Integrating management for old-growth characteristics with enhanced carbon storage of northern hardwood-conifer forests

Sarah Eliot Ford

University of Vermont

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INTEGRATING MANAGEMENT FOR OLD-GROWTH CHARACTERISTICS WITH ENHANCED CARBON STORAGE OF NORTHERN HARDWOOD-CONIFER FORESTS

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Sarah E. Ford

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Thesis Examination Committee:

William S. Keeton, Ph.D., Advisor
Shelly A. Rayback, Ph.D., Chairperson
Gillian L. Galford, Ph.D.
Cynthia J. Forehand, Ph.D., Dean of the Graduate College
ABSTRACT

Forest management practices emphasizing stand structural complexity are of interest across the northern forest region of the United States because of their potential to enhance carbon storage. Our research is nested within a long-term study evaluating how silvicultural treatments promoting late-successional forest characteristics affect aboveground biomass development in northern hardwood forests. We are testing the hypothesis that biomass development (carbon storage) will be greater in structural complexity enhancement (SCE) treatments when compared to conventional uneven-aged treatments. SCE treatments were compared against selection systems (single-tree and group) modified to retain elevated structure. Manipulations and controls were replicated across 2-hectare treatment units at two study areas in Vermont, USA. Data on aboveground biomass pools (live trees and coarse woody material, standing dead and downed wood) were collected pre- and post-harvest then again a decade later in 2013. Species group-specific allometric equations were used to estimate live and standing dead biomass and downed log biomass was estimated volumetrically. We used Forest Vegetation Simulator to project “no-treatment” baselines specific to treatment units, allowing measured carbon responses to be normalized relative to differences in site-specific characteristics and pre-treatment conditions.

Results indicate that 10 years post-harvest biomass development and carbon storage were greatest in SCE treatments compared to conventional treatments, with the greatest increases in coarse woody material (CWM) pools. Structural complexity enhancement treatments contained 12.67 Mg ha\(^{-1}\) carbon in CWM compared to 6.62 Mg ha\(^{-1}\) in conventional treatments and 8.84 Mg ha\(^{-1}\) in areas with no treatment. Percentage differences between post-harvest carbon and baseline values indicate that carbon pool values in SCE treatments returned closest to pre-harvest or untreated levels over conventional treatments. Total carbon storage in SCE aboveground pools was 15.90% below baseline conditions compared to 44.94% less in conventionally treated areas (\(P = 0.006\)). Results from CART models indicated treatment as the strongest predictor of aboveground C storage followed by site-specific variables, suggesting a strong influence of both on carbon pools. Structural enhancement treatments have potential to increase carbon storage in managed northern hardwoods based on these results. They offer an alternative for sustainable management integrating carbon, associated climate change mitigation benefits, and late-successional forest structure.
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CHAPTER 1: SILVICULTURAL MANAGEMENT OF NORTHERN HARDWOOD FORESTS FOR STRUCTURAL COMPLEXITY ENHANCEMENT AND CARBON STORAGE IN ABOVEGROUND BIOMASS

1.1. Introduction

Forest ecosystems protect water quality, cycle nutrients, sequester and store carbon, provide habitat, and help maintain biodiversity. Covering approximately 30% of the land surface on our planet, forests are almost entirely diminished or have effectively disappeared in more than 50 countries worldwide (Hassan et al. 2005). Humans have altered most of the world’s forests though our land-use history, with an estimated net decrease in global forested area of 14 million hectares per year (Houghton 1994, Hassan et al. 2005). Forests globally serve as both a significant source and sink for carbon (Gunn et al. 2014), storing more than 80% of terrestrial carbon (Liu et al. 2011) and are a leading source of carbon emissions due to deforestation and forest degradation (Keith et al. 2009). Established forests offset 30% of global CO₂ emissions (Birdsey and Pan 2015). Forest ecosystems worldwide are threatened directly and indirectly by stresses imposed by climate change, including rising temperatures and increased levels of disturbances such as insect pests and pathogens.

In this thesis, I explore the outcomes of aboveground biomass carbon storage potential in northern hardwood forests following a long-term silvicultural experiment with a goal of enhancing late-successional forest structure. Managing for old-growth/late-successional characteristics is of particular interest across northern New England forests and has the potential to be an important co-benefit to carbon storage and enhanced
To determine the amount of carbon storage potential as a result of this study, we quantified northern hardwood forest aboveground biomass and carbon storage over the 10-year period following an experimental silvicultural treatment, structural complexity enhancement (SCE), and determined how this compared both to conventional selection harvesting systems and passive (no-harvest) management. We also compared carbon outcomes to projected “no-harvest” baselines, allowing measured carbon responses to be normalized relative to differences in site-specific characteristics and pre-treatment conditions. This study provided a unique opportunity to quantify late-successional structure and carbon storage potential, and also the opportunity to test empirical, long-term data against earlier projections (Keeton 2006) and other model simulations (Nunery and Keeton 2010).

1.2. Northeastern U.S. landscape history and impacts to forest cover

The land use history of the Northeast has greatly affected forest cover throughout forest recovery. Human disturbances have affected land-use history across the northern New England region for multiple centuries, with a long history of land clearing, agriculture, and farm abandonment (Ireland et al. 2011). This widespread 19th-century clearing shifted the majority of northeastern U.S. forests from primary to secondary (regenerating) forests. Prior to 19th century clearing, an estimated 70-89% of the forests of the Northeast were in an old-growth condition greater than 150 years of age (Lorimer and White 2003). Witness tree records from lotting surveys completed across northern New England and New York pre-settlement (1763-1820) indicate these forests were dominated by 32% American beech (Fagus grandifolia). In some areas, beech comprised
up to 60% of the tree species (Cogbill 2000). After beech, sugar maple (*Acer saccharum*), red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), and yellow birch (*Betula alleghaniensis*) were the next most dominant, depending on location, ranging from 9 to 14% of species composition (Cogbill 2000). Today’s northern hardwood forests are dominated by sugar maple, American beech, and yellow birch, occurring across New England and northern New York, and across the upper Midwest into southeastern Canada.

Currently, less than 0.5% of northeastern forests have old-growth or late-successional characteristics (Davis 1996). The Northeast’s secondary regenerating forest landscape is mostly even- or multi-aged, less complex structurally, younger in age, has lower densities of large living and dead trees, and lacks the ecological diversity of the former old-growth forested landscape (Keeton et al. 2007b). Topography, soils, and human impact have influenced successional pathways and thus current species distributions throughout northeastern forest recovery (Seischab 1990, Foster 1992, Foster et al. 2004, Thompson et al. 2013).

