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Regeneration responses to management for old-growth characteristics in northern hardwood-conifer forests

Aviva Joy Gottesman

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REGENERATION RESPONSES TO MANAGEMENT FOR OLD-GROWTH CHARACTERISTICS IN NORTHERN HARDWOOD-CONIFER FORESTS

A Thesis Presented

by

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ABSTRACT

Silviculture practices interact with multiple sources of variability to influence regeneration trends in northern hardwood forests. There is uncertainty whether low-intensity selection harvesting techniques will result in desirable tree regeneration. Our research is part of a long-term study that tests the hypothesis that a silvicultural approach called “structural complexity enhancement” (SCE) can promote accelerated development of late-successional forest structure and functions. Our objective is to understand the regeneration dynamics following three uneven-aged forestry treatments modified to increase postharvest structural retention: single-tree selection, group selection, and SCE. In terms of regeneration densities and composition, how do light availability, competition, seedbed, and herbivory interact with overstory treatment effects? To explore these relationships, manipulations and controls were replicated across 2-hectare treatment units at two sites in Vermont, USA. Forest inventory data were collected pre-harvest and 13 years post-harvest. We used linear mixed effects models with repeated measures to evaluate the effects of treatment on seedling and sapling abundances and diversity (Shannon-Weiner $H'$). Multivariate analyses evaluated the relative predictive strength of treatment versus alternative sources of ecological variability.

Thirteen-years post-harvest, the harvested treatments were all successful in recruiting a sapling class with a significantly higher mean than the control. However, in all of the treatments prolific beech regeneration dominated the understory in patches. Seedling densities exhibited pulses of recruitment and mortality with a significant positive treatment effect on all harvested treatments in the first four years post-harvest. Seedling diversity was maintained, while sapling diversity was negatively influenced by herbivory (deer and moose browse) and leaf litter substrate. Multivariate analyses suggest that while treatment had a dominant effect, other factors were strongly influential in driving regeneration responses. Results indicate variants of uneven-aged systems that retain or enhance stand structural complexity, including old-growth characteristics, generally regenerate at adequate and desirable densities depending on site conditions.
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CHAPTER 1: REGENERATION RESPONSES TO SILVICULTURAL MANAGEMENT OF NORTHERN HARDWOOD FORESTS FOR STRUCTURAL COMPLEXITY ENHANCEMENT

1.1. INTRODUCTION

Forest ecosystems make up 30% of the world surface, providing many benefits such as wildlife habitat, nutrient and water cycling, carbon sequestration and storage, and maintenance of global biodiversity (Allen et al. 2010). Due to anthropogenic land use changes as well as global climate change, forested ecosystems are transforming from primary forests to young plantation forests. Although the area of forests designated as legally established protected areas has increased by 200 million hectares, global primary or old-growth forests have decreased every year since 1990 (FAO 2015). Forest plantations have increased about 3.2 million hectares per year since 2010 (FAO 2015). As forest land use change accounts for about 11% of global carbon dioxide emissions (Smith et al. 2014), the future of forests as a carbon sink or as a carbon source is unknown.

To address concerns of climate change, many studies on forest carbon have been implemented in the past decade (Hennigar, MacLean, and Amos-Binks 2008). Alternative silviculture approaches can enhance stand structural complexity, providing increased carbon storage as well as resilience against a more extreme and varied climate by maintaining the ecological integrity of forest systems (Millar, Stephenson, and Stephens 2007). This study examines the regeneration responses to alternative, uneven-aged forestry practices in northern hardwood conifer forests designed to enhance old-growth forest
structure. This comprehensive literature review discusses the current state of research on ecological succession and stand dynamics, traditional and alternative silviculture systems, as well as regeneration responses and limitations to forest management practices. The review concludes with a brief overview of an experimental research program called the Vermont Forest Ecosystem Management Demonstration Project (FEMDP).

1.2. Models of Succession and Forest Stand Development

Ecological succession is often defined as the observation of orderly change within an ecosystem after a disturbance occurs. The study of succession began by observing the sequence of species that successfully invade a site. The Clementsian model of succession emphasized predictable cycles of plant communities that developed toward an equilibrium state called a climax community (Clements 1916). The theory was developed based on observations taken from the development of old, abandoned fields as they progressed along a predictable path of weeds, grassland, shrubland, and forest. This theory of forest succession is a linear, equilibrium model that begins after a disturbance and systematically develops into an old-growth forest (Oliver and Larson 1996).

Assemblages of vegetation were thought to change over time by a process called Relay Floristics. This is described as one group of species colonizing a site after a disturbance, altering the site over time to become less suitable for themselves and more suitable for other groups. A new group of species becomes more competitive and will replace the old group over time. However, Egler (1954) observed a second process of succession, “Initial Floristic Composition,” that has become widely accepted. Initial Floristic Composition differs from Relay Floristics as it assumes that the vegetation that
develops is present in the seedbank before the disturbance occurred. The vegetation is then determined based on a combination of individual life history characteristics, local site factors, and the scale of disturbance (Egler 1954).

Connell and Slatyer (1977) explore these processes further in their three models of succession. Relay Floristics are observed in the facilitation model, which explains that only certain “early succession” species will be able to establish themselves in the newly disturbed site. The vegetation that is suitable for the new, more open environment will thrive and then change the site so that other species will be more suitable to take over. Later successional species will continue colonization and extinction dynamics until the resident species no longer facilitates the invasion and growth of other species. The Tolerance model and the Inhibition model from Connell and Slatyer (1977) begin with the Initial Floristic Composition principle, where any species that arrives or was present is capable of establishing themselves. The Inhibition model differs as early occupants modify the environment, making it unsuitable for anything else to establish itself until another disturbance allows for new establishment. In the Tolerance model early occupants modify the environment to be less suitable for recruiting early successional species; however, it has little to no effect on recruitment of late successional species. Those later successional species are able to invade, or are already present on the site, and can co-exist with early successional species until a climax community is reached (Connell and Slatyer 1977).

Modern concepts of succession have moved away from simple generalizations toward more complex constructs that are site-specific regarding disturbance, environment, propagule availability, and species biology (Spies 1997). More recently, ecologists conceptualize succession in less predictable terms, understanding the diverse changes seen
in the development of vegetative communities. Non-equilibrium models of succession are characterized by varied spatial processes resulting from disturbances and population dynamics such as birth, death, dispersal, and growth under changing environmental conditions (Spies 1997). There are multiple pathways of succession, showing cyclical patterns and complexity based on site-specific environmental changes. This creates a mosaic landscape with vertical and horizontal diversity that was not observed in the succession of abandoned, old fields (Donato, Campbell, and Franklin 2012).

1.2.1 Stand Development

While successional theories are concerned with changes in species assemblages over time, stand development examines changes in forest structure over time. The different approaches to plant successional patterns has led to a variety of models regarding forest stand development. Oliver and Larson (1996) describe stand development as a four-stage, linear process that occurs immediately after a stand-replacing disturbance.

The first stage of development is stand initiation which is influenced by many factors, including a wide range of herbs and woody plants growing together with varied growth patterns. Herbs and shrubs grow laterally, acquiring growing space quickly; however, they typically die off each year while trees continue to add growth. In this stage there are many more species and individuals interacting than other stages, creating patterns of clumped or interspersed regeneration. At this stage, plants are very small compared to their physical surroundings, making them more susceptible to animal damage, freezing or drying soils, and competition from herbaceous plants. The small size of plants also
magnifies effects on growth caused by changes in the microenvironment. As plants grow they dramatically change the environment, making previously unfavorable microsites favorable (Oliver and Larson 1996).

Stand initiation begins with free growth of woody trees and shrubs. Plants get their energy from the originating seed, stump, or root, giving some individuals advantages over others. Once all growing space is occupied, stem exclusion begins. Woody plants initially invade suitable microsites by seeds, sprouts, or advance regeneration. Sometimes suitable sites were previously occupied by annuals or perennials or currently occupied by older plant communities losing vigor. When possible, woody plants invade after any small disturbance releases growing space that was previously occupied. In later development of the stand-initiation phase, taller-growing species will overtop shrubs, increasing low shade and changing the microenvironment. Multiple waves or “seres” of vegetation become dominant, set seed, and disappear, while longer-lived species emerge as dominants (Oliver and Larson 1996).

The stem exclusion phase occurs when space is completely occupied and is characterized by high mortality, resulting in crown differentiation and stratification. In a single-species, single-cohort stand that has no differentiation, wide spacing postpones crown closure and stands accumulate more volume. Narrow spaced stands will grow tall but not wide, and individuals will lose vigor and die. Regardless of density, tree volume growth will slow as trees age and competition for growing space increases (Oliver and Larson 1996). Trees lose lower foliage and branches and the stand enters a stagnation/mortality phase once all the trees uniformly slow in height growth. Differentiation is the process of trees growing into different crown classes: dominant,
codominant, intermediate, and suppressed. It occurs based on variations in tree spacing, microsite, age, genetic makeup, and species characteristics.

After several decades, the overstory changes as soil growing space declines, more swaying leads to crown shyness, and large trees cannot continue to expand their crowns laterally. As large trees become suppressed and die, growing space is released and new growth invades and survives (Oliver and Larson 1996). Minor disturbances will free more growing space as the overstory declines.

According to Oliver and Larson (1996), the fourth stage of forest stand development is the old-growth stage, typically beginning the process at a stand age of 100-500 years in North America. The “true old growth stage” occurs once the trees which invaded immediately after the disturbance have all died, while the “transition old growth” still has trees from previous disturbances. This phase develops as dominant trees begin dying, weakening neighboring trees causing more to die off. The result is a mosaic of young trees regenerating in gaps or dispersed patterns based on regeneration mechanisms, disturbance patterns, and microsite. The old-growth stage describes a process of stand development; however, old-growth can be characterized by a particular structure as well. Oliver and Larson (1996) describe the structure as a Reverse-J diameter distribution with many large old trees at a wide spacing, a variety of species and vegetation, continuous vertical foliage, standing dead trees, and an abundance of coarse woody debris. It is thought to be at an equilibrium with growth and mortality, as well as nutrient conditions (Oliver and Larson 1996). However, alternative models of forest stand development indicate different dynamics exist, resulting in non-equilibrium old-growth that has more productivity and more complex structure.
1.2.2 Alternative Models of Stand Development

Oliver and Larson (1996) provide a framework of stand development that explains the underlying interactions and patterns of growing individuals in a stand; however, the linear, discrete stages of the theory have been re-examined. Most development is observing single-cohort, single-species stands, although touching on multicohort stands. Franklin et al. (2002) found that most structural development processes are continuous and occur throughout the life of the stand. Stand development is described as a cyclical process that takes into account varied disturbances and the creation of biological legacies. Although the development process is broken up into 8 stages, any stage can occur at one time in a stand (Franklin et al. 2002).

The first stage is the disturbance and biological legacy creation stage, which differs from Oliver and Larson (1996), because it does not assume complete removal of the stand. The structures that remain, such as standing live and dead trees, advance regeneration, and coarse woody debris, are described as biological legacies and influence spatial patterning of the invading tree seedlings. The cohort establishment stage follows similar to stand initiation; however, surviving advance regeneration may already occupy significant growing space. Next is the canopy closure stage, which can be brief, occurring more quickly where stands are denser. The biomass accumulation/competitive exclusion stage is characterized by rapid biomass accumulation and competitive exclusion of many organisms. It differs from stem exclusion because many young forests do not grow dense enough to self-thin at this point in development. In the maturation stage, dominant trees begin to die as they reach their maximum height and crown size. The understory is re-established and mortality shifts to density-independent disturbances. The final three stages
are a breakdown of the old-growth stage and describe three developments of old-growth structure: 1. Vertical diversification, 2. Horizontal diversification, 3. Pioneer cohort loss. Vertical diversification produces a continuous canopy of foliage with trees of different tolerances, while horizontal diversification refers to the creation and expansion of gaps. In this model of forest stand development, the final stand is characterized by structural complexity and spatial heterogeneity (Franklin et al. 2002). By retaining structural complexity, the forest stand continues to store carbon, cycle nutrients, support wildlife habitat, and provide a continuous supply of regeneration. Franklin et al. (2002) accepts variability within the eight stages of stand development, implying management should be flexible and creative based on site-specifics and disturbance regimes. While Oliver and Larson (1996) provide a useful framework for timber management, the model by Franklin et al. (2002) is intended for the management of multiple, new objectives.

This process of stand development is a result of competitive interactions. Additionally, disturbance frequency and type influence the pattern of dominant species in the canopy (Oliver and Larson 1996). There are competing hypotheses describing biomass dynamics in the old-growth stage of forest development. The majority of previous studies show a peak and stabilization of biomass in old forests (Bormann and Likens 1979; Tyrrell and Crow 1994); however, new studies have shown the potential for biomass accumulation in northern hardwoods of both greater magnitude and duration than previously understood (Keeton et al. 2011). If older, more structurally complex forest stands continue to increase in biomass, their ability to store carbon will increase as well. The structural and spatial heterogeneity created by persisting living and dead structures seen in stand development, implies that forestry approaches need to emulate the processes giving rise to this
complexity. This has encouraged different approaches to sustainable forestry, including disturbance-based, structural retention silviculture (Gustafsson et al. 2012). This is done by retaining various structures at the time of harvest, longer rotations, and active creation of heterogeneity in the managed stand.

Natural disturbances and other sources of ecological variability interact with stand development processes to create patterns on the landscape that are spatially and temporally-dependent. The intensity, frequency, and amount of overstory removed from a natural disturbance will influence stand development. On the tree-level, a disturbance frees up growing space allowing new individuals to establish or existing individuals to grow bigger. The survival of individuals depends on seed source and regeneration mechanisms of present species, as well as general site conditions (Oliver and Larson 1996). Disturbances affect the heterogeneity of a landscape, creating a mosaic of successional stages depending on the frequency and intensity of the disturbance regime (Spies 1997). The disturbance can create localized patches of regeneration or dispersed uniform regeneration. The size and shape of the disturbed area influences stand development by determining how much of the stand is under the influence of the edge, as well as how easily seeds blow in from adjacent trees. Therefore, the disturbance greatly influences the species composition and structure of the future stand (Oliver and Larson 1996).

