer)	173	*Pinus-Vaccinium-Epigaea* (PVE) plant association in outwash channel landform	Reduce undesirable species such as jack pine, black spruce and red maple	Reduce fuels and promote regeneration of red pine and eastern white pine
2004	2004 (Fall)	114.5	*Pinus-Vaccinium-Epigaea* (PVE) plant association in outwash channel landform	Reduce undesirable species such as jack pine, black spruce and red maple	Reduce fuels and promote regeneration of red pine and eastern white pine
1992	1992 (Winter)	16	*Pinus-Vaccinium-Epigaea* (PVE) plant association in outwash channel landform	Reduce tree species (greater than 1 inch dbh), except northern red oak	Promote red oak regeneration and acorn production to expand food base for wildlife in the winter

Table 4.2 Mean (±1SD) seedling and sapling densities (stems ha^{-1}) in the 2007, 2004, and 1992 stands at Seney National Wildlife Refuge. Nomenclature: http://plants.usda.gov/

	2007 stand		2004 stand		1992 stand	
Species	**Seedling**	**Sapling**	**Seedling**	**Sapling**	**Seedling**	**Sapling**
Red pine	41 ± 161	208 ± 385	291 ± 399	125 ± 258	208 ± 510	1750 ± 2007
Eastern white pine	1708 ± 2283	1500 ± 1471	541 ± 662	2291 ± 2452	3041 ± 2163	23583 ± 11915
Jack pine	416 ± 1124	1083 ± 1627	250 ± 517	1458 ± 2562	0 ± 0	3291 ± 3377
Red maple	3416 ± 5365	83 ± 322	2375 ± 2411	2125 ± 4511	2000 ± 2600	833 ± 1543
Northern red oak	3500 ± 4164	41 ± 161	0 ± 0	0 ± 0	2041 ± 1867	0 ± 0
Quaking aspen	83 ± 322	41 ± 161	500 ± 1007	500 ± 1137	0 ± 0	0 ± 0
Bigtooth aspen	375 ± 845	375 ± 700	208 ± 510	41 ± 161	208 ± 510	8500 ± 20620
Black spruce	0 ± 0	0 ± 0	41 ± 161	41 ± 2007	0 ± 0	0 ± 0
Eastern hemlock	0 ± 0	291 ± 662	41 ± 161	250 ± 517	0 ± 0	0 ± 0
Balsam fir	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	125 ± 258

Table 4.3 Mean (±1SD) ground-flora cover (%) in study plots (16m² plots) in the 2007, 2004, and 1992 stands at Seney National Wildlife Refuge. Nomenclature: http://plants.usda.gov/

Herbs		**2007 Stand**	**2004 Stand**	**1992 Stand**
Bracken fern	*Pteridium aquilinum* (L.) Kuhn	40 ± 17	31 ± 14	28 ± 14
Bunchberry	*Cornus canadensis* L.	0.1 ± 0.3	0 ± 0	0 ± 0
Starflower	*Trientalis borealis* Raf.	0.2 ± 0.3	0.3 ± 0.3	0.2 ± 0.4
Mayflower	*Maianthemum canadense* Desf.	0 ± 0	0.05 ± 0.2	0.07 ± 0.2
Cowwheat	*Melampyrum lineare* Desr.	0.03 ± 0.1	0.3 ± 0.4	0.03 ± 0.1
St. Johns wort	*Hypericum* L.	0.5 ±1.5	0 ± 0	0 ± 0
Bitter lettuce	*Lactuca virosa* L.	0 ± 0	0 ± 0	0.03 ± 0.1
Virginia strawberry	*Fragaria virginiana* Duchesne	0.07 ± 0.2	0 ± 0	0 ± 0
Common sheep sorrel	*Rumex acetosella* L.	0.03 ±0.1	0 ± 0	0 ± 0
Spreading dogbane	*Apocynum androsaemifolium* L.	0.03 ± 0.1	0.1 ± 0.3	0.1 ± 0.3
Shrubs				
Lowbush blueberry	*Vaccinium angustifolium* Aiton	21 ± 15	19 ± 10	19 ± 17
Velvetleaf blueberry	*Vaccinium myrtilloides* Michx.	4 ± 6	8 ± 9	6 ± 13
Blue Ridge blueberry	*Vaccinium vacillans* Kalm ex Torr	0 ± 0	6 ± 7	4 ± 17
Wintergreen	*Gaultheria procumbens* L.	5 ± 5	10 ± 13	0 ± 6
Black huckleberry	*Gaylussacia baccata* (Wangenh.) K. Koch	5 ±10	1 ± 5	17 ± 17
Nannyberry	*Viburnum lentago* L.	0.5 ± 0.5	0.2 ± 0.6	0.3 ± 0.5
Pacific serviceberry	*Amelanchier interior* E.L. Nielsen	0.6 ± 1	0.3 ± 0.6	0.8 ± 0.6
Roundleaf serviceberry	*Amelanchier sanguinea* (Pursh) DC.	0.1 ± 0.2	0 ± 0	0.2 ± 0.4
Low serviceberry	*Amelanchier spicata* (Lam.) K. Koch	0 ± 0	0 ± 0	0.07 ± 0.3
Sweet fern	*Comptonia peregrina* (L.) J.M. Coult.	0.8 ± 3	10 ± 16	0 ± 0
Trailing arbutus	*Epigaea repens* L.	1 ± 5	0.5 ± 1	0.04 ± 0.2
Withe-rod	*Viburnum cassinoides* L.	0 ± 0	0.8 ± 3	0 ± 0
Sandcherry	*Prunus pumila* L.	0 ± 0	0 ± 0	0 ± 0
Pin cherry	*Prunus pensylvanica* L. f.	0.03 ± 0.1	2 ± 6	0.03 ± 0.1
Northern bush honeysuckle	*Diervilla lonicera* Mill.	0.2 ± 0.3	0 ± 0	0 ± 0