1.3. **The significance of late-successional forest structure in a landscape**

An understanding of the significant role of old-growth forests in the landscape can aid the incorporation of such characteristics into management prescriptions. Late-successional or ‘old-growth’ forests can be defined by their function, structure, and disturbance history within a landscape (Wirth et al. 2009). Old-growth structural attributes include large numbers of live and dead trees and basal areas, a high stand biomass, high amounts of coarse woody debris, and a wide decay class distribution of
standing dead and downed woody material. Multiple canopy layers create a vertically differentiated canopy or a complex vertical structure containing large numbers of late-successional or shade-tolerant species. Horizontal structural complexity is achieved through a variation in tree age and size class distribution including the presence of multiple cohorts and variable gap densities and tree distributions (Keeton 2006, Bauhus 2009).

Old-growth forests function to maintain habitat, nutrient cycling, and species biodiversity. Increased coarse woody debris amounts provide important habitat for birds, mammals, herpetofauna, invertebrate decomposers, bryophytes, fungi, and tree seedlings (Keddy and Drummond 1996). Up to one half of the indigenous amphibian and mammal species of northern New England rely on logs for some part of their life history, while an additional 28 birds and 18 mammals use wildlife trees for such functions as perching, foraging, nesting, roosting, and denning (DeGraaf et al. 1992, Keddy and Drummond 1996). Decaying logs provide shelter, denning, nesting, and perching and foraging sites for amphibians and arthropods (Loeb 1996). Large old trees provide important sites for birds and mammals to nest, den, and forage and specialized habitat for arthropods (McGee et al. 1999). Advanced regeneration is triggered by light reaching the forest floor in canopy gaps, increasing species diversity and vertical complexity (Seymour et al. 2002). Old-growth forests cycle nutrients through the slow decomposition of large amounts of coarse woody material. Fungi, bacteria, and invertebrates break down dead organic material slowly releasing nutrients into the soil, where it is cycled back into plant growth. Bacteria fixation in the breakdown of CWD result in increased nitrogen levels, a critical nutrient for plant growth (Franklin et al. 1981). In-stream CWD recruitment in
old-growth forests creates riparian buffers, habitat function, and assists sediment and pollutant movement (Keeton et al. 2007b). It is important to recognize the value of the multitude of ecosystem functions provided by old-growth/late-successional forests considering so little of this forest type remains today within the northeastern forested landscape.

1.4. Silvicultural management approaches for late-successional stand structure

1.4.1. Emulating disturbance regimes

There are multiple management options when the goal is to obtain late-successional forest structure; often a suite of prescriptions can yield more structurally complex and diverse forests. Disturbance-based forest management is one option to promote forest structural complexity in management prescriptions. This type of management is designed to emulate an area’s natural disturbance regime with forestry practices with an understanding of disturbance dynamics and their influence on ecosystem structure and function (North and Keeton 2008). Disturbance agents in the Northeast are predominantly wind, ice, insects, fungal pathogens, beavers (*Castor canadensis*), floods, and fire, which have altered forest landscapes for centuries. Wind disturbances are usually most frequent, occurring at a low intensity, and resulting in fine-scaled canopy gaps. Small canopy gaps allow light to reach the forest floor, releasing advance regeneration and the regeneration of intermediate to shade-tolerant species. This adds structural heterogeneity at the landscape level through the formation of patches and variable horizontal density (Runkle 1984). Other types of wind disturbances of higher
intensities include hurricanes, tornadoes, and microbursts. High intensity wind events result in significant amounts of standing and downed coarse woody material and biological legacies. Legacy structure retention is therefore important if emulating this disturbance type. High intensity disturbances (>10 ha) occur at a low frequency (e.g. return intervals >1000 years) versus low intensity disturbances (0.05 ha), which are high frequency (100 year return intervals) (Seymour et al. 2002). Intermediate disturbances, such as ice storms and microbursts, are not as well researched and are thought to potentially be more prevalent than previously recognized (Hanson and Lorimer 2007). These types of disturbances leave behind significant amounts of residual live and dead trees, which combined with regeneration and release effects, can result in multi-aged stand structures.

The application of disturbance-based practices in the Northeast typically involves creating canopy gaps of varying sizes and frequencies and scales. The goal of this is to produce and maintain complexity in sync with the Northeast’s natural disturbance dynamics. This includes legacy retention to enrich structural complexity over multiple management entries and managing for multi- or uneven-aged structure. Although understood that the historic disturbance regime is characterized by fine-scale canopy gaps, it can be difficult to emulate this across a larger scale in the Northeast due to difficulties with property boundaries and landownership. Also, intermediate disturbances and legacy retention are other important considerations when designing disturbance-based management to promote structural complexity (North and Keeton 2008). There are many examples of disturbance-based silvicultural systems that are helpful when
determining the frequency, scale, and intensity at which to design a prescription to promote late-successional northern hardwood-conifer forest structure.