Northern hardwood forests in the northeast U.S. are a product of a long history of natural and anthropogenic disturbances. These natural disturbances include wind, ice, insects, fungal pathogens, beavers, floods, and fire. Disturbances range in scale and frequency; most dominant are intermediate severity disturbances, such as ice storms and
microbursts (Seymour, White, and deMaynadier 2002). Windstorms are responsible for most major disturbances, although little evidence is available on the exact size range of blowdowns in the northeast (Lorimer and White 2003). These relatively frequent, partial natural disturbances created a finely patterned, diverse mosaic dominated by late successional species and structures (Seymour, White, and deMaynadier 2002).

Seymour et al. (2002) conducted a literature review on disturbances in the northeast and found most disturbances to be either small, frequent events forming canopy gaps, or huge, stand-replacing events that were extremely infrequent. Natural canopy gaps are created every century, while a stand-replacing windstorm impacting 10 + ha only occurs every 1,000 to 100,000 years (Seymour, White, and deMaynadier 2002). When these events were plotted on a graph, the disturbance area increases exponentially as the return interval lengthens, suggesting disturbances in the northeast are spatially and temporally dependent. Although medium size disturbances were not accounted for in Seymour et al. (2002), various studies indicate intermediate intensity disturbances may be more prevalent than previously recognized (Ziegler 2002; Hanson and Lorimer 2007).

The disturbance severity dictates how much of the forest understory, floor and soil is destroyed, which favors certain regeneration mechanisms. Regeneration mechanisms are based on specific species strategies of seed dispersal, frequency of a good seed year, preferred seed bed, seed predation, and competing vegetation. Therefore, disturbances can promote certain species. Minor disturbances and the formation of canopy gaps impact stand development by releasing advance regeneration and establishing new seedlings, generally shade tolerant/intermediate. If trees surrounding the gap are not vigorous, frequent minor disturbances can lead to gap expansion and increased
vertical/horizontal structural diversity (North and Keeton 2008). If nearby trees are strong then there will be accelerated growth of adjacent overstory trees. With a small enough gap, canopy trees will reach crown closure quickly and density-dependent mortality could occur. Ecological variability (climate, soils, invasive vegetation, etc.) impacts stand development in the same way as a disturbance, by modifying the system to benefit certain species regeneration mechanisms and early growth patterns. Geophysical heterogeneity coupled with climate variability and disturbances create a mix of forest development stages, structural conditions and species compositions on the landscape (North and Keeton 2008).

The processes of carbon sequestration and carbon storage in forest ecosystems are often misconstrued due to the complex spatial and temporal dynamics of stand development. Carbon budgets will appear different at a certain point in time, based on the scale of an individual tree or the entire stand. In a young forest, trees grow freely with increasing photosynthetic capacity. At the stem exclusion stage, the stand has the highest rates of carbon uptake (Harmon 2001). Carbon sequestration rates are high for each young tree; however, simultaneously the stand has large amounts of debris from the harvest or from density-dependent mortality that is decomposing and emitting carbon (Harmon 2001). This decomposition and respiration reduces carbon storage rates. With an increase in disturbance frequency (i.e. repeated fires, plantation forestry), more young forests will grow and sequester carbon. However, an older forest stand that matures into a complex structure has greater carbon storage capacity in all of the pools, including soil carbon (Pregitzer and Euskirchen 2004). Observed at the tree-level, older trees are dying regularly.
and lose carbon as an individual tree decomposes, which has led to the assumption old-growth forests are a carbon source due to their dying structural components. Older trees do fix less carbon per unit of light absorbed because there is a reduction in photosynthetic capacity with age (Ryan, Binkley, and Fownes 1997); however, the old-growth stand is actually storing more carbon over time, mostly in aboveground biomass (Harmon 2001; Keeton et al. 2011).

There are competing hypotheses describing biomass dynamics in the old-growth stage of forest development. The majority of previous studies show a peak and stabilization of biomass in old forests (Bormann and Likens 1979; Tyrrell and Crow 1994); however, new studies indicate the potential for biomass accumulation in northern hardwoods of both greater magnitude and duration than previously understood (Keeton et al. 2011). If older, more structurally complex forest stands continue to increase in biomass, their ability to store carbon will increase as well. It has been found that low intensity silvicultural intervention that retains stand structural complexity can accelerate or increase the “old-growthness” of a forest ecosystem (Bauhus, Puettmann, and Messier 2009). There are many studies that show structural complexity can be enhanced to promote multiple functions in a forest, including carbon storage (Keeton 2006).

Forest stand dynamics indicate that species diversity is highest during stand initiation because there is the most available growing space and the least competition (Oliver and Larson 1996). Annuals, perennials and grasses compete among tree seedlings. Once all the growing space is occupied, biodiversity decreases with the increased competition and shaded environment (Oliver and Larson 1996). Studies have shown that
understory plant diversity increases in the mature and old-growth stages of a forest (Gao et al. 2014). The increase in vascular plants with time, peaking in old stands, could be due to fewer stand-replacing disturbances or may be a result of microhabitat heterogeneity (Halpern and Spies 1995). Additionally, with an increase in large, single tree mortality, vertical structural diversity is higher, providing multiple layers of habitat for different plant species groups (Gao et al. 2014).

Nutrient cycling changes through stand development beginning with high rates in young trees because net growth is focused on nutrient rich foliage and root development. An individual tree will rapidly take in nutrients until the canopy closes and then distributes the resources and slows uptake. Once the canopy is developed, two-thirds of the nutrients required for growth are obtained by retranslocation from dead and dying tissues (Miller 1995). Trees also recycle nutrients through the decomposition of leaf litter around the root system. An early peak in nutrients, sometimes earlier than leaf area peak, is balanced and maintained later in stand development through both tree and stand interactions with nutrients (Miller 1995).

The stand level trend shows CWD and microbial N uptake increasing in old-growth and second-growth forests (Fisk, Zak, and Crow 2002). Later in development, there is a large difference between nutrient uptake and nutrient release as abundant litter from die-off decomposes. The new cohort is rapidly taking in nutrients faster than they are producing litter (Sprugel 1984). Due to the sensitive balance of nutrient cycling, nutrient loss can be significant immediately after disturbances (or intense harvests), indicating the importance of retaining structural components that supply nutrients to the system (Sprugel 1984).
1.3. Silviculture

Silviculture is the discipline of providing sought after values from the forest, at the fullest level a site can sustain (Troup 1921). It is an art and a science, as it combines biological knowledge of trees with the anthropogenic needs and desires of humans. Various ecosystem services are valued in forests including wildlife habitat, recreation, timber commodities, carbon storage, and other diverse ecological functions. Through the management of forest stands, silviculturists establish and maintain healthy communities of trees and other vegetation, providing a host of benefits in the form of biological resources. Management includes the control of establishment, composition, structure, and growth in forest stands, based on site and physical environment (Puettmann et al. 2015; Nyland et al. 2007). However, the intention is to foster ecosystem services beyond the stand, at the forest and landscape level. This is done by advising landowners to manage their unit of land in a manner that is sustainable for their needs and for the ecology of the landscape (Nyland et al. 2007).

The silviculture system is managed by changing the tree community based on the desired ecosystem services and forest commodities. Management is performed through a variety of harvest intensities and frequencies, prescribed and completed at different stages of stand or age class development. The silviculturist formulates a management plan for the regeneration, tending, and harvesting of the stand. The decided upon treatment should be ecologically acceptable at all scales (Nyland et al. 2007). Historically, silviculture was based on the management of land to grow and harvest commodities, creating revenue for landowners. The focus was to efficiently regenerate forests that increase wood production and quality (Puettmann et al. 2015). In the late 1950s, major public criticism occurred due
to the management of public lands after World War II. Public reaction to intensive harvesting lead to new policies promoting multiple-use management (Nyland et al. 2007).

1.3.1 Traditional silviculture

Conventional, even-aged forestry treatments are relatively intensive and often produce fully stocked even-aged stands. Clearcutting is the most intensive harvest, which involves removing all of the trees within a designated stand. A silviculture clearcut allows 100 percent full sunlight conditions at the forest floor (Ward et al. 2013). The seed tree method is similar to clearcutting; however, remnant mature trees are left to provide a seed source for a new cohort to regenerate. A shelterwood system retains a sheltering overstory to protect the regenerating seedlings and saplings; while providing a seed source for a new cohort. If over 50% of the next rotation is retained, shelterwoods can be described as a two-aged system that can regenerate mid- to late-successional species (McEvoy 2004).

The irregular shelterwood is designed to mimic small-scale disturbance regimes; however, it is a regeneration method with establishment as the main goal. Regeneration of shade tolerant species will dominate the stand. However, based on objectives and the size and spatial patterns of trees removed, shade intolerant species may also become established. The expanding-gap shelterwood and the extended shelterwood will encourage more shade intolerant species, while the continuous cover promotes 90% tolerant species (Raymond et al. 2009). Many trees are retained in the final removal, promoting the growth of larger size classes. The continuous cover irregular shelterwood system is suitable for developing late-successional characteristics because it promotes shade tolerant and midtolerant species characteristic of mature northern hardwood forests.
The selection system is used to sustain a regular yield of products and values from a stand, by stabilizing forest conditions and structures and by the regular replacement of mature trees with new ones (Nyland et al. 2007). Trees are selected based on timber management goals, and must be consistent with the residual stocking goals. Two common forms of uneven-aged silvicultural systems are the single-tree selection and group selection systems. In single-tree selection, small scattered canopy gaps are created using target diameter distributions to slightly increase filtered sunlight to the forest floor; however, only limited direct solar energy reaches the ground level. The environment remains stable over time, with limited reduction of root competition and small decreases in the withdrawal of moisture and nutrients from the soil. If performed correctly with frequent, low-intensive selection harvests, the structure of the stand should remain relatively stable as well. The group selection system removes clusters of mature trees from a proportion of the stand area, leaving large openings to encourage a new age class to form in groups rather than dispersed among the stand. This allows almost full sunlight conditions near the middle of gaps, promoting middle to low shade tolerant species, while maintaining a balance among age classes (Nyland et al. 2007). A third type of uneven-aged silviculture combines the single-tree and group systems, making the patch-selection method. This system allows for a new age class to regenerate as groups within the patches and uniformly dispersed across the stand. It provides a high degree of vertical structural diversity, as well as a limited component of small-scale horizontal structural diversity.
1.3.2 Alternative approaches to silviculture

The structural and spatial heterogeneity created by persisting living and dead structures (e.g., Biological legacies) informed forestry practices to utilize approaches that emulate the processes giving rise to this complexity. Interest in maintaining multiple ecologic objectives lead to the practice of disturbance-based, structural retention silviculture (Gustafsson et al. 2012). This is done by retaining various structures at the time of harvest, longer rotations, and active creation of heterogeneity in the managed stand. Many uneven-age, multi-species silviculture regeneration systems can be modified to promote late-successional characteristics. This has generated the development of a variety of uneven-aged management strategies including: green tree retention (Franklin et al. 1997), ecological silviculture (Benecke 1996), continuous cover forestry (Garfitt 1995), and near-natural forestry (Benecke 1996). These systems aim to provide ecological functions to increase connectivity across the landscape and to manage the matrix of unprotected forestland, meeting both economic and ecologic objectives.

Variable density thinning (VDT) attempts to distribute both vertical and horizontal structure in a stand, allowing for a site-based spatial arrangement. Using a grid system, the forester applies a thinning treatment on each cell, creating “gaps” where advance regeneration or natural gaps exist, and “skips” in areas with coarse woody debris or unique vegetation. The objectives are to mimic natural disturbance and self-thinning (allogetic and autogenic) mortality. By designating a certain proportion of cells “skips”, “gaps”, and “clumps”, some areas mimic a major disturbance while other parts mimic undisturbed land. Studies have found the spatial heterogeneity of a late-successional forest can be achieved through VDT (O’Hara 1996; Harrington, Roberts, and Brodie 2005).
The continuous cover irregular shelterwood system, also called *Badischer Femelschlag*, is a similar treatment to VDT though varied in objectives. The goal of VDT is ecologically driven, to create natural conditions that sometimes result in suppression of regrowth. The continuous cover shelterwood maintains the appearance of a mature forest, and could appear similar to a patch selection system. Unlike a selection system, the continuous shelterwood does not attempt to create or manage for a diameter distribution (balanced/unbalanced), and the management plan has no formal cutting cycle. Trees are harvested based on the species autecology and site characteristics. This allows for flexibility in management, but produces an inconsistent supply of timber. The irregular shelterwood is an important approach to restoring irregular uneven-aged stands and diversifying northern hardwood forests (Raymond et al. 2009).

Conventional treatments, such as single-tree and group-selection systems, are management options with the potential to be modified to increase late-successional forest structure. Often selection systems are designed to produce a balanced distribution of diameter classes, resembling a Reverse-J distribution; however, a rotated sigmoid distribution can be implemented to re-allocate basal area in larger diameter classes. The rotated sigmoid matches that of old-growth forests in the northeast, depending on disturbance history and species composition (Goff and West 1975; Goodburn and Lorimer 1999; Leak 2002). The traditional BDq marking guide for a selection system can be modified to increase late-successional structural objectives (Keeton 2006). This is done by increasing the residual basal area and setting a large maximum tree diameter. A low $q$-factor of 1.3 results in more big trees and less small trees, promoting a mix of shade-tolerance within the younger trees. Large trees provide extensive benefits to the ecosystem
including nutrient redistribution and increased availability, habitat for plants, fungi, and wildlife, altered microenvironment, and providing a source of propagules and seeds (Lindenmayer and Laurance 2016).

Other structural objectives can be met through a variety of silvicultural techniques. These techniques can be implemented in any of the above silviculture systems or others, to enhance late-successional structures. To create a vertically differentiated canopy, single-tree selection can be implemented in areas where advance regeneration exists or a new cohort could establish. Trees can be girdled to promote mortality at different time intervals and the creation of snags (Keeton 2006). By creating tip-up mounds, foresters can create the pit-and-mound topography characteristic old-growth northern hardwood forests (Dahir and Lorimer 1996). Variable horizontal densities are created by variable density marking and harvesting trees clustered around “release” trees. Full or partial crown release of large trees accelerates growth in even the largest or oldest trees (Singer and Lorimer 1997; Keeton 2006).