Table 4.4 Mean (±1SD) estimates of stand characteristics in the 2007 stand at Seney National Wildlife Refuge

Species	**Overstory BA (m^2/ha)**	**Overstory density (stems/ha)**	**Species IV**	**Other characteristics**
Red pine	4.3 ± 3.8	56 ± 72	29 ± 38	----
Eastern white pine	2.1 ± 2.3	31 ± 24	16 ± 12	----
Jack pine	2.3 ± 2	103 ± 94	52 ± 48	----
Red maple	0.6 ± 0.4	8 ± 20	4 ± 10	----
Northern red oak	6.4 ± 3.5	48 ± 60	25 ± 32	----
Quaking aspen	0 ± 0	0 ± 0	0 ± 0	----
Bigtooth aspen	1.4 ± 0.6	6 ± 14	3 ± 7	----
Black spruce	0 ± 0	5 ± 14	2 ± 7	----
Eastern hemlock	0.6 ± 0.4	0 ± 0	0.04 ± 0.1	----
Balsam fir	0 ± 0	0 ± 0	0 ± 0	----
Paper birch	1.9 ± 0.8	10 ± 20	5 ± 10	----
Other				
% canopy openness				46 ± 9
Distance_red pine (m)				10.7 ± 1.6
Distance_eastern white pine (m)				9.1 ± 4.7
Volume harvested (m^3/ha)				154.3 ± 66.1

*Distance refers to the distance from the observed seedlings to nearest potential seed tree
*BA=overstory basal area
*IV=importance value

Table 4.5 PCA of predictor variables and selected PCs regression with regeneration densities in the 2007 stand at Seney National Wildlife Refuge

	Factor loadings			
Predictor variables	**PC1**	**PC2**	**PC3**	**PC4**
Canopy openness	0.18	**0.67**	-0.09	0.01
Volume harvested	0.12	-0.05	0.03	**0.89**
Overstory basal area	**0.95**	-0.21	-0.03	0.01
Overstory density	**0.91**	0.01	-0.07	0.05
Red pine importance value	0.03	-0.05	**-0.97**	0.19
Eastern white pine importance value	-0.04	-0.16	**-0.87**	0.26
Jack pine importance value	-0.17	**0.84**	0.25	0.21
Red maple importance value	**0.72**	-0.24	0.42	0.08
Northern red oak importance value	-0.03	**-0.72**	**0.52**	-0.02
Herb cover	-0.43	**0.72**	0.03	-0.1
Shrub cover	**-0.88**	-0. 2	0.1	-0.13
Statistics				
Eigen value	3.28	2.36	1.64	1.54
Proportion of variation	0.3	0.21	0.15	0.14
Cumulative variation	0.3	0.51	0.66	0.8

	PC regression with seedling/sapling densities			
	Estimate	**t-value**	**p-value**	**r**
PIRE seedlings				
PC1	0.52	0.79	0.45	0.22
PC2	0.12	0.19	0.86	0.05
PC3	-0.53	-0.80	0.44	-0.22
PC4	-0.80	-1.22	0.25	-0.34
PIST seedlings				
PC1	4.64	1.07	0.31	0.31
PC2	-0.72	-0.17	0.87	-0.05
PC3	3.62	0.84	0.42	0.24
PC4	-2.31	-0.53	0.61	-0.15
PIRE saplings				
PC1	0.14	0.06	0.95	0.01
PC2	-2.23	-0.94	0.37	-0.20
PC3	-8.05	-3.38	0.01	-0.71
PC4	-0.77	-0.33	0.75	-0.06
PIST saplings				
PC1	2.59	0.33	0.33	0.08
PC2	-9.84	-1.26	-1.26	-0.33
PC3	-12.61	-1.61	-1.61	-0.42
PC4	2.87	0.37	0.37	0.09

*Predictor variables represent stand characteristics

* Sign (+/-) before number indicates direction of relationship with principal axis

*PIRE=red pine, PIST=eastern white pine

* *r* = Pearson's correlation coefficient. *r* values indicating strength of correlation were described as follows; < 0.25 = weak, 0.25-0.35 = moderate, and > 0.35 = strong.