**Disturbance-based silviculture examples**

Multiple studies have tested the effects of varied canopy gap sizes on forest response and structural development (Angers et al. 2005, Dyer et al. 2010, Bolton and D'Amato 2011). For instance, a key consideration has been the optimum gap size at both the stand and landscape level when biodiversity and stand structural complexity are primary objectives. Kern et al. (2013) studied the impacts of a range of gap sizes, from 6 to 46 meters in diameter, on forest structure and composition in the northern hardwood forests of the upper Great Lakes region and found that the “optimum” gap size is site specific depending on microsite conditions and site productivity. Thirteen years post-harvest, most small gaps had already closed in the canopy matrix while large gaps remained open. Shrub density increased linearly with gap size, and tree recruitment and density decreased, likely as a result of greater shrub densities. As a result of this study, Kern et al. (2013) recommended using additional treatments, such as the early removal of competing vegetation when using medium to large harvest gaps on productive sites to diversify tree species composition and succeed in establishing a new cohort. These findings were contrary to those of Bolton and D’Amato (2011), who found seedling and sapling densities to increase with increasing gap sizes. This study also examined CWD recruitment within gaps and found that CWD levels were greater in the surrounding intact forest.
The Acadian Forest Ecosystem Research Program (AFERP) in northern Maine provides another example of the application of disturbance-based silvicultural prescriptions emulating the natural disturbance regime (Saunders and Wagner 2005). This project tested two “expanding gap” systems, approximating 1% of the annual disturbance frequency typical to the region. The first, a “large gap” or extended group shelterwood with reserves system, removed 20% of the stand area on a 10-year cutting cycle with 5 entries. Gap sizes were from 320 to 2170 m$^2$, an average of 0.2 ha, expanding previously created gaps at each entry. The goal of this system was to encourage mid shade-tolerant species and maintain the stand at mid-successional status. The small gap system was an “expanding” group selection with 10% of the stand area removed on a 10-year cutting cycle, gap sizes averaging 0.1 ha, and expanding previous entries every 20 years. This system encouraged late-successional states and shade-tolerant species. Reserve trees were maintained at 10% of the pre-harvest basal area within gaps in both systems to retain legacy structure (Arseneault et al. 2011). The AFERP is an area-based system as opposed to many multi-aged silvicultural systems emphasizing size-based target residual stand structure (North and Keeton 2008). Approximating both the spatial and temporal disturbance rate of the region, the treatments included intermediate-scale disturbances as suggested by North and Keeton (2008). Legacy structure retention within gaps included mature trees, rare trees, and standing and downed coarse woody material, a component often lacking in traditional uneven- and even-aged management (Saunders and Wagner 2005).

There were no significant differences in stand-level basal area growth and density between the two gap-based treatments 10 years post-harvest probably as a result of low
replication. However, regeneration of both shade-tolerant and intolerant species increased regardless of gap size likely caused by increasing light availability. Growth and survival of mid-successional species was greater in large gaps and late-successional species in small gaps.

Disturbance-based silviculture as a management option can have a variety of structural and regenerative outcomes, as indicated by these studies. Fine-scale gap dynamics systems may be more appropriate to promote late-successional structure and at smaller scales whereas larger gaps may only be appropriate across a larger landscape. Legacy structure retention within gaps is likely to aid regeneration and maintain elements of species diversity and structural complexity within the landscape.

1.4.2. Structural complexity enhancement

Structural complexity enhancement silvicultural elements at the stand level include a vertically differentiated canopy, variable horizontal density (canopy gaps), crown release around larger trees, legacy tree retention, and recruitment of coarse woody debris. A combination of silvicultural techniques can be used to achieve these structural elements. These include prescriptions with elevated post-harvest target residual basal areas and increasing CWD levels by girdling diseased and unhealthy trees to create standing dead trees and pulling trees over to create tip-up mounds. Single-tree selection harvests with target diameter distributions and variable density marking (Keeton 2006) increase vertical and horizontal heterogeneity. Raising residual live tree diameters to retain legacy trees post-harvest and reserving selections of smaller trees to reach their full
lifespan through retention harvesting are important structural elements for ecosystem
function (McGee et al. 1999, Angers et al. 2005).

Structural complexity is further enhanced by harvest prescriptions with rotated
sigmoid diameter distributions, which allocate growing space to larger diameter classes,
promoting late-successional forest structure. The re-allocation of diameter distributions to
larger size classes supports the growth of large trees, an important element of late-
successional forest structure. Large trees are significant for forest structure, functioning,
and diversity, providing nesting sites and shelter for up to 30% of all vertebrate species
and assisting with forest regeneration by and maintenance of biodiversity (Bastin et al.
2015). Previously assumed to follow the ‘reverse j’ negative exponential self-thinning
distribution curves, size class distributions for old-growth/late-successional forests are
now understood to more closely follow a rotated sigmoid distribution (Goff and West
1975, O'Hara 1996, Goodburn and Lorimer 1999), consisting of three stand-structure
developmental phases during the ‘final’ developmental phase in old-growth/late-
successional stands (see Fig. 1 for details). Example old-growth/late-successional
structural targets (Ducey et al. 2013) include an average basal area of 30–35m2/ha
between 22 and 25cm QMD for trees > 7.5cm dbh, a minimum of 40 live and dead
trees/ha > 40cm dbh (if possible at least 10 > 50cm), and several large downed logs/ha.
Additionally, including gaps is significantly important to promote horizontal complexity
and advanced regeneration.

Silvicultural prescriptions can result in a mix of age classes and structural
conditions at the landscape scale depending on rotation length, frequency, and
management objectives. For example, Hanson et al. (2012) found that raising residual
diameters to 80 cm were most effective at meeting old-growth structural criteria while moderating impacts on timber yield, based on projections completed with the individual-tree, spatially explicit modeling program CANOPY. Elevated residual diameters, permanently reserved legacy trees, variable opening sizes, coarse woody material retention, species harvest restrictions, and occasional moderate-intensity or irregular multi-cohort harvests were compared with conventional single-tree selection harvests. The model was calibrated with data from both young even-aged and mature and old-growth northern hardwood stands across northeastern Wisconsin and western upper Michigan. Stands meeting minimum old-growth structure criteria reduced timber yield by an average of 27-30% compared to conventional single-tree selection treatments. Structural retention treatments maintained elements of mature or late-successional forest structure but those with increased diameter limits resulted in an increase in the abundance of trees with high risks of death, reducing harvest volumes but raising CWD levels.

Maintaining stands at a variety of stocking densities allows for growth to be shifted between size classes depending on desired future stand conditions (Gronewold et al. 2012). At the landscape level, variable retention systems can retain structural elements, such as individual or patches of trees, thereby promoting ecological diversity (Franklin et al. 1997). Retention can be combined with certain conventional systems, like shelterwood and selection-systems, the goal of which is to focus more on what remains rather than what is taken, recognizing the role of structural complexity in maintaining ecosystem function. It is important to note the range of silvicultural options when managing for increased structure and associated co-benefits. While much research has focused on different approaches to enhance structure, including disturbance-based
prescriptions, legacy retention, and low intensity single-tree selection harvests, less research has concentrated on the co-benefit of carbon storage and sequestration associated with managing for late-successional forest structure. These more innovative approaches to forestry that address multiple functions are increasing in significance in the face of rising carbon emissions and global threats to biodiversity.