Structural enrichment forestry, variable retention harvesting, and disturbance-based forestry are three approaches to balance ecological and economic objectives. These techniques share the goal of managing the landscape with forest structures and age classes represented in appropriate densities and spatial distributions for the stand and landscape.

In the northeast, the disturbance regime is dominated by relatively frequent, partial disturbances (Seymour, White, and deMaynadier 2002), such as wind, ice, beavers, pathogens, and insects. Silviculture can alter forest structure by modeling the vertical and horizontal structures created by those natural disturbances and successional dynamics. Many studies examined the size, frequency, and spatial distribution of these natural canopy
gaps in hardwood-hemlock forests (Runkle 1982; Foster and Boose 1992; Boose, Chamberlin, and Foster 2001; Seymour, White, and deMaynadier 2002), providing a guideline for silviculturists in the northeast.

1.4. Forest Regeneration Dynamics

Regeneration and seedling establishment is a critical process in stand development and forest succession, therefore it is an essential aspect of silviculture. Natural regeneration can occur by vegetative methods or by seed dispersal. Seed supply, seedbed, and environment are the three main biophysical factors that influence regeneration success (Stewart and Rose 1990). However, there are often unpredictable limitations to success such as herbivory, competing vegetation, and climatic factors. Natural regeneration can occur when trees produce abundant and viable seeds or vegetative propagules (Nyland et al. 2007). The efficiency of the seed supply depends on the source (e.g. seed trees, shelterwood, uncut timber edge), species type, production of seed, quality (viability), dissemination, and damage to seed supply (e.g. insects, rodents). Under optimal seedbed conditions, seedlings will germinate and establish. This is dependent on the microenvironment. These factors include shade, depth of organic matter, ground vegetation, soil texture, animal damage, disease, erosion and deposition (Stewart and Rose 1990).

There are many environmental factors influencing regeneration success: insolation, moisture, drought, and frost are the most significant. Insolation refers to light intensity, light quality, and heat. Moisture can influence regeneration success from
changing snow patterns to summer storms. Frost can lead to physiological damage, soil detachment, and frost heaving. The impacts of these factors may increase or decrease depending on a physiographic site (e.g. aspect and elevation). These impediments can be divided into the categories of external agents and intrinsic site factors, both determining the success of regeneration (Nyland et al. 2007).

Each species has its own silvic characteristics including shade tolerance, early relative height growth, site requirements, and good seed crop time intervals. A recent study at Hubbard Brook observed that the establishment of sugar maple regeneration is determined primarily by biotic factors such as size of seedlings and the prevalence of pathogenic fungi and caterpillar herbivory (Cleavitt et al. 2014). These factors coupled with abiotic factors (e.g. elevation and slope) revealed complex interactions influencing the long-term (7-year) survivorship of seedlings (Cleavitt et al. 2014).

Mixed northern forests are comprised of hardwood and conifer species in the northeast. A mixed species stand can support diverse species with a range of regeneration mechanisms and requirements. Three hardwood species that make-up a large component of mixed northern forests are sugar maple (Acer saccharum), American beech (Fagus grandifolia), and yellow birch (Betula alleghaniensis). These three species together are often found in mid- and late-succession forests, although yellow birch can be found in early-successional forests as well (Beaudet and Messier 2008). Each species has different regeneration niches that allow it to survive as a component of the system; however, changing stand dynamics can lead to increased competition for growing space between species.
Sugar maple is a very shade tolerant species that requires high moisture, nutrient rich soils (Colombo, Wagner, and Ontario. Ministry of Natural Resources 2001). Sugar maple seeds are wind dispersed and medium in weight, therefore a litter seedbed is preferred. Seeds are dispersed around a hundred meters in the late summer, between August and September. Sugar maple seeds can survive two years. Sugar maple can also regenerate by stump sprouting; however, sprouting abilities are not particularly strong.

American beech is the most shade tolerant species with a wide range of soil preferences (Colombo, Wagner, and Ontario. Ministry of Natural Resources 2001). It prefers a medium amount of moisture and nutrients, but can survive on many different types. Beech also prefers a litter seedbed type; however, is much more prolific at regenerating vegetatively through root sprouts. This gives beech an advantage on poor sites with low nutrients. Beech seeds are heavy and drop locally around the seed source, although animals, such as bear, are dependent on the nuts and can disperse seeds across larger ranges (Wagner et al. 2010).

Yellow birch is an intermediate shade tolerant species, that requires high moisture and very high nutrients in the soil. Yellow birch prefers a humus mix seed bed, often germinating on coarse woody debris (Marx and Walters 2006), mossy rocks, and scarified forest floor. Unlike the previous two species, yellow birch cannot regenerate on leaf litter. Yellow birch seeds are very light and can travel over four times the distance of a sugar maple seed. Both beech and yellow birch disperse their seeds in early winter, around November, and their seeds can live for a year. Yellow birch has weak stump sprouting abilities, but it does occur.
Sugar maple has the longest time between good seed crops, as well as the most variability between good seed crop years. Yellow birch has a good seed crop between one and three years; beech is between the two. Once the seeds have germinated, American beech has slow early relative height growth; while sugar maple is a bit faster, and yellow birch (which grows moderately fast) is the fastest out of the three species (Colombo, Wagner, and Ontario. Ministry of Natural Resources 2001).

The diverse regeneration mechanisms of beech, yellow birch, and sugar maple allow for this mix of hardwoods to grow together without completely outcompeting each other. Each requires a different level of canopy removal, yellow birch will regenerate with 0.1 ha gaps and 40% stand density (Colombo, Wagner, and Ontario. Ministry of Natural Resources 2001). Sugar maple and yellow birch only need 0.05 ha gaps with 60% (maple) and 75% (beech) canopy density retained (Colombo, Wagner, and Ontario. Ministry of Natural Resources 2001). After a harvest or natural disturbance, intermediate intolerant yellow birch occupies tip-up mounds, downed logs, and other humus-mix substrates, which are often abundant after disturbances. It grows quickly, taking advantage of the available light and soil space. Simultaneously, sugar maple advanced regeneration can remain in the mid-canopy from before the disturbance, growing tall when light and nutrients are available (Leak 2005). Depending on the disturbance, beech may aggressively root sprout and remain as advance regeneration, potentially outcompeting the sugar maple. The regeneration dynamics of these species differs enough to promote co-existence; however, still similar enough that interspecies competition can dictate future stand development (Ward et al. 2013).
1.4.1 Limitations to Regeneration in Northern Hardwoods

In New England there are observed trends of climate change showing an increase in temperature and precipitation, projected to continue at rates dependent on emission scenarios (Rustad et al. 2012). Increased heavy rain events have occurred over the past century, and will continue in the future, along with more drought events in the growing season. It is still unknown how forests will respond to the sudden changes including: longer growing seasons, increased drought, increased storm events, changing suitable habitats, high atmospheric CO2, and new pests and diseases (Rustad et al. 2012). With multiple stressors occurring more frequently, it is uncertain what the combined influences will be on natural regeneration dynamics.

Long-term research and management experience in northern hardwood forests are critical to determine the regeneration dynamics of silvicultural systems. Limitations to regeneration in northern hardwood forests include, interfering species, disease, pests, herbivory, and climate change (Ward et al. 2013). With combined natural and anthropogenic stressors impacting forest dynamics, it is important to gain insight on regeneration responses to silvicultural treatments.

The main regeneration dynamics to be concerned with when managing for late-successional characteristics is sustaining shade intolerant and intermediate species. With low-intensity harvests and high structural retention, it could be challenging to create conditions that provide enough light for species such as birch, aspen, cherry, or oak. These species are high-value hardwoods often desirable for timber production.

Species that interfere with regeneration in northern hardwoods are American beech (*Fagus grandifolia*), striped maple (*Acer pensylvanicum*), hobblebush (*Viburnum*...
*alnifolium*), hay-scented fern (*Dennstaedtia punctilobula*), New York fern (*Thelypteris noveborecensis*), bracken fern (*Pteridium aquilinum*), raspberries (*Rubus* spp.), and pin cherry (*Prunus pensylvanica*) (Bashant et al. 2005). When shared resources are reduced through inter-specific competition, these species are advantageous in rapid growth, tall stature, and persistence. At high densities, these interfering species may cast such a heavy shade that smaller seedlings of any other species may die or become suppressed (Maguire and Forman 1983). Hay-scented fern does this by creating a root mat and dense frond litter that prevents adequate root development, reduces light quality, and employs allelopathy to prevent seedlings from establishment. Altering or disturbing the forest through increased understory light, abundant soil moisture, fire, and herbivory all promote fern proliferation (Bashant et al. 2005).

American beech thickets are a result of compounding effects of beech bark disease, herbivory, and forest management history. Through a combined effort of scale (*Cryptococcus fagisuga*), canker-causing fungus (*Nectria coccinea* var. *faginata*) and heart rot fungi, the disease decimated the largest beech trees and weakened young American beech populations (Houston 1975). American beech is a canopy species that dominates in northern hardwood forests along the North American east coast. In 1932, beech bark disease moved down from Nova Scotia into Maine (Ehrlich 1934) and now affects most of northern New England. The cumulative effect is a rapid decrease of large overstory beech trees and a drastic increase of understory beech density resulting from the species regeneration advantages. Beech reproduce both sexually and vegetatively. Beech vegetative reproduction (i.e. root suckering, sprouting) occurs when shallow roots are wounded, due to freeze-thaw patterns, logging, and disease (Wagner et al. 2010). As a
highly shade-tolerant species, they outcompete other species and can persist below a full canopy (including its own canopy) for years in light levels that inhibit development of less shade-tolerant species (Beaudet and Messier 2008). In northern hardwood forests, altered disturbance regimes have permitted the combination of these two regeneration advantages to enhance beech fecundity, forming pure beech thickets, resulting in not only the abundance of beech saplings but the suppressed regeneration of other tree species, thus reducing forest diversity. Light cuttings tend to promote the development of beech thickets to the exclusion of other species.

Herbivory by deer and moose can enhance the problem of beech thickets and interfering shrub species. Deer prefer to browse species such as sugar and red maple, oaks, white pine, hemlock, and white ash (Bashant et al. 2005). Overabundant deer populations combined with selective cutting practices causes stands to shift to a species mix dominated by beech, red maple, and non-commercial species (Bashant et al. 2005). Moose herbivory can also impact the regeneration of commercial species, by selecting hardwood species of value and suppressing sapling growth (Faison et al. 2010). Similar to deer, the presence of moose may shift forest species to be softwood dominated by selectively browsing hardwood species (Andreozzi, Pekins, and Langlais 2014).

1.5. Regeneration Responses to Silviculture Systems

There are a variety of long-term research studies on the effects of silvicultural treatments in northern hardwood forests. Dating back to 1923, research from the Dukes Forest primarily, as well as the Argonne Experimental Forest in northern Michigan, was responsible for the “Arbogast Guide”, one of the most influential guides for single-tree
selection (Kern et al. 2014). The Partial Cutting Study installed in 1926 at Dukes EF was created in response to a shift in the cultural paradigm away from clearcutting towards “near natural” forestry practices (Gronewold, D’Amato, and Palik 2010). This was done by promoting multiple age classes within stands through the creation and maintenance of a Reverse-J diameter distribution. In the long-term, single-tree selection increased the dominance of shade-tolerant sugar maple, leading to the development of special cutting practices for mid-tolerant species (Eyre & Zillgitt 1953; Metzger & Tubbs 1971; Kern et al. 2014). Even-aged stands could regenerate less shade-tolerant species and increase tree species richness under a shelterwood system with release and thinning. Uneven-aged stands were able to regenerate yellow birch successfully within group openings (0.04 ha) near seed trees, and with scarification (Kern, Montgomery, et al. 2014). Although group selection openings can fill with competing vegetation, fall harvesting has been found to give yellow birch an advantage for recruitment (Falk et al. 2010).

Studies from experimental forests help inform management practices and silvicultural guidelines for northern hardwood forests throughout the Northeast. Early results from the Bartlett Experimental Forest indicated 3 years post-harvest regeneration in young even-aged hardwoods might not be successful because of vegetative understory competition (Marquis 1965). However, after 47 years patches showed yellow and paper birch were dominant species in patch centers. The experimental treatment included 10 patches that averaged 0.2 ha each, removing all existing beech thickets within each patch. Results suggest patches can successfully regenerate yellow and paper birches, however, the removal of vigorous beech thickets may be a critical component (Leak 2003).
In a two-stage shelterwood system, three important factors found to regenerate desirable northern hardwood species include: hunting to control deer density, killing of heavy beech understories, and retaining adequate basal area (Kelty and Nyland 1981). The influence of deer browse, understory vegetation, overstory removal, and silvicultural treatment were tested on regeneration at the Huntington Forest in the Adirondack Mountains in New York (Ray, Nyland, and Yanai 1999). Silvicultural treatment included understory removal and beech removal from the stand. Intensive hunting reduced deer populations to reduce browsing of vegetation. Successful regeneration occurred with densities above the minimum criteria suggested by Tubbs (Tubbs 1977), and equal numbers of established tolerant sugar maple and beech, and less-tolerant yellow birch and white ash (Kelty and Nyland 1981).

In a selection system, uneven-aged northern hardwood stands with a well-balanced diameter distribution can be repeatedly cut at 12- to 15- year intervals (Mader and Nyland 1984). Additionally, sapling growth under the selection system could be 10 years ahead of planted saplings, enhancing structural stability of uneven-aged stands (Donoso, Nyland, and Zhang 2000). The treatment included the removal of all financially mature trees; regeneration of a new age class to replace the mature trees; and tending of the immature classes to stimulate growth and control development. After six years, 60-70 percent of saplings 6ft tall to 1 in dbh, or 1 to 2 dbh, were commercially valuable species (sugar maple, white ash, yellow birch, black cherry).