Table 4.6 Mean (±1SD) estimates of stand characteristics in the 2004 stand at Seney National Wildlife Refuge

Species	Overstory BA (m^2/ha)	Overstory density (stems/ha)	Species IV	Other characteristics
Red pine	6.1 ± 5	58 ± 56	31 ± 30	----
Eastern white pine	2 ± 2.1	45 ± 85	23 ± 43	----
Jack pine	2.2 ± 2	35 ± 80	17 ± 41	----
Red maple	1.8 ± 1.3	23 ± 42	11 ± 21	----
Northern red oak	0 ± 0	0 ± 0	0 ± 0	----
Quaking aspen	5.4 ± 4.2	50 ± 88	26 ± 46	----
Bigtooth aspen	1.9 ± 1.4	13 ± 32	6 ± 16	----
Black spruce	0.7 ± 0.3	11 ± 28	5 ± 14	----
Eastern hemlock	0.9 ± 0.5	5 ± 10	2 ± 5	----
Balsam fir	0 ± 0	0 ± 0	0 ± 0	----
Paper birch	0 ± 0	0 ± 0	0 ± 0	----
Other				
% canopy openness				44 ± 12
Distance_red pine (m)				7.9 ± 3.4
Distance_eastern white pine (m)				8.9 ± 5.2
Volume harvested (m^3/ha)				5743 ± 6511
Harvested patch size (m^2)				136.3 ± 57.7

*Distance refers to the distance from the observed seedlings to nearest potential seed tree
*BA=overstory basal area
*IV=importance value

Table 4.7 PCA of predictor variables and selected PCs regression with regeneration densities in the 2004 stand at Seney National Wildlife Refuge

	Factor loadings			
Predictor variables	**PC1**	**PC2**	**PC3**	**PC4**
Canopy openness	-0.39	0.25	-0.15	**0.72**
Volume harvested	0.19	-0.1	-0.29	**0.85**
Overstory basal area	**0.95**	0.14	-0.05	-0.07
Overstory density	**0.94**	0.2	0.09	0.04
Red pine importance value	-0.2	-0.4	**-0.79**	0.16
Eastern white pine importance value	0.26	**0.58**	-0.17	-0.16
Jack pine importance value	-0.14	-0.3	**0.89**	0.2
Red maple importance value	0.07	-0.13	**0.51**	**-0.61**
Gap size	0.24	**0.76**	-0.04	0.32
Herb cover	-0.37	**0.73**	0.17	0.1
Shrub cover	**-0.67**	**0.52**	-0.06	0.08
Statistics				
Eigen value	2.75	2.12	1.86	1.82
Proportion of variation	0.25	0.18	0.17	0.17
Cumulative variation	0.25	0.44	0.61	0.78

	PC regression with seedling/sapling densities			
	Estimate	**t-value**	**p-value**	**r**
PIRE seedlings				
PC1	-7.30	-1.78	0.11	-0.42
PC2	-0.49	-0.12	0.91	-0.02
PC3	8.34	2.04	0.07	0.48
PC4	-2.34	-0.57	0.58	-0.13
PIST seedlings				
PC1	3.22	0.67	0.52	0.19
PC2	-5.56	-1.15	0.28	-0.32
PC3	2.37	0.49	0.63	0.14
PC4	3.79	0.79	0.45	0.22
PIRE saplings				
PC1	-8.27	-1.23	0.25	-0.32
PC2	1.42	0.21	0.84	-0.06
PC3	-8.91	-1.33	0.21	-0.34
PC4	7.79	1.16	0.27	0.30
PIST saplings				
PC1	6.42	0.84	0.42	0.21
PC2	4.81	0.63	0.54	0.16
PC3	9.64	1.26	0.24	0.32
PC4	12.23	1.60	0.14	0.41

*Predictor variables represent stand characteristics

* Sign (+/-) before number indicates direction of relationship with principal axis

*PIRE=red pine, PIST=eastern white pine

* *r* = Pearson's correlation coefficient. *r* values indicating strength of correlation were described as follows; < 0.25 = weak, 0.25-0.35 = moderate, and > 0.35 = strong.

Table 4.8 Mean (±1SD) estimates of stand characteristics in the 1992 stand at Seney National Wildlife Refuge

Species	**Overstory BA (m^2/ha)**	**Overstory density (stems/ha)**	**Species IV**	**Other characteristics**
Red pine	1.5 ± 0.6	8 ± 22	4 ± 11	----
Eastern white pine	1.9 ± 2.5	73 ± 62	37 ± 31	----
Jack pine	0.4 ± 0.2	6 ± 14	3 ± 7	----
Red maple	2.7 ± 1.6	26 ± 56	13 ± 28	----
Northern red oak	9.6 ± 6.3	158 ± 130	82 ± 68	----
Quaking aspen	0 ± 0	0 ± 0	0 ± 0	----
Bigtooth aspen	0.2 ± 0.6	2 ± 6	0.9 ± 3	----
Black spruce	0 ± 0	0 ± 0	0 ± 0	----
Eastern hemlock	0 ± 0	0 ± 0	0 ± 0	----
Balsam fir	0.02 ± 0.1	2 ± 6	0.8 ± 3	----
Paper birch	3.2 ± 1.3	13 ± 36	6 ± 18	----
Other				
% canopy openness				37 ± 6
Distance_red pine (m)				11 ± 4.6
Distance_eastern white pine (m)				6.4 ± 2.5
Volume harvested (m^3/ha)				200.3 ± 135.6