1.5. The temperate forest carbon sink

Silvicultural prescriptions that promote late-successional forest structure have the potential to significantly affect carbon storage. Late-successional/old-growth forests have greater aboveground carbon storage compared to young and mature stands. This is because high live tree biomass amounts indicative of old-growth structure store a disproportionate amount of carbon, in addition to carbon stored in larger amounts of standing and downed wood biomass (Krankina and Harmon 1994, Keeton et al. 2011). As forests age, biomass accumulates (Keeton 2011), and growth rates and productivity were previously assumed to slow (Weiner and Thomas 2001, Meinzer et al. 2011). However, recent research (Stephenson et al. 2014) analyzing 403 tropical and temperate trees species indicates that tree growth rate increases continuously with size, as does C sequestration and storage for most trees. This adds to the significance of old-growth forests functioning as long-term carbon sinks (Carey 2001), not only in maintaining high biomass amounts, but also increased productivity.

The conversion of old-growth forests to second-growth forests is a substantial loss of carbon storage capacity. In the 1990s, almost 20% of global carbon dioxide emissions
were from changes in land use and land management, mostly through deforestation (Hassan et al. 2005). Harmon et al. (1990) has suggested that 58% of the C from old-growth stands harvested in the Pacific Northwest (PNW) is lost to the atmosphere from paper production, fuel consumption, or decomposition. The deforestation of PNW old-growth stands has contributed 2% of the total carbon released to the atmosphere over the last 100 years. Although many assume reforesting with younger, faster growing stands will sequester greater amounts of carbon than older, slower growing stands, the live and dead biomass amounts of old-growth forests far surpass that of younger forests. Accounting for carbon stored in wood products, the conversion of old-growth forests to younger forests still resulted in a net C loss (305 Mg C/ha) over a 60-year rotation period (Harmon et al. 1990). The conversion of old-growth forests to second-growth forests that ultimately store less carbon is therefore making these areas a net carbon source (Krankina and Harmon 1994). It is estimated that during 2000 to 2009, approximately 1 Pg of C was lost globally each year as a result of land-use land-cover change from the combined effects of harvests, deforestation, forest degradation, forest regeneration, and decomposition of dead wood (Houghton et al. 2012). Between 1990 and 2005, it is estimated global forest area decreased by 1.7%, with a conversion of 6 million hectares per year from forest to other land uses between 2000 and 2005, twice what it was between 1990 and 2000 (FAO and JRC 2012). United States forests have only recently transitioned back to a net carbon sink following centuries of forest clearing, currently offsetting approximately 16% of anthropogenic CO₂ emissions (Joyce et al. 2014) (see Fig. 2).
The process of carbon sequestration or uptake in terrestrial forests occurs through photosynthetic processes, in which carbon is transformed into “solid carbon” or photosynthates in forest biomass (trunks, branches, leaves, and roots of trees) with up to 50% transferred to the forest floor and soil (Turner et al. 1995). Carbon storage components in the forest are called “C pools” and often divided between aboveground (live trees, standing dead and downed wood, fine litter), and belowground (soil and roots). Carbon is released into the atmosphere through the decomposition of dead wood by fungi and heterotrophs, bacteria fixation, and respiration. If carbon uptake is less than release, an ecosystem becomes a net source instead of a sink (McComb and Lindenmayer 1999, Dyer et al. 2010). Carbon fluxes to the atmosphere through deforestation, forest degradation, and land conversion, and is sequestered through tree planting and regrowth, resulting in a net offset about 30% of CO₂ emissions by forests globally (Pan et al. 2011), with the potential to increase gross terrestrial C uptake by ~2 Pg C annually (from 4 Pg to 6.2 Pg) (Birdsey and Pan 2015).

1.6. Carbon forestry

Carbon forestry employs silvicultural prescriptions of varying intensities and frequencies, with one goal being the enhancement of carbon storage potential, typically focused on aboveground biomass. The issue of forest management for carbon storage is actively debated among researchers (Harmon et al. 1990, Fahey et al. 2010, Birdsey and Pan 2015). Some suggest management scenarios with increased growth rates yield greater levels of carbon sequestration (Ruddell et al. 2007), while others propose limited or
passive management techniques to maximize structural complexity and carbon storage, promoting maintenance of old-growth forests for maximum carbon uptake (e.g. Krankina and Harmon 1994, Luyssaert et al. 2008, Nunery and Keeton 2010).

1.6.1. Reduced harvests, extended rotations, and structural enhancement

Low-intensity treatments with increased post-harvest residual basal areas, longer rotations, and fewer entry cycles are likely to increase carbon storage potential over the long term (Gustafsson et al. 2012, Palik et al. 2014). Less intensive management focused on structural enhancement provides an ecosystem approach to climate mitigation by maintaining habitat and biodiversity, enhancing water and nutrient cycling, and promoting biodiversity, lending resilience to alterations in temperature, precipitation, and disturbance. Silvicultural prescriptions that focus on enhancing forest biomass and structure have been successful at increasing carbon uptake and storage (Harmon 2001, Nunery and Keeton 2010).