More recent studies explore the regeneration dynamics in disturbance-based silvicultural treatments (Bolton and D’Amato 2011; Arseneault et al. 2011; Forrester et al. 2014). In Northeastern Minnesota, the regeneration response to disturbance-based harvest
gap treatments was observed after 6 or 7 years post-harvest. Gaps were 0.008 to 0.07 ha, mimicking the natural disturbance patterns of the region. It was found that gap size and downed coarse woody debris influenced regeneration rates. Density of seedlings and saplings was greatest in large gaps (>0.02 ha) compared to small gaps in the intact forest floor. Sugar maple dominated the seedling (37%) and sapling (82%) layers with highest relative density among combined stem densities (Bolton and D’Amato 2011). Another disturbance-based silviculture experiment is the Acadian Forest Ecosystem Research Program in the coniferous/mixed deciduous-coniferous forest of central Maine. According to Arseneault et al. (2011), two treatments were studied including: large-gap (0.1-0.2 ha) extended group shelterwood with reserves, and small-gap (0.05-0.1 ha) “expanding” group selection. Results indicated both treatments increased shade-tolerant and shade-intolerant species indiscriminately. Larger gaps favored the growth and survival of mid-successional species such as red maple and white pine, while small gaps favored late-successional species such as eastern hemlock and spruce. The increase in light availability was found to be a more significant influence than treatment, as different sized gaps encouraged different species (Arseneault et al. 2011).

The regeneration response to modified group-selection openings (group selection with seed tree reserves) nine years post-treatment in upper Michigan, suggest openings enhance the representation of mid-tolerant species, though the long-term forest composition may not be impacted. Plant dynamics in canopy gaps may be exceedingly controlled by prior stand conditions. Gap size, along with environmental conditions of past and present were the greatest indicators of regeneration success, as the experimental treatment involved building gaps around yellow birch seed trees. Sugar and red maple
regeneration dominated all sites, in greater densities in the group-selection openings, compared with the single-tree selection sites. Yellow birch densities increased with opening size; however, survival and growth were inhibited by multiple years of drought conditions (Poznanovic, Webster, and Bump 2013).

Other regeneration studies suggest there may be no consistent trends in the relative growth responses of shade-tolerant and midtolerant tree species to increased light and gap size. A series of small (0.005), medium (0.02 ha), and large (0.038 ha) sized gaps were harvested at the Flambeau River State Forest, in Wisconsin, and deer fences were installed on 10 plots to measure the influence of herbivory on sapling growth. Gap size was not a significant factor to sapling growth rate, for both shade-tolerance groups. Deer browse affected the sprout layer; however, sugar maple advance regeneration was above browsing height and predominated in the upper height classes (Forrester et al. 2014).

There are fewer studies in northern hardwood forests that specifically study the regeneration response of structural retention to accelerate old-growth characteristics. In one study, results indicate seedling densities are significantly impacted by the patch selection treatment (0.12 ha gaps), with tolerant species (maple and beech) dominating regeneration. The highest seedling densities were in the ‘no retention’ treatment, then the ‘legacy retention’ treatment, then the ‘downed woody debris’ treatment, with the control containing the lowest seedling density (D’Amato, Catanzaro, and Fletcher 2015).

Regeneration results tend to be variable and dependent on multiple factors. In a sugar maple-yellow birch stand, regeneration was positively influenced by harvest gaps, however densities depended on understory vegetation control as well as soil scarification (Gauthier, Lambert, and Bédard 2016). Another study found yellow birch establishment to
be more successful and highly dependent on deadwood rather than mineral soil alone (Lambert et al. 2016). From managing diverse seed beds to understanding herbivory patterns, there are many challenges for successful regeneration of desirable species in gap-based silviculture due to many limitations beyond the light environment (Kern et al. 2016). Factors such as temperature and overstory tree size diversity have been assessed and determined to play an important role in regeneration species richness and density (Bose et al. 2016). Regeneration is already highly variable based on all of these factors, therefore the additional uncertainty of climate change will have a variety of species-specific impacts. Species such as sugar maple, red maple, yellow birch, and American beech are predicted to establish successfully with an increasing soil water deficit, while key conifer species may decline under the same conditions (Canham and Murphy 2016). Warmer, wetter climates in the eastern U.S. predicted under climate models will likely result in higher seedling mortality regardless of competition (Canham and Murphy 2016).

1.6. The Vermont Forest Ecosystem Management Demonstration Project (FEMDP)

The critical shift from traditional logging practices to more ecological forestry has begun; however, it is a challenge based in cultural goals and traditional practices (Gustafsson et al. 2012). The Vermont Forest Ecosystem Management Demonstration Project (FEMDP) is a long-term study that explores forestry techniques balancing ecological and economic forest management objectives. The FEMDP is testing the
hypothesis that structure-based and disturbance-based silviculture can sustain a broader array of ecological functions and biodiversity, while providing economic opportunities through timber revenue generation (Keeton 2006; K. J. Smith et al. 2008; Ford and Keeton 2016).

Although similarly designed to retain structure, the treatments differ in harvest approach through varied spatial patterning, level of retention, and the specific type of structures retained (K. J. Smith et al. 2008). The treatments include two conventional uneven-aged prescriptions, single-tree selection (STS) and group selection (GS), which were modified to increase post-harvest structural retention. The modifications for single-tree selection were based on a target residual basal area of 18.4 m2 ha-1, maximum diameter of 60 cm, and $q$-factor of 1.3. The group selection treatment follows the same BDq, but was applied through spatially aggregated harvesting. The patches averaged 0.05 ha, based on estimates of average fine-scale natural disturbance patterns in New England (Seymour, White, and deMaynadier 2002) resulting in eight to nine groups per treatment unit (Keeton 2006).

The third treatment is an approach termed “structural complexity enhancement” (SCE), which promotes accelerated development of late-successional forest structure and function (K. J. Smith et al. 2008; Keeton 2006). The treatment is based on a rotated sigmoid diameter distribution to re-allocate basal area into larger diameter classes. This distribution could reflect one of many distributions of old-growth forests in the northeast, depending on disturbance history, species composition, and other variables (Goodburn and Lorimer 1999). Other structural objectives include vertically differentiated canopies, elevated large snags, downed woody debris, variable horizontal density, and accelerated growth in the
largest trees. These structural objectives were met through unconventional silviculture techniques, for example, uprooting trees to mimic the pit-and-mound topography characteristic of old-growth northern hardwood forests (Dahir and Lorimer 1996).

Prior research has explored this projects economic tradeoffs (Keeton and Troy 2005), harvest effects on stand structure (Keeton 2006), and elements of late-successional biodiversity. Research has shown structural complexity enhancement can support herpetofauna populations (McKenny, Keeton, and Donovan 2006), diverse herbaceous plant communities (Smith et al. 2008), and increase fungal diversity (Dove and Keeton 2015).

More research is needed to better understand the long-term dynamics of structure-based, unconventional forest management techniques. Our knowledge of the regeneration responses in systems designed to enhance late-successional/old-growth characteristics is limited, regarding the interacting influences of treatment, interfering vegetation, herbivory, pests, disease, and climate. The goal of this project is to further increase our understanding of forest responses by examining natural regeneration dynamics. Our primary objective is to understand the regeneration dynamics following three uneven-aged forestry practices modified to increase postharvest structural retention: single-tree selection, group selection, and structural complexity enhancement (SCE). This study examines the natural regeneration response of these three structurally modified treatments, in the thirteen years after harvest, to understand the effect of these management techniques on the establishment of future cohorts.
CHAPTER 2: REGENERATION RESPONSES TO MANAGEMENT FOR OLD-
GROWTH CHARACTERISTICS IN NORTHERN HARDWOOD-CONIFER 
FORESTS

2.1. ABSTRACT

Forest management practices interact with multiple sources of variability to influence regeneration trends in northern hardwood forests. There is uncertainty whether low-intensity selection harvesting techniques will result in adequate and desirable regeneration. Our research is part of a long-term study that tests the hypothesis that a silvicultural approach called “structural complexity enhancement” (SCE) can accelerate the development of late-successional forest structure and functions. Our objective is to understand the regeneration dynamics following three uneven-aged forestry treatments modified to increase postharvest structural retention: single-tree selection, group selection, and SCE. Regeneration density and diversity can be limited by differing treatments effects on or interactions among light availability, competitive environment, substrate, and herbivory. To explore these relationships, manipulations and controls were replicated across 2-hectare treatment units at two Vermont sites. Forest inventory data were collected pre-harvest and periodically over 13 years postharvest. We used mixed effects models with repeated measures to evaluate the effect of treatment on seedling and sapling density and diversity (Shannon-Weiner H’). The treatments were all successful in recruiting a sapling class with significantly higher sapling densities compared to the controls. However, due to high spatial variability, prolific beech (Fagus americana) sprouting dominates some
patches in the understory of all the treatments. Multivariate analyses suggest that while treatment had a dominant effect, other factors were influential in driving regeneration responses. These results indicate variants of uneven-aged systems that retain or enhance elements of stand structural complexity, including old-growth characteristics, generally foster abundant regeneration of important late successional tree species depending on site conditions, but that beech control will be needed where this inhibits desired regeneration.

2.1.1 INTRODUCTION

Sustainable forest management provides an important opportunity to help mitigate the effects of climate change, while providing many social, economic, and ecological co-benefits. Forests in the United States, covering 34% of the landscape, currently sequester approximately 15% of U.S. annual CO2 emissions from fossil fuel combustion (Woodall et al. 2016; US EPA 2016). Forestry practices could increase or decrease this number, turning forest ecosystems into a stronger sink or a carbon source (Harmon 2001). One approach proposed for carbon forestry is to manage for high biomass stand structures like those often found in old-growth forests (Nunery and Keeton 2010; Burrascano et al. 2013). This could entail, for example, emulating – through various retention forestry techniques – the type of natural disturbances and stand development processes leading to the development of high biomass conditions (Franklin et al. 2000; North and Keeton 2008). Pre-European settlement, forests in the northeastern U.S. were dominated by relatively frequent, gap-forming and partial disturbances that created a finely patterned mosaic of successional conditions (Cogbill, Burk, and Motzkin 2002; Kern et al. 2016). These were dominated by late successional/old-growth stand structures (Lorimer
and White 2003), providing higher levels of some ecosystem functions, such as high levels of carbon storage (Keeton et al. 2011; Gunn, Ducey, and Whitman 2014; Thompson et al. 2013) and riparian functionality (Keeton, Kraft, and Warren 2007; Warren et al. 2009; Warren et al. 2016), in comparison to the younger, secondary forests that predominate today.

Structural retention systems are of great interest as a means for providing a broad array of biodiversity and ecosystem services in managed forests (Aubry et al. 1999; Keeton 2006; Choi, Lorimer, and Vanderwerker 2007; Hanson and Lorimer 2007; Bauhus, Puettmann, and Messier 2009; Outerbridge and Trofymow 2009; D’Amato et al. 2011; Lindenmayer et al. 2012; Gustafsson et al. 2012), but successful regeneration outcomes are required for wider adoption by the forestry profession. For example, in the northern hardwood region of eastern North America, the increased canopy cover and shade associated with high levels of retention, particularly in the context of selection harvesting systems, poses challenges for regenerating economically and ecologically desirable tree species, even though many of these are shade tolerant. Our research investigates the question of whether a silvicultural practice promoting old-growth characteristics, termed “Structural Complexity Enhancement,” can regenerate desirable tree species and establish a new cohort of saplings at sufficient densities to be sustainable in comparison to conventional uneven-aged prescriptions. Additionally, we are interested in whether the regeneration responses are influenced by other sources of variability, such as herbivory, substrate, light intensity, and climate, that might interact with treatment effects.

In the U.S. Northeast, forest structure and composition in pre-European settlement landscapes were spatially and temporally variable due to climate variability, disturbances
(natural and anthropogenic), and geophysical variability (Foster and Aber 2004). With a land-use history of forest clearing for agriculture in the 18th and 19th centuries, followed by land abandonment, reforestation, and 20th century forest management, northern hardwood forests are now mostly second growth forests with a median age of 70 years (Lorimer and White 2003; Gough et al. 2016). Consequently, one objective proposed for sustainable forest management is to increase the landscape representation of late-successional and old-growth forests (Keeton 2006; Gunn, Ducey, and Whitman 2014).

There are a number of late-successional attributes indicative of stand structural complexity in northern hardwoods that could be promoted through retention forestry (Singer and Lorimer 1997; Franklin et al. 2002; Lorimer and White 2003; Keeton 2006; Choi, Lorimer, and Vanderwerker 2007; Hanson and Lorimer 2007; Dyer et al. 2010; Hanson et al. 2012; D’Amato, Catanzaro, and Fletcher 2015; Fassnacht et al. 2015). These include greater availability of large downed and standing woody debris, larger sized trees, tip-up mounds, horizontal variation in stand density (e.g., gaps of varying sizes and shapes), vertically complex canopies, and advanced regeneration (McGee, Leopold, and Nyland 1999; Keeton, Kraft, and Warren 2007; Burrascoano et al. 2013). In managing for structurally complex stand structures, silviculturists might promote a variety of ecological functions, including habitat for late-successionally-associated wildlife, hydrologic regulation (Wirth et al. 2009), and increased carbon storage potential (Keeton et al. 2011; McGarvey et al. 2015; Ford and Keeton 2016).

Disturbance- and retention-based silvicultural treatments have demonstrated effectiveness for accelerating the development of late-successional characteristics in managed forests, which some have termed “old-growthness” (Lindenmayer, Margules, and
Botkin 2000; Keeton 2006; Bauhus, Puettmann, and Messier 2009; Puettmann et al. 2015; Sullivan and Sullivan 2016). For example, research has shown that Structural Complexity Enhancement can increase herbaceous understory plant diversity (K. J. Smith et al. 2008), terrestrial amphibian populations (McKenny, Keeton, and Donovan 2006), and fungal species richness (Dove and Keeton 2015), while enhancing stand structural complexity and promoting late-successional functions like carbon storage (Keeton 2006).