*Distance refers to the distance from the observed seedlings to nearest potential seed tree
*BA=overstory basal area
*IV=importance value

Table 4.9 PCA of predictor variables and selected PCs regression with regeneration densities in the 1992 stand at Seney National Wildlife Refuge

Predictor variables	Factor loadings PC1	PC2	PC3	PC4
Canopy openness	-0.4	**0.81**	0.35	-0.15
Volume harvested	0.07	**0.86**	0.09	0.06
Overstory basal area	**-0.42**	-0.17	-0.04	**0.79**
Overstory density	0.13	0.04	-0.05	**0.94**
Red pine importance value	0.13	-0.21	**0.82**	0.01
Eastern white pine importance value	0.18	0.25	**0.83**	0
Jack pine importance value	**0.78**	0.36	0.06	0.17
Red maple importance value	**0.9**	-0.18	-0.14	-0.22
Northern red oak importance value	**-0.72**	-0.02	**-0.56**	0.17
Herb cover	0.33	**0.69**	-0.03	-0.13
Shrub cover	-0.11	**0.48**	**-0.61**	0.13
Statistics				
Eigen value	2.5	2.41	2.21	1.68
Proportion of variation	0.23	0.22	0.2	0.15
Cumulative variation	0.23	0.45	0.65	0.8

PC regression with seedling/sapling densities	Estimate	t-value	p-value	r
PIRE seedlings				
PC1	-0.96	-0.91	0.39	-0.25
PC2	-0.15	-0.15	0.89	-0.04
PC3	-1.19	-1.12	0.29	-0.32
PC4	-0.78	-0.73	0.48	-0.21
PIST seedlings				
PC1	-6.20	-0.91	0.38	-0.20
PC2	-14.49	-2.14	0.06	-0.48
PC3	-0.62	-0.09	0.93	-0.02
PC4	14.40	2.12	0.06	-0.47
PIRE saplings				
PC1	-1.58	-0.85	0.42	-0.25
PC2	0.45	0.24	0.81	0.07
PC3	0.97	0.52	0.61	0.15
PC4	1.14	0.61	0.55	0.18
PIST saplings				
PC1	-6.20	-0.91	0.38	-0.20
PC2	-14.49	-2.14	0.06	-0.48
PC3	-0.06	0.09	0.93	-0.02
PC4	14.40	2.12	0.06	0.47

*Predictor variables represent stand characteristics

* Sign (+/-) before number indicates direction of relationship with principal axis

*PIRE=red pine, PIST=eastern white pine

* r = Pearson's correlation coefficient. r values indicating strength of correlation were described as follows; < 0.25 = weak, 0.25-0.35 = moderate, and > 0.35 = strong.

Figure 4.1 Images of the 2007 stand showing the dispersed harvesting pattern and retention of red pine trees (A), the 2004 stand depicting gaps created within the residual stand during harvesting (B), and the 1992 stand with a major component of eastern white pine in the sapling layer (C).