While passive or no-management options have been found to yield the greatest carbon uptake benefit (Nunery and Keeton 2010), it is possible that forest management focusing on structural retention and biomass development will accelerate carbon storage potential beyond that of no-management options (Bauhus et al. 2009). Chen et al. (2015) compared clear-cut, no-harvest, uneven-aged single-tree selection, and uneven-aged group selection treatments over an 18-year study period in the Missouri Ozarks oak-hickory forest. The group selection treatments resulted in the highest biomass amounts of all harvest types compared at the end of the study period, with a mean aboveground
biomass of 148.7 Mg ha\(^{-1}\) compared to 139.5 Mg ha\(^{-1}\) in the un-harvested treatments. The net aboveground biomass growth increased from 2 to 3 Mg ha\(^{-1}\) yr\(^{-1}\) during the first 15 years post-harvest with all alternative treatments, which is higher than the average accumulation. Biomass amounts in the low-intensity single-tree selection treatments returned to pre-harvest levels only 9 years post-harvest. This study indicates the potential for alternative harvest methods to promote carbon storage potential in eastern hardwood forests, especially in low-intensity treatments such as single-tree selection. This was further supported by Man et al. (2013), who showed that reduced harvests stored significantly more carbon over a 100-year rotation length. Swanson et al. (2009) had similar but slightly contrasting findings after evaluating the effects of timber harvests on carbon storage in the southern beech (\textit{Nothofagus blume}) forests of Tierra Del Fuego, Chile. Simulations projected increases in carbon stocks at the landscape level (live tree pool) for clearcut treatments with rapid regeneration of the understory following clearcutting with an extended 200-year rotation period, but decreases in carbon stocks in the CWD pool for overstory retention treatments over 100-year rotation periods. However, the over-story retention treatments retained stored carbon in standing trees, future sources of CWD, and a spatially distributed seed source for regeneration. Clearcutting treatments relying on natural regeneration had the greatest decreases in C stocks. Although there is some level of variability in the findings of Swanson et al. (2009), Mann et al. (2013), and Chen et al. (2015), all suggest that overall, reduced harvests and extended rotations stand enhance carbon storage in aboveground pools at both the stand and landscape levels.
Research has shown that C storage can increase by 6% over 140 years as a result of switching from even-aged to uneven-aged management systems (Taylor et al. 2008). Increasing rotation length by 50% has the potential to increase carbon storage by 23% over 160 years (Nunery and Keeton 2010), a rotation length increase of 100% can increase C storage by 31% over 500 years (Peng et al. 2002), and if rotation length is increased by 200% C storage can increase by 81% over 300 years (Harmon and Marks 2002). All results are influenced by intensity, level of disturbance, and management regime. These among other studies have focused on reduced harvests and extended rotations as a carbon forestry technique, yet not included structural complexity enhancement as an additional silvicultural option for increased carbon storage potential. The integration of these objectives in silvicultural prescriptions can allow for the co-benefits of enhanced late-successional characteristics combined with carbon forestry.

1.6.2. Intensified forest management

Alternatively, some argue increased management will elevate carbon sequestration potential by increasing growth rates and carbon sequestered in harvested wood products (Ruddell et al. 2007). However, intensively managed forested areas can have a more homogenous structure and lack the biodiversity associated with a heterogeneous or late-successional forest structure (Hanson et al. 2012). More intensive treatments often focus on maximizing stocking with shorter rotations and more frequent entries, with a goal of increased productivity and C sequestration. Research aimed at strategies to increase growth rates has found that using genetically improved stock can increase carbon storage by 13% over 40 years (Aspinwall et al. 2012) and 9% after 300
years with the use of fertilizers (Seely et al. 2002). Ruddell et al. (2007) suggests forest management stability for long-term carbon sequestration. This includes sustainable forest management practices defined as encouraging maximum forest growth over time including harvesting to increase growth rates. According to Ruddell et al. (2007), managed forests have the ability to sequester more carbon than unmanaged forests through the delay of the decay of the CWD pool and therefore C loss. Harvested wood products with long life cycles can store carbon for decades. This is contrary to the previously stated findings (Harmon and Marks 2002, Houghton et al. 2012), encouraging extended rotations, reduced harvests, and CWD recruitment for increased C storage.

Although reduced harvesting frequency (Chen et al. 2015) and passive management (Nunery and Keeton 2010) have shown promise for increased C storage, multiple studies have evaluated the potential for increased growth rates to maximize forest C sequestration. One example is afforestation. Zhou et al. (2014) projected plantation forestry established through China’s National Forest Protection program to increase carbon storage by 6.24 Tg C/yr by 2020. Objectives of the program include decreasing and adjusting timber yield, but also increasing plantation establishment on degraded lands. In northwestern Ecuador, Olschewski and Benitez (2009) suggest rotation lengths of 30 years for plantations of fast-growing Cordia alliodora to optimize C sequestration and timber production. While plantation forestry with increased growth rates and C sequestration can be an effective approach for climate mitigation in the short term, this approach can lead to a less complex stand-structure lacking the co-benefits of late-successional forests. Increased growth and yield also has obvious economic
incentives, but when the goal is to promote old-growth characteristics, intensified management may not be the best option.

1.7. Northeastern U.S. aboveground forest carbon

1.7.1. Regional carbon estimates for aboveground biomass pools

Regional forest carbon stock estimates are an important measure of forest productivity and can be indicative of structural complexity in aboveground pools. The USDA Forest Service (2015) recently reported mature northern hardwood mean live tree C to be between 60 and 80 Mg ha\(^{-1}\), standing dead C between 2 and 4 Mg ha\(^{-1}\), and downed log C between 6 and 9 Mg ha\(^{-1}\). Other studies specific to northern New England report comparable values (Keeton et al. 2011). Bradford et al. (2010) found northern New Hampshire mature hardwood forests (maximum age of 120 years) to contain 96 Mg ha\(^{-1}\) live tree C and 18 Mg ha\(^{-1}\) C in coarse woody material. Whitman and Hagan (2007) reported higher levels in mature northern hardwood forests in Maine, 113 Mg ha\(^{-1}\) live tree C, 10 Mg ha\(^{-1}\) standing dead C, and 12 Mg ha\(^{-1}\) downed log C. Vermont’s old-growth live tree C has been reported at 139 Mg ha\(^{-1}\), 6 Mg ha\(^{-1}\) in the standing dead pool, and 12 Mg ha\(^{-1}\) in the downed log pool. For a more detailed overview of regional C stock estimates, please refer to Table 1.

1.7.2. Aboveground carbon modeling projections

Forest stand development models serve as a useful tool to simulate forest growth and harvest scenarios and when available, compare projected outcomes with
empirical data. Forest Vegetation Simulator (FVS) is a widely accepted and well-recognized distance-independent and individual tree-based field model, designed for even- and uneven-aged stands, best suited to the forest growth parameters of this study. FVS was selected as a modeling program for my study because of its wide use and acceptability in forest management to project forest stand development for a variety of management applications (Crookston and Dixon 2005).