Regeneration responses remain as a key source of uncertainty in predicting the long-term viability and efficacy of disturbance or retention-based treatments (e.g. (Price et al., n.d.; Bergeron et al. 2006; Shindler and Mallon 2006; Dodson, Burton, and Puettmann 2014; Koivula et al. 2014; Kneeshaw and Bergeron 2016)), including old-growth silviculture (Aplet and Keeton 1999; Palik, Mitchell, and Hiers 2002; Bauhus, Puettmann, and Messier 2009; Fassnacht et al. 2015). A key indicator of success in any silvicultural system is the ability of regeneration harvests to recruit and establish new cohorts of trees, the most fundamental requisite for achieving all long-term objectives including sustained growth and yield. Challenges to successful regeneration of desirable species in selection harvesting, including gap-based silviculture, go beyond the light environment and include seed availability, desirable substrate, and completion with herbaceous cover, and advanced regeneration (Kern et al. 2016). Herbivory by white-tailed deer (Odocoileus virginianus), moose (Alces alces), and eastern cottontail rabbit (Sylvilagus floridanus) can strongly influence regeneration responses and redirect compositional development (Augustine and McNaughton 1998; Collins 2003; Andreozzi, Pekins, and Langlais 2014).

Moreover, tree regeneration in the Northeast is increasingly limited by competition with American beech (Fagus Americana) due to its high shade tolerance and
vegetative sprouting response to beech bark disease (BBD, *Nectria coccinea var. faginata*), causing many (Leak, Yamasaki, and Holleran 2014) to be skeptical of the ability of single-tree selection harvesting systems to regenerate desirable shade tolerant (e.g. sugar maples [*Acer saccharum*]) and intermediate tolerant (e.g. yellow birch [*Betula alleghaniensis*]) species. The vigorous root sprouting mechanism of beech leads to the formation of dense beech thickets (Houston 1975). Beech thickets alter stand species composition through competition for light and other resources, while providing a substrate for BBD to spread from older diseased trees to the sapling class (Giencke et al. 2014).

Due to the uncertainty of beech regeneration effects on the understory competitive environment, we are particularly interested in the recruitment response of common beech associates, such as sugar maple and yellow birch. Regeneration of sugar maple and yellow birch following harvesting tends to be spatially and temporally variable and dependent on interactions among multiple factors. Harvest gaps, as well as soil scarification and deadwood availability, can positively influence yellow birch establishment (Gauthier, Lambert, and Bédard 2016; Lambert et al. 2016). Sugar maple regenerates well on rich soils with partial canopy cover. Acid deposition can substantially deplete soil calcium on poorly buffered soils and limit sugar maple growth in some areas, another factor that could favor beech over time (Huggett et al. 2007).

### 2.1.2 Hypothesis

Ability to accurately predict regeneration responses to disturbance and retention-based silvicultural approaches remains highly limited in northern hardwood-conifer systems. The goal of this project is to explore the potential of silvicultural techniques
retaining and promoting old-growth structure to successfully regenerate desirable tree species. We define successful as the establishment of seedlings (approx. 12,300/ha minimum as suggested by Nyland (Nyland et al. 2007)) and the recruitment of seedlings into the sapling class. We define desirable as maintaining overall species diversity, but including an abundance of intermediate and shade-tolerant commercially important (i.e. for wood products and syrup production) species (sugar maple, red maple [Acer rubrum], and yellow birch), to ensure the development of a new cohort. Furthermore, we explore important factors that may limit regeneration responses, including those that might be modified through silvicultural practices. Specifically, our study investigates regeneration dynamics following three uneven-aged silvicultural treatments modified to increase post-harvest structural retention, emulate finely-scaled natural disturbance effects, and increase the representation of late-successional structural elements within managed stands. We hypothesize that SCE will have temporally dynamic effects on the densities and diversity of seedlings and saplings similar to the conventional uneven-aged practices. Additionally, we hypothesize that multiple sources of ecological variability, such as canopy cover, substrate composition, climate, light intensity, and herbivory, will interact with the silvicultural treatments to influence the regeneration dynamics.
2.2. METHODS

2.2.1 Study Area

The Vermont Forest Ecosystem Management Demonstration Project (FEMDP) is a study testing the long-term stand dynamics, biodiversity responses, and ecosystem service outcomes of experimental treatments designed to emulate fine-scale natural disturbance effects and promote development of late-successional/old-growth characteristics. There are two main study areas: these are located at the Mount Mansfield State Forest and the University of Vermont’s Jericho Research Forest (Figure 1, Table 1). Both sites are mature (ca. 70-100 years), multi-aged northern hardwood-conifer forests. There are no records for either sites pre-settlement forest composition prior to 1790 (Hannah 1999). In the 1900’s there were between four and six recorded management entries in the study areas (Hannah 1999). Additionally, the multi-aged forest structure was confirmed through pre-treatment coring as reported in Keeton (2006). In 1940, JRF was purchased by the University of Vermont and the university established conifer plantations on abandoned fields. There was no harvesting activity until 1956 when improvement cuts were made removing poor quality hardwoods such as hophornbeam (Ostrya virginiana), still a minor component today. The Jericho Research Forest (44°26’43.70”N; 72°59’44.15”W) is located in the foothills of the Green Mountains at 200 to 250 m a.b.s.l.
Soils are Adams and Windsor loamy sands or sandy loams. At Jericho Research Forest, *Tsuga canadensis* (eastern hemlock) is also co-dominant, with minor components of *Acer rubrum* (red maple) and *Quercus rubra* (red oak).

The Mount Mansfield State Forest (MMSF, 44°30′23.03″N; 72°50′11.24″W) is on the western slopes of the Green Mountain Range, a northern extension of the Appalachians, in northern Vermont. Elevations at the study area range from 470-660 m a.b.s.l. Soils are primarily Peru extremely stony loams. MMSF was heavily cut beginning in the 1800’s, followed by selection cuts and improvement thinning in the 20th century (Hannah 1999). The overstory at both sites is dominated by *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), and *Betula alleghaniensis* (yellow birch). Red spruce (*Picea rubens*) is a minor element of the canopy at Mount Mansfield State Forest (Keeton 2006).

### 2.2.2 Study Design

The FEMDP investigates three uneven-aged silvicultural techniques which were modified to retain post-harvest structure such as standing dead snags, coarse woody debris, and gaps of advanced regeneration. These were assigned to 2 ha treatment units in a randomized block design. One of the treatments, an approach termed “Structural Complexity Enhancement” (SCE), was specifically designed to accelerate the development of late-successional forest structure and function, targeting stand structure attributes derived from previous research on old-growth forests in the U.S. Northeast (Tyrrell and Crow 1994; Dahir and Lorimer 1996; Hunter Jr and White 1997; Singer and Lorimer 1997;
O’Hara 1998; Lorimer and White 2003; Keeton and Troy 2005; Ziegler 2002). Effects on stand structure (Keeton 2006; Kern et al. 2016), elements of biodiversity (McKenny, Keeton, and Donovan 2006; K. J. Smith et al. 2008; Dove and Keeton 2015), and carbon cycling (Ford and Keeton 2016) have been explored previously. At MMSF the three treatments are all replicated twice; at JRF the SCE treatment is replicated twice. Both sites have two un-manipulated control units (N = 4 units per treatment in total). To prevent soil damage and erosion, experimental manipulations (i.e. logging) were conducted in deep snow on frozen ground in the winter (January-February 2003). Marking guidelines specifically targeted retention of disease resistant beech, larger trees showing evidence of wildlife use (e.g. black bear [Ursus americanus] activity, cavity excavation, etc.), and tree species diversity.

Although all three treatments in the FEMDP shared structural retention as an objective, they differed in harvest approach, for example in the degree of uniform vs variable density tree marking, silvicultural gap size and configuration, and amount of live and dead tree retention (Keeton 2006; Kern et al. 2016; D’Amato, Catanzaro, and Fletcher 2015). The treatments include two conventional uneven-aged prescriptions, single-tree selection (STS) and group selection (GS), which were modified to increase post-harvest structural retention compared to the parameters typical for the region (Table 2). The modifications for single-tree selection set retention targets of 18.4 m² ha⁻¹ in residual basal area, a maximum tree diameter of 60 cm at breast height (dbh, 1.37 m), and a q-factor of 1.3 to re-allocate basal area into larger diameter classes. The group selection treatment followed the same BDq prescription, but was applied through spatially aggregated harvesting. The group patches averaged 0.05 ha in size, a prescription intended to emulate
the average size of canopy openings created by fine-scale natural disturbance in New England based on work summarized by Seymour et al. (Seymour, White, and deMaynadier 2002). Group openings were variable in shape and some had light retention, consisting primarily of large snags and, occasionally, large diameter beech exhibiting resistance to beech bark disease (*Nectria coccinea* var. *faginata*). The treatment resulted in eight to nine groups per treatment unit, with the matrix between groups left unharvested (Keeton 2006).

The third treatment, SCE, employed a rotated sigmoid target (or post-harvest) diameter distribution (see (Goff and West 1975; Goodburn and Lorimer 1999)) defined by a high residual basal area (34 m$^2$ ha$^{-1}$), large maximum tree size (90 cm), and a variable q-factor applied to three portions of the diameter distribution (2.0 in the smallest size class, 1.1 in the medium size class, and 1.3 in the largest size class). The combined effect was a re-allocation of basal area and growing space into larger diameter classes, while retaining abundant stems across all sizes and ages. Other structural objectives included vertically differentiated canopies, elevated large snags, downed woody debris, variable horizontal density including small (mean size of 0.02 ha) gaps, and accelerated growth in the largest trees. The latter was achieved through partial or full crown release (Singer and Lorimer 1997). At one unit in each of the two study areas, trees were pulled (or pushed) over to create the tip-up mounds characteristic of old-growth northern hardwood forests.

**2.2.3 Data Collection**

Each two-hectare treatment unit contains five randomly placed 0.1 ha permanent sampling plots. The plots are buffered from edge effects through placement of at least 15 m on the interior of unit boundaries and collectively represent 25% of each unit’s total area.
For this study, we used one year of pre-treatment (2001) data, six intervals of post-harvest seedling data (2003, 2004, 2006, 2007, 2013, 2015), and three years of post-harvest sapling data (2003, 2004, 2015). Tree seedlings <1 m in height were identified and counted along two 1-m wide and 31.64 m long belt transects bisecting the 0.1 ha plots. Tree saplings >1 m in height and < 5 cm dbh were identified and counted within a plot (0.02 ha) nested within the 0.1 ha plots. All live and dead trees > 5 cm dbh within the 0.1 ha sampling plots were tagged, measured, and identified.

Additional variables hypothesized to influence seedling establishment and survival were inventoried in 2015. These included substrate and understory composition, light intensity, soil pH, herbivory, and stand structure. Herbaceous and woody shrub cover by species was measured using an ocular estimate designed to ensure precision and consistency in estimation (Peet, Wentworth, and White 1998). Understory plant cover data was measured with thirteen 1-m² quadrats placed systematically along plot transects. The substrate data was inventoried using the same quadrats and estimation methodology as the understory data. The substrate data presented here for the purpose of assessing seed beds are categorized as fine litter, mineral soil, and coarse woody debris (>10cm diameter). Soil samples were collected at two locations placed systematically in each plot, measured using the Lovibond Soil pH Test Kit. For each sapling inventoried in the 0.02 ha sapling plot, branches were assessed for the presence of deer or moose herbivory (browse). Saplings that were unequivocally browsed (i.e. torn, ragged) at any stem height (not distinguishing between moose and deer) were recorded as having the presence of browse (Faison et al. 2010).
To quantify light conditions in each treatment, hemispheric canopy photography was used to estimate the proportion of direct light (DSF) transmitted through the canopy. The camera was mounted on a tripod with a self-leveling mechanism set at 1-m height and two photographs were taken at the center of each plot. All analyses and photo selections were conducted by the same lab technician to minimize and systematize any error associated with selecting thresholds during analyses. The canopy photographs were processed and analyzed using HemiView canopy analysis software (Delta-T Devices 1999).

The Palmer Drought Severity Index (PDSI) was obtained for climate region 2 (western) using the Earth System Research Laboratory of the National Oceanic and Atmospheric Administration (NOAA ; http://www.esrl.noaa.gov/psd/data/timeseries/). PDSI data from 2001-2013 was used as a coarse estimate of climatic conditions including relative dryness and drought potential. PDSI has been used previously to develop predictions of seedling success under different drought scenarios (Zwolinski et al. 1994).

2.2.4 Statistical Analysis

Due to uneven treatment replication among the two study areas, analyses were performed separately by site. Multivariate analyses were used to determine if treatment had an effect on trends in the regeneration response variables over time. We used Statistical Analysis Software (SAS Institute Inc.) to build a linear mixed effects model (LME) to model the diversity response (Shannon-Wiener H’) of seedling and saplings. Because seedling and sapling abundance estimates were not normally distributed, we used a generalized linear mixed model (GLIMMIX) to model total seedling and sapling densities,
as well as sugar maple, red maple, yellow birch and beech responses over time. GLIMMIX use multivariate analyses to test for effects in non-normal data and is most appropriate for analyzing repeated measures (Bolker et al. 2009; Zuur, Ieno, and Smith 2007). We assumed a negative binomial distribution and a first order autoregressive covariance structure for the repeated measures. Treatment and year were modeled as fixed effects, while plots and units were modeled as random effects. Following the model design of Smith et al. (K. J. Smith et al. 2008), plots were nested within units and units within sites. The model output provided parameter estimates for the fixed effects and covariance estimates for the random effects, as well as a pairwise comparison test of the treatments at each time point to compare mean estimates between the treatments. All models were adjusted using pre-treatment values as continuous covariates to normalize data and allow for standardized comparisons among treatments across a range of inherent site variability. Percentage differences between pre-treatment, peak abundance, and thirteen years post-harvest were calculated following Littlefield and Keeton (Littlefield and Keeton 2012) using the equation:

\[
\text{Percentage difference} = \left[ \frac{(V_H - V_B)}{(V_H + V_B)/2} \right] \times 100
\]

where \( V_H \) is the post-harvest value and \( V_B \) is the pre-treatment “baseline” value.

To test for the interaction among ecological variables having a possible influence on tree regeneration, time was removed from the model and we focused on the 2015 data. Predictor variables included in the model were percent leaf litter, percent browse, Direct Site Factor (DSF, obtained through analysis of hemispheric photographs), and Curtis relative-density structure index (Curtis 1982). We chose DSF as a proxy for light
conditions; it represents the proportion of direct solar radiation that reaches each plot, relative to that location with no sky obstructions (open canopy). The Curtis-relative density index is an aggregated stand structure index that integrates quadratic mean diameter and stem density. It is a good indicator of canopy retention as it depicts the total occupation of growing space based on tree density and size and can be used for uneven-aged management (Curtis 1982, 198). A coarse estimate of climate using PDSI was analyzed with the Durbin-Watson statistical test which detects the presence of autocorrelation in the residuals from a time series regression analysis (Durbin and Watson 1971).