Figure 4.1 continued

Figure 4.1 continued

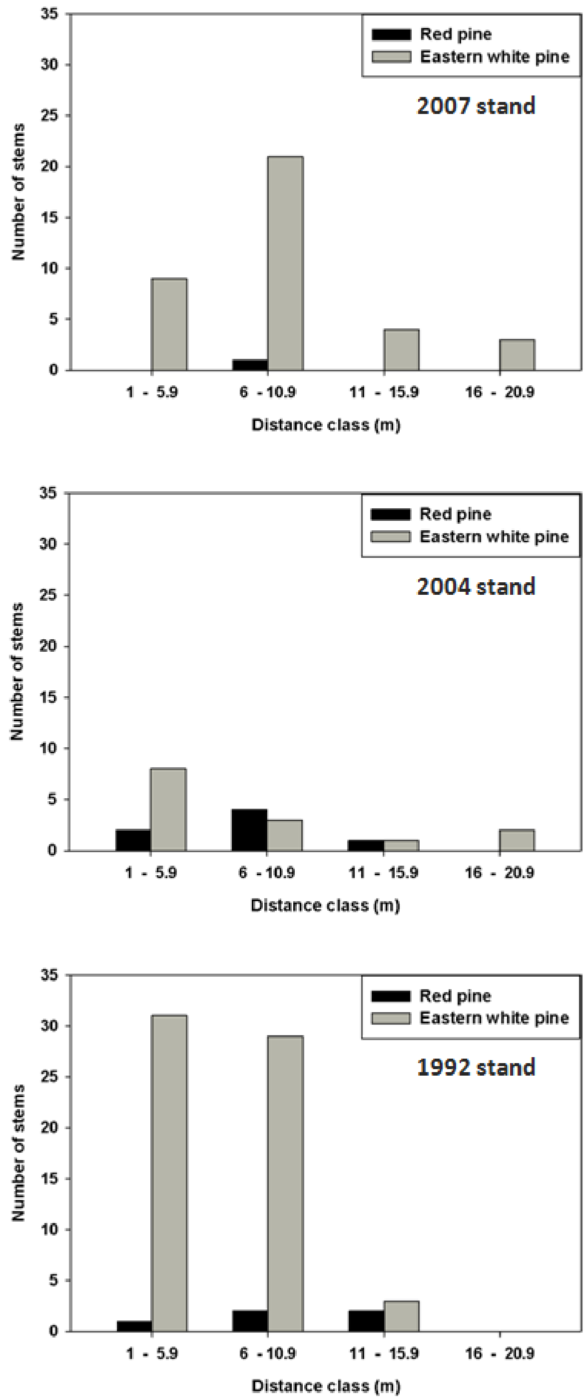

Figure 4.2 Red pine and eastern white pine seedling stem counts by distance from potential seed tree in the 2007, 2004, and 1992 stands at Seney National Wildlife Refuge.

Chapter 5: Management Implications

Resource managers across the northern Lake Lakes experience a number of challenges in their efforts to restore mixed-pine forest ecosystems dominated by red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.) (Wilson et al., 2009). Such challenges include competing interagency management objectives, land ownership, and a public that may be skeptical of proposed restoration treatments (Wilson et al., 2009). These challenges are further compounded by the current condition of some forests, with high stem densities, shifts in species composition (e.g., increased jack pine (*P. banksiana* Lamb.), and high fuel loadings outside of the natural range of variability (Corace et al., In Press; Drobyshev et al., 2008b), all of which may limit use of prescribed fire as a management tool in many areas. While initial steps have been made to address these issues through efforts to enhance exchange of information about fire and fuel issues (Kocher et al., 2012; Miesel et al., 2012), and encourage adoption of emerging forest management approaches (Franklin et al., 2007), there are considerable knowledge gaps in our understanding of fire effects and how to approach barriers to prescribed fire use in the region.

One important framework that may assist in specific efforts to restore mixed-pine forests in the northern Lake States is a focus on ecological forestry (Corace and Goebel, 2010). The "three-legged stool" concept of ecological forestry proposed by Franklin et al. (2007) emphasizes three key principles in cases where silvicultural treatments are to be implemented: 1) retention of biological legacies during harvest; 2) intermediate treatments that enhance stand heterogeneity; and 3) allowing for appropriate recovery periods between regeneration harvests. These ideas, coupled with increased efforts by land managers to focus on ecosystem-based resource management (Corace et al., 2009), and increasing public support for ecologically based management objectives (Shindler et al., 2009; Wilson et al., 2009) suggest opportunities exist to contribute to restoration efforts in these altered forest ecosystems. A critical component of this effort is the sharing of information from field-based experimental studies with land managers to facilitate decision making, treatment selection, and treatment implementation. The results of both descriptive and experimental studies in this dissertation build on these restoration and management efforts by 1) advancing our knowledge of fire and fuel issues within the region, 2) enhancing the adoption of emerging restoration techniques as well as integration of ecological forestry principles, and 3) encouraging monitoring and adaptive management as ways to assess and improve the effectiveness of restoration treatments.

Reintroduction of fire as a long term objective

Mixed-pine forest types were historically maintained by a frequent mixed-severity surface fire regime that played a critical role in the regeneration and dominance of red pine and eastern white pine (Drobyshev et al., 2008a). These frequent mixed-severity surface fires were highly variable, however, with a mean return interval of 32.7±19.2 years for pre-EuroAmerican settlement period (Drobyshev et al., 2008a). Our results indicate a negative relationship between red pine seedling density with time since last fire, and most of the red pine seedlings found in the altered stands are in areas that have experienced about 6-10 fires over the past 142 years. Further, we found that occurrence of fires that we hypothesized were of higher severity (although determining severity from the dendrochronological record is difficult) favored other species such as jack pine more than they did for red pine and eastern white pine (see Chapter 2).

Our results suggest that fire history and legacies of changes to the natural fire regime are important factors that influence regeneration patterns of current altered stands. More broadly, these findings underscore the fact that it is highly probable that not only will fire be needed to create conditions for regeneration of red pine and eastern white pine, but reintroducing fires with characteristics (e.g., frequency, severity, seasonality) that resemble those prior to alteration of the regime may be most effective at achieving these objectives, and will need to be part of the long-term management strategy. Emphasizing the importance of including fire in management plans, Allen et al. (2002) argues that the reintroduction of fire, either by restoring the actual natural fire regime, or emulating it with prescribed fires may be the best way to determine if management objectives are being met in these fire-adapted ecosystems.

Need for silvicultural treatments

As mentioned earlier, the current shifts in species composition, high stand densities, and high accumulations of both live and down fuels may preclude the use of prescribed fire as a restoration and fuels reduction treatment. Consequently, there is likely to be greater need to rely on silvicultural treatments aimed at reducing fuels, improving regeneration of target species and creating stand structures that are conducive to use of prescribed fire as a management tool. Our suggestions are consistent with other studies that have suggested that the reintroduction of fire ought to be a long-term management objective, however, other immediate interventions including mechanical treatments need to be considered (Drobyshev et al., 2008a; Goebel et al., 2005). Such silvicultural treatments should aim to restore the resilience and functionality of the ecosystem within the context of desired future conditions (Franklin and Johnson, 2012) by incrementally moving it along a trajectory towards a state that is within an historic range of conditions (Landres et al., 1999).