In certain situations, FVS has been known to over-predict carbon amounts. Gunn et al. (2014), found FVS to over estimate carbons stocks in both late-successional and old-growth northeastern forests, likely due to a lack of calibration data because of the rarity of these forest types across the Northeast and also increased disturbance amounts within these forests not accounted for by FVS. However, MacLean et al. (2014) found that uncalibrated regional FVS tended to under predict carbon for FIA plots across the northeastern United States. Differences in FVS projected outcomes for northeastern tree growth and C stocking suggest an inherent need to continue to work on calibration methods and an overall awareness of differences in methods for conducting carbon stock assessments and calculations. Additionally, the effects of disturbance (e.g. beech bark disease) and climate change (e.g. changes in species distributions) on forest stand development in the Northeast also need to be considered for when projecting future forest conditions. Our study proposes using field inventory regeneration and site-specific stand compositional data to assess model accuracy. We plan to use FVS to project no-harvest baseline conditions to normalize site variability and compare against measured post-harvest carbon outcomes.
1.8. Climate change and northeastern forests

Climate change is having both gradual and long-term effects, direct and indirect on forests (Fig. 3), including changes to biodiversity, productivity, forest structure, and ecosystem services. Direct effects of climate change on forests include increased water use and evaporation as a result of warmer winters and longer growing seasons. Increased water use will decrease soil moisture, contributing to dry spells during summer, and decreased forest productivity. This could result in increased susceptibility of trees to disease, invasive species infestations, and threaten silvicultural resources (Rustad et al. 2012). New England’s forests in particular are vulnerable to increasing infestations by invasive species and damage from more severe and frequent forest disturbances as a result of climate change. Habitat ranges of certain tree species are at risk as temperatures increase with the potential to be pushed northward by the end of the century.

The Northeast’s climate has warmed almost 2 degrees F between 1895 and 2011, an average of 0.16 degrees F per decade, and is projected to rise 5 to 10 degrees F by the end of the 21st century under all emissions scenarios (Horton et al. 2014). Precipitation is projected to increase 5 to 10% (up to 4 inches) by the end of this century, with a greater increase in the winter than summer and an increase in short and medium term droughts (Frumhoff et al. 2007). Additionally, the Northeast is experiencing a greater number of stronger precipitation events, windstorms, and extended cold periods or “polar vortexes” over the past 10 to 20 years (Frumhoff et al. 2007, Galford et al. 2014).

The effects of changing precipitation and alterations in temperatures are significant for northeastern forest ecosystems, including exacerbating conditions favoring pest and pathogen invasions and changing disturbance frequencies and severities. The
hemlock woolly adelgid (*Adelges tsugae*) has already expanded its range north to Maine and into southern Vermont due to a more favorable climate over the last decade (Paradis et al. 2007), and is likely to continue expanding northward with warming temperatures. A reduction in snowpack has caused an increase in northeastern deer populations, resulting in increased browse effects on forest understories (Horton et al. 2014). Spring leaf-out is occurring earlier as a result of shorter winters. Research from northern hardwood forests at Hubbard Brook Experimental Forest in New Hampshire found significantly earlier spring leaf-out with an increase in green canopy of 10 days over a 47-year period (Richardson et al. 2006). Although extended growth periods should increase productivity, other stressors (water, heat, disease, pests, and acid deposition) often limit the extent to which forests are able to take advantage of longer growing seasons.

Northeastern forests have experienced transitions in climate and species composition for tens of thousands of years (Foster et al. 2004). Forests are slow to respond to such variations, and it is therefore difficult to accurately model future forest species distributions as a result of climate change as humans accelerate the degree to which climate transitions are occurring. Trees have long life spans, slow dispersal rates, and the ability to adapt genetically to changing climate, adding to the complexity of modeling future suitable ranges based on such factors as increasing temperature and alterations in precipitation amounts (Rustad et al. 2012). Human-accelerated climate change is making it even less clear how forests will respond to changes in suitable habitat. Climate models project dramatic range shifts of dominant tree species in the northeastern U.S. over the next 100 years (Iverson et al. 2008). High elevation spruce-fir forests are most vulnerable to rising temperatures associated with some of the long-term
effects of climate change, and climate models project their suitable habitat to be virtually nonexistent in the Northeast within 100 years under all emissions scenarios (Rustad et al. 2012). Oak-pine forests, which are more tolerant to warmer temperatures, are projected to expand northward throughout the Northeast, replacing current dominant hardwood species like maple and birch (Rustad et al. 2012). However, the combination of changing precipitation, temperature, disturbance, and biogeochemical cycles add to the complexities of projecting how northern U.S. forests will respond. Holistic management approaches that focus on promoting species diversity, structural complexity, and carbon storage can serve as an option for climate mitigation.

1.9. Integration of old-growth characteristics with enhanced carbon storage

Silvicultural treatments that enhance carbon storage while providing other co-benefits, such as late-successional biodiversity associated with stand structural complexity are of interest both domestically and abroad (e.g. Gustafsson et al. 2012, Ducey et al. 2013, Chen et al. 2015). Prior studies (Angers et al. 2005, Bauhus et al. 2009, Puettmann et al. 2015) suggest that silvicultural treatments promoting or accelerating the development of late-successional structure may offer particular potential for this type of multi-functional forestry.

A combination of silvicultural approaches can elevate carbon storage potential at the landscape level while also providing opportunities for timber harvest and other co-benefits (Schwenk et al. 2012). For example, irregular shelterwoods and selection systems maintain carbon stores in large trees and when combined with thinning treatments increase spatial heterogeneity and structural complexity (D'Amato et al. 2011).
Carbon sequestration is increased through tree regeneration and carbon stores are maintained through large tree retention. There are tradeoffs, however, when maximizing the potential of both stand structural complexity and carbon storage benefits. D’Amato et al. (2011) found that with increased stocking, stand structural complexity decreased in the upper Great Lakes region. Live tree carbon increment rates were also lowest in stands with the highest stocking levels, even though these stand conditions maximized carbon stores. Alternatively, increasing northeastern carbon storage in existing forests has been suggested through increases in live tree stocking (Heath and Hoover 2011), with mean live tree C storage measuring from 74 to 106 Mg/ha in fully stocked forests, 94.1 Mg/ha in Vermont forests. Considering an estimated 49% of northeastern timberlands are below their live tree stocking potential (Hoover and Heath 2011), there is a need for research on multi-functional silvicultural approaches that increase stocking, complexity, and carbon stores in northern hardwood forests.