2.3. RESULTS

2.3.1 Recruitment of Seedlings into Sapling Class

Management for old-growth characteristics performed as well as conventional selection harvest systems in terms of establishing diverse and desirable regeneration, despite retention of high levels of canopy cover. The linear mixed models employed for the time series analysis provided insight on the patterns of change by comparing the way treatments changed over time. In the Type 3 Test of Effects output, a significant treatment*time effect indicated the treatments changed in different patterns over time (Table 3); however, the model output did not specify if the treatment effect was positive or negative because results often alternated between a positive and negative treatment effect depending on the observed time point (Figure 2, Figure 3).
Analysis of total seedling density trends over time using the generalized linear mixed effects model resulted in different patterns of regeneration by site (Figure 2). At Jericho Research Forest (JRF), SCE did not increase regeneration significantly over background rates. The control units at JRF had regeneration occurring in natural gaps thirteen-years post-harvest which could explain the lack of difference. At Mount Mansfield State Forest (MMSF), the three harvested treatments had significantly more seedlings than the control for the first four years post-harvest (P<.0001). After 13 years, total seedling means were similar across all treatments. Seedling densities in the Control units were highly variable year to year, exhibiting pulses of recruitment and mortality, such that densities fluctuated from 2,925 seedlings/ha to 92,757 seedlings/ha.

While total seedling densities initially increased and then declined to the background rate detected in the Control over the 13-year period, total sapling densities display the opposite trend (Table 4). At MMSF, total sapling densities did not increase significantly over the first two years post-treatment. But after 13 years all treatments were successful at regenerating and recruiting a new cohort into the sapling class, at densities significantly greater than the controls (Figure 3). Sapling densities in the Control declined over the 13-year time series, while GS, STS, and SCE increased after the initial two-year time lag. Although not significantly different, GS had the highest mean (and standard error), followed by STS and then SCE.

At JRF, although sapling means are not significantly different between the Control and SCE at each time point, the SCE treatment had an increase in sapling densities while the Control had a decrease in sapling densities over the 13-year time period.
(P=0.0195). Pre-treatment sapling densities had a significant effect on these trends (P=0.0079).

2.3.2 Maintaining Species Diversity

Regeneration species diversity was an outcome of particular interest because there is uncertainty whether low-intensity selection systems can regenerate a range of intermediate and shade-tolerant species. In our hypotheses, we defined successful regeneration as maintaining diverse species composition in the seedling and sapling classes. We found that there were significant differences in treatment effects on species diversity. At JRF there was no significant treatment*time effect. However, both the Control and SCE increased in seedling diversity (H’), with SCE having slightly higher seedling diversity than the control at all time intervals. At MMSF, SCE and GS showed a positive treatment*time effect, while STS had a negative treatment*time effect. The GS treatment almost doubled in seedling diversity over the 13-year time series, while STS had an increase in the first four years and then after 13 years declined to the level immediately post-harvest. The SCE treatment increased seedling diversity from year 1 to year 2 following harvest, and then leveled off, remaining constant to year 13 post-treatment. The Control varied only slightly from year to year, remaining around the same level of seedling diversity and showing no treatment*time effect. In the first year post-harvest, seedling diversity was lowest in the GS, followed by SCE, STS, and Control. After thirteen years, SCE had the highest seedling diversity, followed by the Control, then GS and finally STS (Table 4, Figure 4). In addition to the treatment effect, the seedling diversity pre-treatment
(year 2001) had a significant effect (P=0.0012) on the seedling diversity trends observed over the time series. Plots with higher species diversity in the seedling class pre-treatment exhibited significantly higher diversity post-treatment, suggesting an interaction between starting condition and treatment.

Sapling diversity at JRF declined for both the SCE and Control treatments over the 13-year time series. Although there was no treatment effect, the pre-treatment sapling diversity had a significant influence on resulting sapling diversity. At MMSF, the pre-treatment sapling diversity also had a significant effect on resulting sapling diversity. The Control declined in sapling diversity (P=0.0015) over the 13-year time series, indicating regeneration limitations occurred regardless of the harvest. GS Units showed an initial increase in sapling diversity 2 years following the harvest and then declines significantly after 13 years post-harvest (P=0.0042). SCE performed comparably to STS in regenerating and maintaining a diverse sapling cohort as demonstrated by the insignificant treatment * time effect, indicating both treatments did not decline in sapling diversity as did the Control and GS units (see Table A1 for full species list).

2.3.3 Competition and Species Response

The regeneration response of beech was a result of great importance due to its competitive reproductive strategies that could inhibit the establishment of other northern hardwood species. At JRF, beech seedlings had a treatment*time effect (P=0.0216). The Control had a higher mean of beech seedlings for year 1 through year 11 post-harvest; however, the means were not significantly different between the treatments for the entire
time series. At MMSF, there was a significant treatment*time effect (P<.0001). GS and SCE resulted in seedling recruitment responses that reached similar levels after 13 years, while STS and the Control had similar beech seedling densities from year to year. GS and SCE units had significantly more beech seedlings than STS and Control units, even though GS and SCE both showed decreasing beech seedling densities over the 13 years monitored.

At MMSF, there was a significant Treatment*Time effect (P=0.0040) on beech sapling densities. Immediately post-harvest, SCE units had significantly greater beech saplings than STS units (P=.0257); by year two none of the treatment means were significantly different. However, after 13 years the Control had significantly less beech saplings than GS (P=.0020) and SCE (P=.0244). Following the beech seedling trend at MMSF, GS and SCE displayed similar sapling densities while the Control and STS had similar sapling densities. SCE and STS treatments resulted in beech sapling densities that were not significantly different from each other 13 years post-harvest, while GS resulted in significantly more beech saplings than STS units (P=.0089).

To assess regeneration responses of those species (termed “desirable”) for which there is regional concern regarding regeneration success following selection harvesting, we combined sugar maple, red maple, and yellow birch regeneration into a single response variable, termed “SM_RM_YB”. At JRF, seedling densities for SM_RM_YB were not significantly different between the Control and SCE. At MMSF, there was a significant Treatment*Time effect (P<.0001) on SM_RM_YB, as well as a significant effect from the pre-treatment SM_RM_YB densities (P=0.0358). After 4 years, the Control units had significantly fewer SM_RM_YB seedlings than the other three treatments; however, by the following year the densities had stabilized at levels that were not significantly different
from one another. After 11 years, the GS treatment had significantly fewer of these species in the seedling class than SCE and STS. Following the pattern of total seedling densities, by year 13 all treatment means were not significantly different from each other (Figure 5). Although insignificant, the harvested treatments all have more SM_RM_YB seedlings than the Control. STS had a higher density of SM_RM_YB seedlings than SCE, while SCE had a higher density than GS.

2.3.5 Effects of Herbivory, Substrate and Climate

While mean densities of seedlings were similar after 13 years across all the treatments, plot level data showed large spatial variation or patchiness within the treatments (Table 4). Across both sites, the two factors found to have the most significant effect on sapling recruitment were percent browse (herbivory) and percent fine litter substrate (Table 5).

Thirteen-years post-harvest, percent browse on saplings had a positive impact on seedling diversity (P=0.0286) and a negative impact on sapling diversity (P=0.0403). The positive impact of browse on seedling diversity could be a result of disproportionate browse on common, palatable species giving rare species seedlings a competitive advantage (Paine & Beck 2007). This effect may be short-lived as seedlings move into the sapling class and there is greater competition for resources. Increasing percent browse was negatively correlated with sapling diversity, while it was positively correlated with the density of beech (P=0.0512) and sugar maple saplings (P=0.0443).
Percent fine litter had an influence on regeneration response similar to that of percent browse. Our data showed a positive relationship between fine litter substrate and beech sapling density (P=.0369), while there was a significantly negative relationship with sapling diversity (P=.0213).

Total seedling densities were not significantly correlated with any of the variables presenting possible non-treatment influences on regeneration dynamics. There was a significant treatment effect on total sapling densities (P=0.0327), indicating that after light conditions (DSF), substrate (fine litter), herbivory, and Curtis-RD were accounted for in the model, the treatment still had the greatest effect on the amount of saplings (Table 5).

The Palmer Drought Severity Index (PDSI) values for northwestern Vermont indicated moist, non-drought conditions for most of the duration of the study. However, in the growing season (Jun-Aug) of 2001, the year the study was established, the PDSI was -1.927 which is categorized as a mild drought. This declined to a severe drought with a PDSI of -3.350 in the fall (Sept-Nov). PDSI remained high with no drought until 2012 when there was a mild drought that decreased into an incipient (developing) drought in the spring of 2013.

In the Durban-Watson analysis, species diversity ($H'$) in the SCE treatment at JRF was significantly correlated with PDSI values indicative of high moisture, (DW statistic = 1.056, p = 0.05). None of the other treatments showed a correlation between PDSI and the diversity index. For all the treatments, the total density of seedlings was not significantly correlated with PDSI.
2.4. DISCUSSION

Silvicultural techniques promoting the development of late-successional/old growth structure in northern hardwood-conifer forests have the potential to regenerate and establish a diverse new cohort of trees, including desirable species, such as sugar maple, red maple, and yellow birch, despite the relatively high levels of structural retention typical of selection harvesting systems. The effects of SCE were highly variable spatially, with successful regeneration in certain patches, while other areas were dominated by dense beech thickets. This was due primarily to the patchy light environment created through variable density harvesting and small gap creation. These results supported the hypothesis that SCE and other silvicultural approaches specifically intended to increase horizontal complexity in stand structure (see (Franklin et al. 2002)), dependent on site conditions and other factors, have the potential to achieve regeneration levels close to or even greater than conventional uneven-aged practices, including selection systems employing larger group openings. They lend support to the efficacy of old-growth silviculture (Bauhus, Puettmann, and Messier 2009) for long-term sustainable management from a regeneration and recruitment perspective.

And yet, as with previous research on selection harvesting (Mader and Nyland 1984; Jones, Nyland, and Raynal 1989; Donoso, Nyland, and Zhang 2000; Matonis, Walters, and Millington 2011; Poznanovic, Webster, and Bump 2013; D’Amato, Catanzaro, and Fletcher 2015), clearly regeneration success was mixed and strongly affected by competition with beech sprouting especially. Regeneration of desirable species, in particular, ranged among patches and sites from absent or poor to very abundant. These
findings further supported our hypothesis that multiple sources of variability interact with treatment effect (Bashant et al. 2005; Nyland et al. 2006; Arseneault et al. 2011; Bolton and D’Amato 2011; Forrester et al. 2014; Nolet 2016) to influence regeneration response following the types of modified selection harvesting systems we tested.

2.4.1 Regeneration Response to Old-Growth Management

We found variants of uneven aged silviculture systems designed to enhance structural complexity and old-growth characteristics adequately regenerate late-successional tree species, depending on site conditions and patch-scale controls. Although the seedling and sapling response was not as abundant as conventional even-aged systems, the total regeneration density was sufficient to reach full stocking according to the minimum threshold recommended by Nyland (Nyland et al. 2007). Regeneration dynamics in all the harvested treatments showed an initial pulse of recruitment (GS increasing by 103%, STS increasing by 113%, and SCE by 53% from pre-treatment baseline densities) in the seedling class. After thirteen years all treatments returned (GS decreasing -33%, STS decreasing -76%, and SCE decreasing -17% from peak abundance) to a similar mean seedling density. The decline from peak abundance (achieved in year 4 post-treatment) in seedling density can be attributed to a combination of factors, including partial canopy closure and reduced light availability, competition and density-dependent mortality, and recruitment into the sapling class (Poznanovic et al. 2013). The treatments were all successful in recruiting a sapling class (GS increased 79%, STS by 60%, and SCE by 4% at MMSF and 54% at JRF) over the thirteen years post-harvest. However, 62% of the
sapling layer was made up of dense beech (1,843/ha on average) thickets after 13 years, a trend we found across all treatments. Beech thickets were most abundant in the GS treatment, intermediate in the SCE treatment, and least prevalent in the STS treatment.

Species diversity in the seedling class increased across all harvested treatments. Pre-treatment species diversity was as predictive as treatment type, suggesting a strong influence of initial site conditions and past stand development history on community composition. At the FEMDP sites the spatially heterogeneous regeneration pattern for some species, such as sugar maple, red maple, and yellow birch, is clearly influenced both by light availability and competition with beech thickets, the latter being present in all treatments. Beech seedlings in all treatments showed a very large initial increase immediately post-harvest and then declined after a decade, most likely due to recruitment into the sapling class.

Due to relatively small sample size (N = 4 per treatment type), we did not find a statistically significant relationship (positive or negative) between beech and sugar maple regeneration densities. Previous studies have found that maple and beech tend to replace each other in stands uninfected with beach bark disease in the Upper Lake states, with saplings often occurring beneath the canopy of the other species (Woods 1979; Whittaker and Levin 1977). Both beech and sugar maple have been found to outcompete one another following a disturbance or harvest, depending on site conditions. Sugar maple typically has faster growth rates than beech under higher light conditions in gaps (e.g. (McClure, Lee, and Leak 2000; Ricard et al. 2003; Nolet 2016)). However, due to asexual reproduction through root sprouting and shared belowground nutritional supply, beech can often outcompete sugar maple in the understory, ultimately overtopping sexually reproduced
maple (Beaudet and Messier 1998; Beaudet et al. 1999; Gasser et al. 2010). In addition to outcompeting sugar maple, beech produces abundant beech leaf litter which contains leachate with phytotoxins that inhibit the development of sugar maple seedlings (Hane et al. 2003).

**2.4.2 Sources of Variability in Regeneration Dynamics**

Consistent with previous reports from northern hardwood forests, regeneration limitations in our study were linked to multiple factors including competition from dense beech understories and deer browse (Sage, Porter, and Underwood 2003; Horsley, Stout, and DeCalesta 2003). Adding the ecological variables into the linear mixed model showed that increasing herbivory and leaf litter were negatively associated with sapling diversity and positively associated with beech sapling densities. There was a positive association between herbivory and seedling diversity, found also in previous studies when deer populations are about 3-6 deer/km² (Healy 1997). Although beech is palatable to deer, it is less preferentially browsed in comparison to yellow birch and sugar maple. Browse and litter substrate were positively associated with beech sapling density at the FEMDP sites. Browse pressure (deer, moose, and rabbit) was highest in GS (ranging from 80%-97%), intermediate in SCE (43%-92%), and lowest in STS (45%-91%).