Our findings associated with the initial two-year ecosystem response to variable-retention harvesting as one such treatment indicates its potential as a restoration and fuel reduction technique (see Chapter 3). Although the initial trend was low establishment of red pine, we found significantly higher densities of eastern white pine in treated stands compared to controls (representing an increase in newly established seedlings after treatment implementation, based on our age discrimination; i.e., seedlings 1 or 2 years old). Our results suggest that negative effects exerted by sprouting species such as red maple (*Acer rubrum* L.), deciduous species in the overstory, and the down woody material on the forest floor may have contributed to the low response of red pine to the treatment, and are important factors that need to be taken into consideration. A negative relationship between overstory characteristics and seedling and sapling densities of red pine and eastern white pine was found in all our studies, suggesting that manipulating the overstory to favor regeneration of target species should be an important area of focus for land managers. Creating favorable conditions for regeneration of red pine need to not only reduce competing vegetation, but timing harvesting to impact the soil surface so that mineral seedbeds are exposed may also be needed (D'Amato et al., 2012). We further suggest that treating the slash or using prescribed fires can potentially improve conditions and favor regeneration of red pine. Additionally, land managers should ensure that adequate seed trees are left in place during harvest treatments to act as seed sources (e.g., by accurately determining initial mature stem densities, age and basal area prior to harvesting).

Although we did not find significant differences in regeneration responses of our target species between the two spatial patterns of retention (aggregate vs dispersed), the observed similarity in response suggests land managers could have flexibility to explore both patterns especially where the scale of treatment and management objectives allow. The two retention patterns are important in the efforts to emulate patterns created by natural disturbance processes; for example, aggregate retention emulates the patchy mosaic pattern created by natural fire events. Although some studies suggest that the drastic changes in environmental conditions in open gaps created by the aggregate pattern could favor intolerant pine species (Palik and Zasada, 2003; Palik et al. 1997), others suggest that the extreme conditions in such gaps could favor regeneration of other species (e.g., jack pine) and cause initial mortality of pines targeted for restoration (Peck et al., 2012). These potential effects might be ameliorated by dispersed retention pattern. In addition to creating conditions for regeneration of target species, both patterns could also be useful in achieving a variety of other management objectives, including improving structural complexity (of age classes and stem sizes) as well as creating wildlife habitat. For example, early seral communities created in the gaps of the aggregate pattern and the open understory structure in the dispersed treatment may benefit species such as the American woodcock (*Scolopax minor*).

Our findings also suggest variable-retention harvesting is a viable technique where fuel reduction is a management objective. With the harvest treatment targeted to remove jack pine as part of a live fuel reduction strategy, we found up to 92% reduction in live jack pine basal area in treated stands. These findings are encouraging, especially in cases where the likelihood of severe fires facilitated by the vertical fuel continuity provided by jack pine is a concern. Land managers planning to use variable-retention harvesting for fuel reduction will thus need to target such species as jack pine, along with other fire-sensitive species such as red maple during harvesting. Overall, although they are in the initial stages of adoption, silvicultural treatments such as variable-retention harvesting likely will be integral components to the overall restoration efforts of mixed-pine forest ecosystems in the northern Lake States. Our findings suggest that variable-retention harvesting is a useful technique to achieve both restoration and fuel reduction objectives. We suggest that complimentary studies, such as effects of treatment on wildlife, or effects of harvest operations on remnant tree may advance the knowledge from our studies and provide land managers a broader scope of other factors to consider when implementing these treatments.

Location, management objectives, and spatial scale considerations

While the underlying principles for the design and implementation of restoration treatments may be largely similar for a given ecosystem type, treatment prescriptions may be most effective when tailored to meet specific management objectives in a given geographical location. There is potential for local differences in factors that influence stand dynamics even within the same ecoregion. Density of beaked hazel (*Corylus cornuta* Marsh.), for example, is likely to be a factor to consider in the understory of some pine-dominated stands in Minnesota (Peck et al., 2012), which is not often the case for mixed-pine forest ecosystems in eastern Upper Michigan. Silvicultural practices such as variable-retention harvesting have also been implemented mostly in managed ecosystems within the northern Lake States, where the primary objective is to enhance structural complexity within stands. Land managers in unmanaged ecosystems on the other hand, may have additional objectives including improving natural regeneration of historically dominant pine species and fuel reduction. Restoration treatments will also need to increasingly focus on larger spatial scales, recognizing the interconnectedness of ecosystems across the landscape, landscape-level processes and biodiversity considerations (Corace et al., 2009; 2012; Franklin, 1993; Franklin and Johnson, 2012).

This is particularly true for areas that are dominated by large tracts of public lands that provide opportunities to implement restoration treatments at larger spatial scales (Corace et al., 2012).