Structural enhancement treatments present an option for continued management coinciding with the northeastern forest natural disturbance regime (Seymour et al. 2002), as previously discussed. U.S. forests recover and store approximately 15% of all carbon dioxide from U.S. emission sources, but with improved forest management this could increase to 25% (EPA 2014). Disturbance-based/alternative stand structural management promoting legacy tree retention, inputs to coarse woody debris pools, and increased vertical and horizontal heterogeneity and biomass levels are options for maximizing C storage potential (Franklin and Pelt 2004, Gustafsson et al. 2012) in addition to providing habitat function and maintaining biodiversity (Lindenmayer et al. 2000, Keith et al. 2009).
1.10. Project overview

Prior research has focused on harvest effects on stand structure (Keeton 2006) and elements of late-successional biodiversity, including herpetofauna (McKenny et al. 2006), herbaceous plant communities (Smith et al. 2008), and fungal response (Dove and Keeton 2015), but has not evaluated carbon storage. This study proposes using the 10-year time span of inventory data post-treatment to further evaluate the effectiveness of treatments tested on biomass retention and carbon storage in experimentally treated areas on Mount Mansfield and in Jericho. Analysis of inventory data can determine factors influencing differences between treatments (site conditions, initial species composition, treatment types, fluxes between carbon pools, etc.). Results from this study will address the need for more research on the effects of silvicultural treatments on carbon fluxes in aboveground biomass pools (Gunn et al. 2014), provide carbon and forest structure management tools for landowners, and also highlight areas for continued research opportunities on this project.

1.11. Conclusions

Climate mitigation is now an integral part of sustainable forest management. With climate change projected to significantly raise temperatures and alter precipitation patterns under all emissions scenarios across the northeastern U.S. by the end of this century (IPCC 2013), this is adding to the complexities of forest management considering the effects on forest ecosystems are still uncertain. Projected impacts on tree growth and species distributions indicate potential shifts from our northern hardwood maple-beech-
birch forest to a southern oak-hickory forest with suitable high elevation spruce-fir habitat disappearing. Research is needed to project how the effects of climate change will affect carbon storage potentials of stands under future conditions (Hoover and Heath 2011).

A more widespread adoption of silvicultural practices with a focus on structural complexity enhancement, biomass development, ecosystem function, and diversity in species composition stands to promote resilience to climate change and also address the issue of global decline in biodiversity and carbon stocks (Lindenmayer et al. 2012). Silvicultural treatments that enhance structure and carbon storage can offer a variety of ecosystem services and management tools for landowners at multiple scales. Global carbon markets, temperature and precipitation alterations, and shifts in disturbance frequencies and intensities are increasing the necessity for landowners and forest managers to be prepared with a suite of management alternatives. These include the modification of harvests to increase retention and rotation length, in addition to the emulation of natural disturbance regimes. Forest clearing for agriculture, development, and other forms of land use conversion is reducing carbon storage potentials and transitioning old-growth/late-successional forested areas from a net carbon sink to source. Silvicultural treatments evaluated in this study present a range of alternative carbon forest management options including resilience and adaptation to climate change, structural enhancement, and maintenance of biodiversity.
Table 1. Northeastern United States regional carbon stock comparisons (live tree, standing dead, and downed log pools).

<table>
<thead>
<tr>
<th>Live tree</th>
<th>Standing dead</th>
<th>Downed log</th>
<th>Location</th>
<th>Forest Type</th>
<th>Age</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>96</td>
<td>18 (both dead wood pools)</td>
<td>12</td>
<td>Northern NH</td>
<td>Northern hardwood</td>
<td>120 (max)</td>
<td>Bradford et al. 2010</td>
</tr>
<tr>
<td>113</td>
<td>10</td>
<td>12</td>
<td>Maine</td>
<td>Northern hardwood</td>
<td>Mature</td>
<td>Whitman and Hagan 2007</td>
</tr>
<tr>
<td>83</td>
<td>12</td>
<td>15</td>
<td>New York</td>
<td>Northern hardwood-conifer</td>
<td>Mature</td>
<td>Keeton et al. 2011</td>
</tr>
<tr>
<td>60-80</td>
<td>2-4</td>
<td>6-9</td>
<td>Northern NE</td>
<td>Northern hardwood</td>
<td>Mature</td>
<td>USDA Forest Service 2015</td>
</tr>
<tr>
<td>116</td>
<td>8</td>
<td>12</td>
<td>Northern NE</td>
<td>Northern hardwood</td>
<td>150-400+</td>
<td>Hoover et al. 2012</td>
</tr>
<tr>
<td>125</td>
<td>13</td>
<td>9</td>
<td>Northern NE</td>
<td>Tsuga, Picea, Abies</td>
<td>150-400+</td>
<td>Hoover et al. 2012</td>
</tr>
<tr>
<td>139</td>
<td>6</td>
<td>12</td>
<td>Vermont</td>
<td>Hardwood</td>
<td>Old-growth</td>
<td>Hoover et al. 2012</td>
</tr>
<tr>
<td>131</td>
<td>14</td>
<td>13</td>
<td>Michigan</td>
<td>Northern hardwood</td>
<td>200-300</td>
<td>Fisk et al. 2002</td>
</tr>
<tr>
<td>4</td>
<td>14</td>
<td>10</td>
<td>Michigan</td>
<td>Northern hardwood</td>
<td>Old-growth</td>
<td>Goodburn and Lorimer 1998</td>
</tr>
<tr>
<td>5</td>
<td>10</td>
<td>12</td>
<td>Michigan</td>
<td>Hemlock hardwood</td>
<td>Old-growth</td>
<td>Goodburn and Lorimer 1998</td>
</tr>
<tr>
<td>6 (CWD)</td>
<td>Vermont</td>
<td>21</td>
<td>Northern hardwood</td>
<td>Mature</td>
<td>Woodall et al. 2013</td>
<td></td>
</tr>
<tr>
<td>122</td>
<td>22</td>
<td>11</td>
<td>New York</td>
<td>Northern hardwood-conifer</td>
<td>Old-growth</td>
<td>Keeton et al. 2011</td>
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<tr>
<td>141</td>
<td>15</td>
<td>14</td>
<td>Maine</td>
<td>Northern hardwood</td>
<td>Old-growth</td>
<td>Whitman and Hagan 2007</td>
</tr>
<tr>
<td>102</td>
<td>18</td>
<td>11</td>
<td>Maine</td>
<td>Northern hardwood-conifer</td>
<td>Old-growth</td>
<td>Gunn et al. 2014</td>
</tr>
<tr>
<td>96</td>
<td>12</td>
<td>5</td>
<td>Maine</td>
<td>Northern hardwood-conifer</td>
<td>Late-successional</td>
<td>Gunn et al. 2014</td>
</tr>
</tbody>
</table>
Figure 1: Example reverse-J and rotated sigmoid diameter distributions. A reverse-J distribution contains a constant q-factor (the ratio of number of trees in each successively larger size class), with equal growing space allotted to each size class (O’Hara 1998). Rotated sigmoid distributions have three q-factors, indicative of three indistinct phases of development common to old-growth stand-structure (Goff and West 1975).
Figure 2: United States net forest CO$_2$ emissions/sequestration corresponding with the change in forest land area over time. Carbon emissions/sequestration are represented by the blue line and change in forest cover by the green shaded area. Forest CO$_2$ emissions peak in the early 1900s coinciding with the height of forest clearing in the U.S. Adapted from Joyce et al. (2014).
Figure 3: Direct and indirect effects of climate change on forests. Adapted from Keeton et al. (2007).
2.1. Abstract