In the FEMDP experiment, the SCE treatment initially increased coarse woody debris (CWD) volumes by 140% (Keeton 2006), though these later declined due to decay [37]. In addition to mineral soil, partially decayed softwood coarse woody debris is a preferred seedbed for yellow birch establishment and is a substrate that provides a
competitive advantage for birch by altering the sapling morphology (i.e. multilayered crowns) for improved shade-tolerance (Marx and Walters 2006; Lambert et al. 2016). Beech control in the treatment units could allow established yellow birch saplings to grow into merchantable size classes, such as on the CWD substrate.

**2.4.3 Effects of climate variability and drought**

Although we did not see a significant treatment effect on seedling diversity at JRF, there was a relationship between climate and SCE seedling diversity. This implies there may be an influence of drought stress, as measured by PDSI, on regeneration trends in the structural complexity enhancement treatment (Zwolsinski et al. 1994). Mild spring drought conditions in recent years could influence early seedling establishment, potentially causing a decline in regeneration diversity. In the winter of 2012, 2013, and 2015 the PDSI indicated an incipient drought, which could relate to lower amounts of precipitations in the form of snow. A decline in snow depth can lead to decreased seedling survival due to increased browse and soil freezing stresses (Decker et al. 2003; Christenson et al. 2013). Increased sapling mortality has also been associated with root exposure due to declining snow pack (Drescher and Thomas 2013).

Climate change models predict that increased temperatures and higher drought deficits will influence regeneration dynamics in the eastern U.S. (Millar, Stephenson, and Stephens 2007; Huntington et al. 2009; Rustad et al. 2012; Canham and Murphy 2016). Some models suggest that now dominant northern hardwood and conifer species may decline due to water deficits (Iverson, Prasad, and Matthews 2008). However, sugar maple,
red maple, yellow birch, and American beech, surprisingly, showed enhanced seedling survival with increasing water deficit between 25mm and 625mm across their entire range between (Canham and Murphy 2016). These may be transient effects; if conditions become too dry or too wet seedling mortality may increase (N. A. Fisichelli, Frelich, and Reich 2013; N. Fisichelli et al. 2014). However, maintaining tree species diversity, as the FEMDP treatments did, at stand and landscape scales is an important strategy conferring ecosystem resilience to climate related stresses (D’Amato et al. 2011).

2.4.4 Management Implications

Our research suggests that management for old-growth characteristics in northern hardwood-conifer forests can promote adequate regeneration; however, site specific modifications are recommended for successful recruitment of species other than beech. Some silviculturists recommend patch- or clear-cutting to prevent prolific beech regeneration (Leak, Yamasaki, and Holleran 2014). However, in our study beech sprouting is most abundant in the group selection openings, even though advanced beech regeneration was cut (or cleaned) at the time of harvest, suggesting that more aggressive beech control would be needed for a desirable regeneration outcome. Based on our results, we suggest that low-intensity selection systems can regenerate at desirable densities (Nyland et al. 2007), but may require beech control to sustain a diversity of intermediate- and shade-tolerant species. While all the treatments resulted in total seedling densities above the minimums recommended by regional silvicultural guides, densities of sugar
maple and yellow birch rarely exceeded the accepted minimum seedling densities. If regenerating commercially valuable species is the primary management objective, alternative silvicultural systems may be preferable. However, where timber is integrated with other management objectives, such as late-successional wildlife habitat, non-timber forest products, riparian functionality, or carbon storage, the regeneration densities and mixed composition resulting from selection systems modified to retain and enhance structural complexity might be considered acceptable.

Removal of beech saplings alone may not be sufficient to promote sugar maple seedling establishment under selection harvesting (Nolet 2016). Precutting of beech saplings and repeated cleaning entries post-harvest are potential applications of beech control (Nyland et al. 2006). Repeated cutting of beech before overstory harvest can still promote beech suckering; however, beech regeneration may remain shorter than sugar maple and yellow birch (Nyland et al. 2006). As an alternative, several studies have tested limited herbicide treatments (e.g. (Mallett 2002; Kochenderfer et al. 2001) and found them to be highly effective. Broad range application of glyphosate or triclopyr in the summer months is the most efficient and most effective treatment suggested by Nyland et al. (Nyland et al. 2006) based on a literature review of experimental treatments to eliminate understory interferences. Glyphosate treatments were also found to be successful at maintaining desirable species such as sugar maple and yellow birch, while minimizing American beech in a northern Maine study (Nelson and Wagner 2011). However, herbicide application carries risks that some managers may find unacceptable. Combined beech removal and deer exclusion, though expensive and thus often not practical, offers another means for improving regeneration outcomes (Forrester et al. 2014).
Gap size can strongly influence regeneration dynamics (Arseneault et al. 2011). For example, a study of northern hardwoods in Minnesota found that gaps greater than 0.02 ha had the highest regeneration densities (Bolton and D’Amato 2011). Another long-term silvicultural study found better sugar maple establishment and survival under single-tree selection in comparison to large and medium sized group-selection openings, while yellow birch seedlings followed the reverse trend, with higher densities in larger gaps compared to smaller gaps (Poznanovic, Webster, and Bump 2013). However, these study sites were uninfected with beech bark disease. Canopy gaps increase light levels which is thought to increase species diversity (Kern, Montgomery, et al. 2014). However, other sources of variability may lead to unanticipated regeneration responses to gap-based silviculture (Bobiec 2007; Bolton and D’Amato 2011; Kern et al. 2012; Poznanovic, Webster, and Bump 2013). These include seed availability, presence or absence of a seedbank, and seed predation (Kern et al. 2016). As a consequence, the regeneration objective remains challenging. However, in a review of gap-based silviculture by Kern et al. (Kern et al. 2016) suggest moving towards a continuum of gap sizes, shapes, and within-gap retention, emulating the complexity associated with partial disturbances. Based on our findings, we support this suggestion and recommend utilizing a range of gap sizes, with smaller gaps on better quality sites and larger gaps implementing beech control on poorer sites.

Managing forests for old-growth and late-successional characteristics is an option some managers are considering that would provide a broader range of habitat conditions and ecosystem service co-benefits approaches (Harmon, Ferrell, and Franklin 1990, 199; Goodburn and Lorimer 1999; Keeton 2006; Choi, Lorimer, and Vanderwerker 2007; Bauhus, Puettmann, and Messier 2009; Gronewold, D’Amato, and Palik 2010; Fassnacht
et al. 2015; Halpin and Lorimer 2016; Sullivan and Sullivan 2016). Our research shows that SCE like other disturbance- and retention-based systems, is sustainable from a regeneration perspective and thus provides a viable approach that could be integrated into holistic forest management.

2.5. Acknowledgements

This research would not have been possible without support from the Northeastern States Research Cooperative. Prior support for the FEMDP was provided by the Vermont Monitoring Cooperative, the USDA McIntire-Stennis Forest Research program, and the USDA National Research Initiative. Thanks especially to Timothy Perkins, and Anthony D’Amato for extensive input on this paper. Valuable reviews were also provided by Garrett Meigs, Sarah Ford, Andrea Urbano, and the UVM Carbon Dynamics Laboratory. Finally, we wish to thank Alan Howard for assistance with statistical modeling and analysis.
2.6. TABLES

Table 1. Site characteristics of experimental treatment units located in the Mansfield and Jericho study areas of the Forest Ecosystem Management Demonstration Project Adapted from Ford and Keeton (*in press*).

<table>
<thead>
<tr>
<th>Site</th>
<th>Unit</th>
<th>Treatment</th>
<th>Site Index</th>
<th>Slope (%)</th>
<th>Aspect (deg)</th>
<th>% Hardwood</th>
<th>Total BA (sq. m/ha)</th>
<th>Total Stem Density (trees/ha)</th>
<th>Live QMD (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mansfield</td>
<td>1</td>
<td>Control</td>
<td>70</td>
<td>28.8</td>
<td>276</td>
<td>99.70</td>
<td>33.5</td>
<td>728</td>
<td>24.2</td>
</tr>
<tr>
<td>Mansfield</td>
<td>2</td>
<td>SCE</td>
<td>55</td>
<td>22.2</td>
<td>290</td>
<td>99.73</td>
<td>36.4</td>
<td>1044</td>
<td>21.1</td>
</tr>
<tr>
<td>Mansfield</td>
<td>3</td>
<td>SCE</td>
<td>55</td>
<td>13.0</td>
<td>260</td>
<td>99.65</td>
<td>28.5</td>
<td>1056</td>
<td>18.5</td>
</tr>
<tr>
<td>Mansfield</td>
<td>4</td>
<td>Single Tree</td>
<td>60</td>
<td>29.6</td>
<td>272</td>
<td>95.87</td>
<td>33.9</td>
<td>750</td>
<td>24</td>
</tr>
<tr>
<td>Mansfield</td>
<td>5</td>
<td>Single Tree</td>
<td>60</td>
<td>37.0</td>
<td>273</td>
<td>97.49</td>
<td>31.9</td>
<td>750</td>
<td>23.3</td>
</tr>
<tr>
<td>Mansfield</td>
<td>6</td>
<td>Group</td>
<td>60</td>
<td>19.4</td>
<td>249</td>
<td>98.67</td>
<td>30.1</td>
<td>1140</td>
<td>18.3</td>
</tr>
<tr>
<td>Mansfield</td>
<td>7</td>
<td>Group</td>
<td>60</td>
<td>26.4</td>
<td>250</td>
<td>99.35</td>
<td>30.8</td>
<td>1144</td>
<td>18.5</td>
</tr>
<tr>
<td>Mansfield</td>
<td>8</td>
<td>Control</td>
<td>55</td>
<td>22.3</td>
<td>320</td>
<td>98.19</td>
<td>27.6</td>
<td>1066</td>
<td>18.2</td>
</tr>
<tr>
<td>Jericho</td>
<td>1</td>
<td>Control</td>
<td>60</td>
<td>27.125</td>
<td>188</td>
<td>53.11</td>
<td>35.4</td>
<td>1186</td>
<td>19.5</td>
</tr>
<tr>
<td>Jericho</td>
<td>2</td>
<td>SCE</td>
<td>60</td>
<td>27.75</td>
<td>146</td>
<td>82.99</td>
<td>33.5</td>
<td>1040</td>
<td>20.2</td>
</tr>
<tr>
<td>Jericho</td>
<td>3</td>
<td>SCE</td>
<td>60</td>
<td>42.6</td>
<td>147</td>
<td>54.77</td>
<td>44</td>
<td>1034</td>
<td>23.3</td>
</tr>
<tr>
<td>Jericho</td>
<td>4</td>
<td>Control</td>
<td>60</td>
<td>34.2</td>
<td>99</td>
<td>74.17</td>
<td>30.2</td>
<td>940</td>
<td>20.2</td>
</tr>
</tbody>
</table>
Table 2. Silvicultural prescription details for experimental treatment manipulations at the MMSF and JRF study areas. Listed in the table is the target BDq for each treatment. The BDq is the residual basal area (B), maximum target diameter (D), and q-factor (q). The q-factor is equal to the ratio of number trees in each successively larger size class. Adapted from Keeton (2006) and Ford and Keeton (in press).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Target residual basal area (m² ha⁻¹)</th>
<th>Max diameter (cm)</th>
<th>q-factor</th>
<th>Structural objective</th>
<th>Silvicultural prescriptions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single-Tree Selection</td>
<td>18.4</td>
<td>60</td>
<td>1.3</td>
<td>Increased post-harvest target structural retention</td>
<td>• Elevated target residual basal area</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>• Slash/unmerchantable bole retention</td>
</tr>
<tr>
<td>Group Selection</td>
<td>18.4</td>
<td>60</td>
<td>1.3</td>
<td>Increased post-harvest target structural retention</td>
<td>• Elevated target residual basal area</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>• Slash/unmerchantable bole retention</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Variable horizontal density</td>
<td>• Variable density marking</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Vertically differentiated canopy</td>
<td>• Release advanced regeneration</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>• Spatially aggregated harvest (patches ~ 0.05 ha)</td>
</tr>
<tr>
<td>SCE</td>
<td>34</td>
<td>90</td>
<td>2.0/1.1/1.3</td>
<td>Increased horizontal complexity</td>
<td>• Rotated sigmoid diameter dist.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Re-allocation of basal area to larger size class</td>
<td>• High max. D and target basal area</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Vertically differentiated canopy</td>
<td>• Retention of trees &gt;60 cm dbh</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Growth acceleration of larger trees</td>
<td>• Single-tree sel. with target diameter distribution</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>• Release advanced regeneration</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Elevated coarse woody material inputs for added structure</td>
<td>• Full (3- or 4-sided) and partial (2-sided) crown release</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>• Tree girdling/felling and leaving trees</td>
</tr>
</tbody>
</table>
Table 3. Generalized Linear Mixed Model results including the Type 3 Tests of Fixed Effects and selected results from the pairwise comparison of Treatment* Time for total seedling (top) and sapling (bottom) densities at Mt. Mansfield. Estimate represents the transformed and adjusted stem counts (least squares mean). The outputs shown are immediately post-harvest (2003), and thirteen years post-harvest (2015). The three harvested treatments have significantly more seedlings than the Control initially and converge around a similar mean after thirteen years. The saplings show the opposite pattern, beginning at a similar mean and then diverging after thirteen years from the control. This suggests the initial burst of seedlings translated into a recruitment of the sapling class thirteen-years post-harvest.