Adaptive management and recovery periods

Our descriptive study of the effects of harvest practices over the past 20 years (see Chapter 4) underscores the need for adaptive management as part of restoration efforts in these mixed-pine ecosystems. Our findings suggest that, despite the harvest treatments, overstory composition is still an important factor that may be negatively influencing regeneration patterns of red pine and eastern white pine in current stands. This type of post-treatment information is critical to land managers as it provides the much needed feedback that then allows for adaptive management strategies to be implemented in a restoration framework. The land manager could decide to conduct additional harvesting, depending on what species are targeted for restoration alongside other management objectives. More broadly, Holling (1978) suggests that land managers may achieve their restoration objectives more effectively by learning from treatment experiences and adjusting their approaches through time.

Closely related to adaptive management is the need for managers to consider the temporal dimensions of resource management. It has been suggested that ecological restoration may be an incremental process whose objectives could take a long time to fully achieve, especially in the efforts to restore ecosystem characteristics that resemble those prior to modification (Allen et al., 2002). Indeed one of the key components of ecological forestry proposed by Franklin et al. (2007) is the need for managers to allow for appropriate recovery periods between regeneration harvests. The studies described as part of this dissertation provide valuable initial responses that can be used for adaptive management. Additional longer-term measurements may, however, be needed to make assessments about post-treatment stand development.

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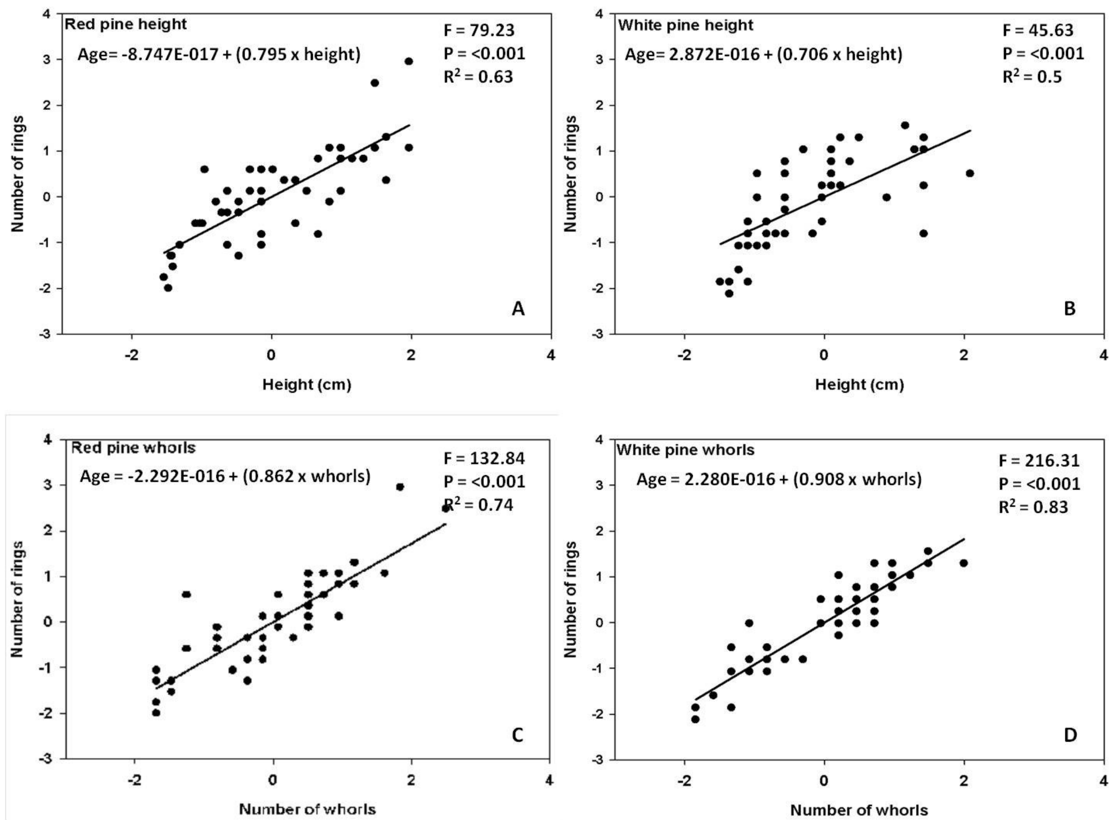
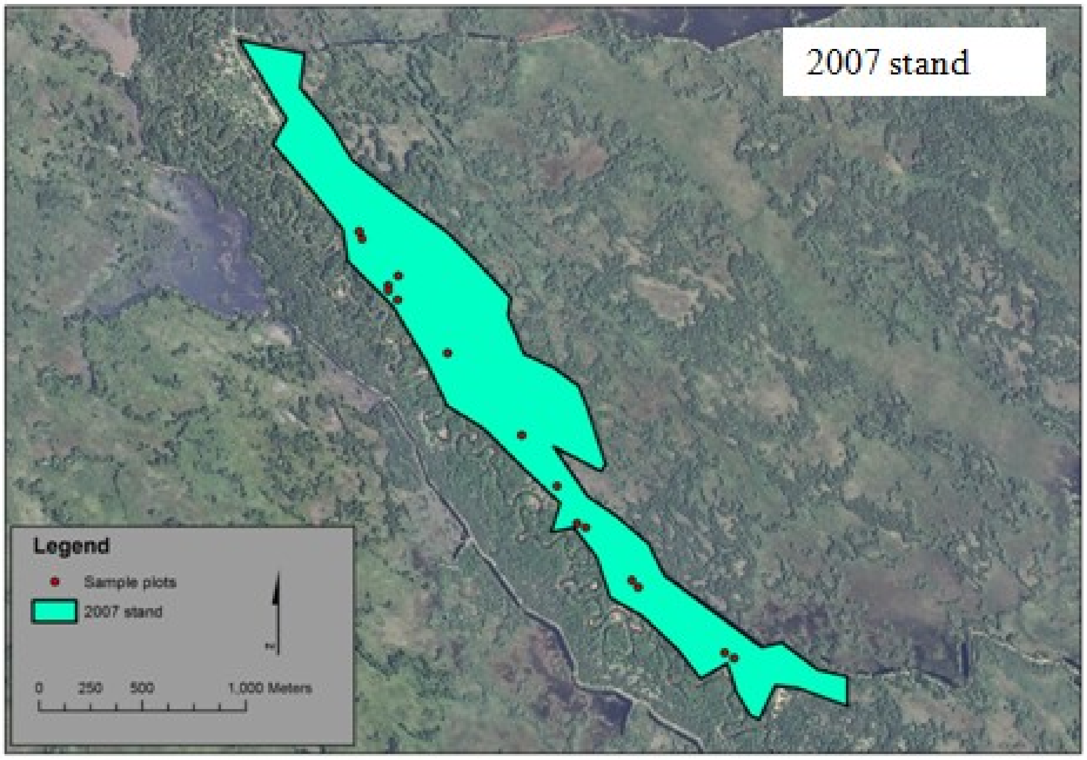
Appendix