### Type III Tests of Fixed Effects

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-treatment</td>
<td>1</td>
<td>208</td>
<td>31.94</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Treatment</td>
<td>3</td>
<td>208</td>
<td>24.73</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Time</td>
<td>5</td>
<td>208</td>
<td>22.43</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Treatment*Time</td>
<td>15</td>
<td>208</td>
<td>5.72</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>

### Treatment*Time

| Time 1 Treatment | Treatment | Estimate | Standard Error | DF  | t Value | Pr>|t| |
|------------------|-----------|----------|----------------|-----|---------|-----|
| Control          | Group     | -2.0489  | 0.3068         | 208 | -6.68   | <.0001 |
| Control          | SCE       | -1.8638  | 0.2964         | 208 | -6.29   | <.0001 |
| Control          | STS       | -0.9610  | 0.3079         | 208 | -3.12   | 0.0021 |
| Group            | SCE       | 0.1851   | 0.3039         | 208 | 0.61    | 0.5431 |
| Group            | STS       | 1.0878   | 0.3059         | 208 | 3.56    | 0.0005 |
| SCE              | STS       | 0.9027   | 0.3060         | 208 | 2.95    | 0.0035 |

| Time 13 Treatment | Treatment  | Estimate  | Standard Error | DF  | t Value  | Pr>|t| |
|-------------------|------------|-----------|----------------|-----|----------|-----|
| Control           | Group      | -0.0363   | 0.3065         | 208 | -0.12    | 0.9060 |
| Control           | SCE        | -0.4215   | 0.2959         | 208 | -1.42    | 0.1559 |
| Control           | STS        | -0.2814   | 0.3072         | 208 | -0.92    | 0.3607 |
| Group             | SCE        | -0.3852   | 0.3045         | 208 | -1.27    | 0.2072 |
| Group             | STS        | -0.2451   | 0.3063         | 208 | -0.80    | 0.4244 |
## Type III Tests of Fixed Effects

**MMSF Saplings**

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-treatment</td>
<td>1</td>
<td>36.85</td>
<td>0.17</td>
<td>0.6861</td>
</tr>
<tr>
<td>Treatment</td>
<td>3</td>
<td>3.244</td>
<td>0.65</td>
<td>0.6315</td>
</tr>
<tr>
<td>Time</td>
<td>2</td>
<td>61.74</td>
<td>2.91</td>
<td>0.0618</td>
</tr>
<tr>
<td>Treatment*Time</td>
<td>6</td>
<td>64.33</td>
<td>6.66</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>

| Simple Effect Level | Treatment | Treatment | Estimate | Standard Error | DF | t Value | Pr>|t| |
|---------------------|-----------|-----------|----------|----------------|----|---------|-------|
| **Time 1**          | Control   | Group     | 0.1478   | 0.3502         | 10.19 | 0.42 | 0.6818 |
|                     | Control   | SCE       | -0.0792  | 0.3333         | 8.811 | -0.24 | 0.8177 |
|                     | Control   | STS       | 0.3746   | 0.3398         | 9.447 | 1.10 | 0.2977 |
|                     | Group     | SCE       | -0.2269  | 0.3504         | 10.2  | -0.65 | 0.5315 |
|                     | Group     | STS       | 0.2268   | 0.3596         | 11.1  | 0.63 | 0.5411 |
|                     | SCE       | STS       | 0.4537   | 0.3398         | 9.445 | 1.34 | 0.2131 |
| **Time 13**         | Control   | Group     | -1.6099  | 0.3426         | 9.484 | -4.70 | 0.0010 |
|                     | Control   | SCE       | -1.0472  | 0.3333         | 8.815 | -3.14 | 0.0122 |
|                     | Control   | STS       | -1.1555  | 0.3398         | 9.449 | -3.40 | 0.0073 |
|                     | Group     | SCE       | 0.5627   | 0.3427         | 9.49  | 1.64 | 0.1333 |
|                     | Group     | STS       | 0.4544   | 0.3518         | 10.35 | 1.29 | 0.2246 |
|                     | SCE       | STS       | -0.1083  | 0.3398         | 9.443 | -0.32 | 0.7569 |
|                     | SCE       | STS       | 0.1401   | 0.3060         | 208   | 0.46 | 0.6476 |
Table 4. Summary of seedling and sapling response thirteen years post-harvest at both sites. Table includes the mean of all species combined total stems/ha, minimum, and maximum values; mean American beech stems/ha; mean sugar maple, red maple, yellow birch combined; and the Shannon-Weiner ($H'$) value. All means shown with ±1 standard error. Saplings in harvested treatments are significantly greater than the control. N represents the number of plots within the treatments.

### SEEDLINGS

<table>
<thead>
<tr>
<th>Site</th>
<th>Treatment</th>
<th>N</th>
<th>Total Mean Stems/ha</th>
<th>Beech</th>
<th>SM_RM_YB</th>
<th>H-Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>JRF</td>
<td>Control</td>
<td>10</td>
<td>23687 ± 5128</td>
<td>3004 ± 1382</td>
<td>17204 ± 4201</td>
<td>1.1 ± 0.14</td>
</tr>
<tr>
<td>SCE</td>
<td>10</td>
<td>38726 ± 11438</td>
<td>1850 ± 464</td>
<td>27973 ± 10809</td>
<td>1.42 ± 0.11</td>
<td></td>
</tr>
<tr>
<td>MMSF</td>
<td>Control</td>
<td>10</td>
<td>25206 ± 4089</td>
<td>1265 ± 294</td>
<td>21743 ± 4271</td>
<td>1 ± 0.13</td>
</tr>
<tr>
<td></td>
<td>Group</td>
<td>10</td>
<td>15939 ± 2454</td>
<td>3447 ± 553</td>
<td>11196 ± 2554</td>
<td>1.12 ± 0.09</td>
</tr>
<tr>
<td></td>
<td>SCE</td>
<td>10</td>
<td>39374 ± 9506</td>
<td>6578 ± 1983</td>
<td>29823 ± 9687</td>
<td>1.16 ± 0.08</td>
</tr>
<tr>
<td></td>
<td>Single-Tree</td>
<td>9</td>
<td>28586 ± 7812</td>
<td>1125 ± 289</td>
<td>26320 ± 7592</td>
<td>0.81 ± 0.1</td>
</tr>
</tbody>
</table>

### SAPLINGS

<table>
<thead>
<tr>
<th>Site</th>
<th>Treatment</th>
<th>N</th>
<th>Total Mean Stems/ha</th>
<th>Beech</th>
<th>SM_RM_YB</th>
<th>H-Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>JRF</td>
<td>Control</td>
<td>10</td>
<td>1036 ± 226</td>
<td>768 ± 238</td>
<td>92 ± 70</td>
<td>0.56 ± 0.12</td>
</tr>
<tr>
<td>SCE</td>
<td>10</td>
<td>2260 ± 471</td>
<td>1596 ± 501</td>
<td>16 ± 12</td>
<td>0.63 ± 0.12</td>
<td></td>
</tr>
<tr>
<td>MMSF</td>
<td>Control</td>
<td>10</td>
<td>1204 ± 208</td>
<td>736 ± 144</td>
<td>292 ± 100</td>
<td>0.93 ± 0.10</td>
</tr>
<tr>
<td></td>
<td>Group</td>
<td>10</td>
<td>5912 ± 1874</td>
<td>4788 ± 1831</td>
<td>652 ± 206</td>
<td>0.67 ± 0.09</td>
</tr>
<tr>
<td></td>
<td>SCE</td>
<td>10</td>
<td>3228 ± 382</td>
<td>2240 ± 433</td>
<td>476 ± 206</td>
<td>0.81 ± 0.12</td>
</tr>
<tr>
<td></td>
<td>Single-Tree</td>
<td>9</td>
<td>3609 ± 674</td>
<td>964 ± 117</td>
<td>1662 ± 549</td>
<td>1.25 ± 0.06</td>
</tr>
</tbody>
</table>
Table 5. Results from the GLIMMIX show that increasing browse and increasing fine litter substrate both resulted in a decline in sapling diversity ($H'$) and an increase in American beech saplings. Direct Solar Fraction and Curtis Relative-Density Index were not significant in the model.

| Dependent Variable | Effect                  | Estimate | Standard Error | DF  | t Value | Pr > |t| |
|--------------------|-------------------------|----------|----------------|-----|---------|------|---|
| Sapling Diversity  | Percent Browse          | -0.00447 | 0.002122       | 48.7| -2.11   | 0.0403|
|                    | Percent Fine Litter Substrate | -0.01230 | 0.005158       | 46.3| -2.38   | 0.0213|
|                    | DSF                     | -0.02103 | 0.7502         | 46.4| -0.03   | 0.9778|
|                    | Curtis RD               | -0.00542 | 0.03665        | 47.6| 0.15    | 0.8830|
| Beech sapling      | Percent Browse          | 0.01130  | 0.005656       | 49  | 2.00    | 0.0512|
|                    | Percent Fine Litter Substrate | 0.02944 | 0.01371        | 46.55| 2.15   | 0.0369|
|                    | DSF                     | 0.4978   | 1.9390         | 46.31| 0.26   | 0.7985|
|                    | Curtis RD               | -0.06259 | 0.09770        | 48.21| -0.64  | 0.5248|
2.5. FIGURES

Figure 1. Regional map with locations of the two project study sites: Mt. Mansfield State Forest (A) and Jericho Research Forest (B). Also shown are treatment unit layout maps of the two study areas. Mansfield treatment manipulations: Units 1 and 8, Control; 2-3, SCE; 4-5, Single-Tree Selection; 6-7 Group Selection. Jericho manipulations: 1 and 4, Control; 2-3 SCE.
Figure 2. Total seedlings/ha by treatment over time at JRF (a) and MMSF (b). The two treatments at JRF (SCE and Control) are changing in the same way over time, while the treatments at MMSF are initially significantly greater than the control. Error bars represent +/- 1 standard error from the mean.
Figure 3. Total saplings/ha by treatment over time at JRF (a) and MMSF (b). JRF treatments are changing differently over time due to initial site conditions (Treatment*Time $P=0.0195$, pre-treatment value effect $P=0.0079$), however the means are not significantly different at each time interval. MMSF harvested treatments had significantly more saplings than the control thirteen years post-harvest showing all treatments were successful in recruiting a sapling class. Error bars represent +/- 1 standard error.
Figure 4. MMSF seedling (top) and sapling (bottom) species diversity ($H'$) thirteen years post-harvest. Outlier boxplot showing data distribution.
Figure 5. MMSF treatments thirteen years post-harvest showing American beech saplings (white) in comparison to red maple, sugar maple, yellow birch combined (grey) sapling means. Group selection (GS) had the highest range and mean of beech saplings/ha, and the highest outlier (21,080 saplings/ha not depicted on figure) while SCE exhibited high variability with patches made up of high densities of American beech displayed by the large error bars. (Tukey) outlier box plot showing data distribution.
Literature Cited


Beaudet, M., and C. Messier. 1998. “Growth and Morphological Responses of Yellow Birch, Sugar Maple, and Beech Seedlings Growing under a Natural Light


Savolainen, S. Schlömer, C. von Stechow, T. Zwickel and J.C. Minx (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.


Appendix

Table A1. Seedling and sapling densities thirteen years post-harvest by species, treatment means (± 1 standard error). In Group, Control, SCE the n=10, in Single-Tree the n=9.

<table>
<thead>
<tr>
<th>Site</th>
<th>Treatment</th>
<th>JRF</th>
<th>SCE</th>
<th>MMSF</th>
<th>Group</th>
<th>SCE</th>
<th>Single-Tree</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seedlings</td>
<td></td>
<td>Control</td>
<td>SCE</td>
<td>Control</td>
<td>Group</td>
<td>SCE</td>
<td>Single-Tree</td>
</tr>
<tr>
<td>Striped maple</td>
<td></td>
<td>727 ± 421</td>
<td>1471 ± 424</td>
<td>885 ± 220</td>
<td>269 ± 82</td>
<td>617 ± 267</td>
<td>422 ± 115</td>
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<tr>
<td>Red maple</td>
<td></td>
<td>9899 ± 3826</td>
<td>22359 ± 9863</td>
<td>32 ± 32</td>
<td>95 ± 63</td>
<td>1439 ± 1184</td>
<td>53 ± 37</td>
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<tr>
<td>Sugar maple</td>
<td>Mountain maple</td>
<td>3052 ± 1278</td>
<td>4206 ± 2084</td>
<td>15591 ± 4930</td>
<td>4096 ± 2357</td>
<td>18770 ± 9065</td>
<td>19889 ± 8417</td>
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<tr>
<td>Yellow birch</td>
<td></td>
<td>0 ± 0</td>
<td>0 ± 0</td>
<td>395 ± 195</td>
<td>127 ± 66</td>
<td>300 ± 166</td>
<td>158 ± 83</td>
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<tr>
<td>Sweet birch</td>
<td></td>
<td>4254 ± 2298</td>
<td>1407 ± 838</td>
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<td>7005 ± 1390</td>
<td>9614 ± 1953</td>
<td>6378 ± 1665</td>
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<tr>
<td>Mountain maple</td>
<td>Bitternut hickory</td>
<td>3004 ± 1382</td>
<td>1850 ± 464</td>
<td>1265 ± 294</td>
<td>3447 ± 553</td>
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<tr>
<td>White ash</td>
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<td>901 ± 329</td>
<td>2325 ± 720</td>
<td>32 ± 21</td>
<td>348 ± 196</td>
<td>680 ± 236</td>
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<td>Hop hornbeam</td>
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<td>1344 ± 680</td>
<td>2625 ± 1078</td>
<td>16 ± 16</td>
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<td>0 ± 0</td>
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<tr>
<td>Red spruce</td>
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<td>0 ± 0</td>
<td>0 ± 0</td>
<td>411 ± 177</td>
<td>174 ± 60</td>
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<td>White pine</td>
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<td>32 ± 21</td>
<td>79 ± 35</td>
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<td>Red oak</td>
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<td>63 ± 35</td>
<td>1502 ± 346</td>
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<td>Striped maple</td>
<td>20 ± 14</td>
<td>296 ± 84</td>
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<td>4 ± 4</td>
<td>56 ± 25</td>
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<td>98 ± 46</td>
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<td>0 ± 0</td>
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<td>Sweet birch</td>
<td>American beech</td>
<td>12 ± 12</td>
<td>12 ± 9</td>
<td>236 ± 93</td>
<td>648 ± 205</td>
<td>360 ± 160</td>
<td>1564 ± 559</td>
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91
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<tr>
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<td>96 ± 46</td>
<td>0 ± 0</td>
<td>0 ± 0</td>
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