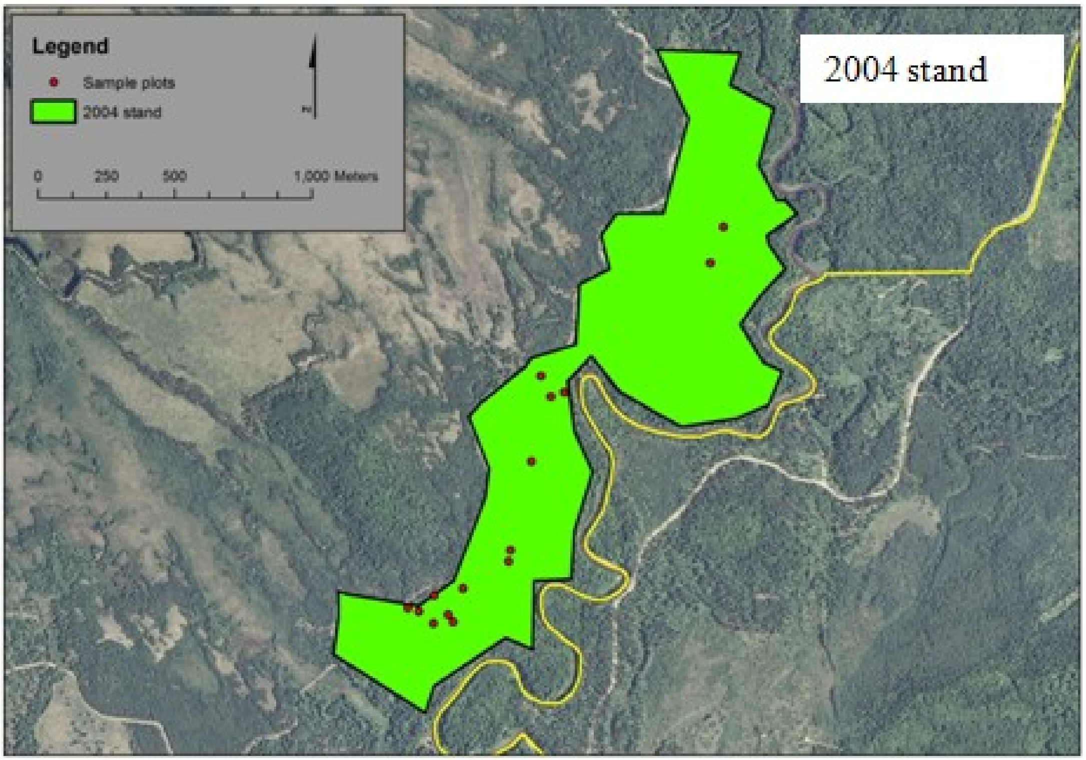
Appendix A. Regression models and equations relating height (A and B) and number of whorls (C and D) to age for both red pine and eastern white pine at Seney National Wildlife Refuge.



Appendix B. Polygons of harvested areas of the 2007 stand and distribution of plots used in the study at Seney National Wildlife Refuge.



Appendix C. Polygons of harvested areas of the 2004 stand and distribution of plots used in the study at Seney National Wildlife Refuge.



Appendix D. Polygons of harvested areas of the 1992 stand and distribution of plots used in the study at Seney National Wildlife Refuge.