Forest management practices emphasizing stand structural complexity are of interest across the northern forest region of the United States because of their potential to enhance carbon storage. Our research is nested within a long-term study evaluating how silvicultural treatments promoting late-successional forest characteristics affect aboveground biomass development in northern hardwood forests. We are testing the hypothesis that biomass development (carbon storage) will be greater in structural complexity enhancement (SCE) treatments when compared to conventional uneven-aged treatments. SCE treatments were compared against selection systems (single-tree and group) modified to retain elevated structure. Manipulations and controls were replicated across 2-hectare treatment units at two study areas in Vermont, USA. Data on aboveground biomass pools (live trees and coarse woody material, standing dead and downed wood) were collected pre- and post-harvest then again a decade later in 2013. Species group-specific allometric equations were used to estimate live and standing dead biomass and downed log biomass was estimated volumetrically. We used Forest Vegetation Simulator to project “no-treatment” baselines specific to treatment units, allowing measured carbon responses to be normalized relative to differences in site-
specific characteristics and pre-treatment conditions.

Results indicate that 10 years post-harvest biomass development and carbon storage were greatest in SCE treatments compared to conventional treatments, with the greatest increases in coarse woody material (CWM) pools. Structural complexity enhancement treatments contained 12.67 Mg ha\(^{-1}\) carbon in CWM compared to 6.62 Mg ha\(^{-1}\) in conventional treatments and 8.84 Mg ha\(^{-1}\) in areas with no treatment. Percentage differences between post-harvest carbon and baseline values indicate that carbon pool values in SCE treatments returned closest to pre-harvest or untreated levels over conventional treatments. Total carbon storage in SCE aboveground pools was 15.90% below baseline conditions compared to 44.94% less in conventionally treated areas \((P = 0.006)\). Results from CART models indicated treatment as the strongest predictor of aboveground C storage followed by site-specific variables, suggesting a strong influence of both on carbon pools. Structural enhancement treatments have the potential to increase carbon storage in managed northern hardwoods based on the results. They offer an alternative for sustainable management integrating carbon, associated climate change mitigation benefits, and late-successional forest structure.

### 2.2. Key words
Carbon storage; Carbon forestry; Alternative silviculture; Northern hardwoods; Structural complexity enhancement; Forest Vegetation Simulator; Late-successional/old-growth forestry
2.3. Introduction

Forests globally function as a significant carbon sink, storing ~45% of terrestrial carbon (Bonan 2008), yet are a leading source of carbon emissions due to deforestation and forest degradation (Keith et al. 2009). An estimated 36% of the historical extent of the world’s forests have declined (16.4 million km$^2$) over the last 200 years (Meiyappan and Jain 2012). Although widely acknowledged that forest ecosystems of greater maturity and structural complexity maintain high levels of carbon storage (Harmon et al. 1990, Luyssaert et al. 2008, Keeton et al. 2011, Hoover et al. 2012, Cunningham et al. 2015), there is ongoing debate regarding the effects of different silvicultural approaches on carbon storage (Ruddell et al. 2007, Thomas et al. 2007, Nunery and Keeton 2010). Managing for old-growth/late-successional forest structure has the potential to be an important co-benefit to carbon storage and enhanced biomass development, and is of particular interest across northern New England, U.S.A. In this study, we quantified aboveground biomass and carbon storage in northern hardwood-conifer forests over a 10-year period following an experimental silvicultural treatment, structural complexity enhancement (SCE), and determined how this compared both to conventional selection harvesting systems and passive (no-harvest) management. This study also provides an opportunity to test empirical, long-term data against earlier projections (Keeton 2006) and other model simulations (Nunery and Keeton 2010).

Prior to 19$^{th}$ century clearing, an estimated 70-89% of the forests that covered the Northeast were old-growth hardwood forests, greater than 150 years of age (Lorimer and White 2003). Today less than 0.5% of northeastern forests have old growth or late-
successional characteristics (Davis 1996) as a result of widespread 19th century clearing for agriculture (Lorimer and White 2003). Compared to primary or late-successional forests, secondary forests are often younger in age, lack vertical and horizontal complexity, and have lower densities of both live and dead trees (Keeton et al. 2007b). Late-successional forests have greater amounts of vertical and horizontal structure, tree age and size class distributions, and diversity in species composition, lending to greater levels of complexity (McGee et al. 1999, Franklin et al. 2002 D’Amato et al. 2011, McElhinny et al. 2005). Structurally complex temperate forests are known to maintain higher levels of biological diversity (Lindenmayer et al. 2000), hydrologic regulation (Wirth et al. 2009), and carbon storage (Keeton et al. 2011, Hoover et al. 2012, McGarvey et al. 2015). Over the past decade several studies have investigated forest management practices specifically designed to promote late-successional/old-growth forest characteristics, both in the U.S and internationally (Lindenmayer et al. 2000, Bauhus et al. 2009, Ducey et al. 2013, Duveneck et al. 2014). However, less well understood is whether these approaches would also have utility for carbon management, and thus, this question is the focus of this paper.

Silviculture is the act of forest management by controlling tree growth and establishment to meet a multitude of long term goals, needs, and values (Smith 1962). Carbon forestry employs silvicultural prescriptions of varying intensities and frequencies with one goal being the enhancement of carbon storage potential in aboveground biomass. Silvicultural treatments that enhance carbon storage while providing other co-benefits, such as late-successional biodiversity associated with stand structural complexity are of interest both domestically and abroad (e.g. Gustafsson et al. 2012,
Ducey et al. 2013, Chen et al. 2015). Prior studies (Angers et al. 2005, Bauhus et al. 2009, Puettmann et al. 2015) suggest that silvicultural treatments promoting or accelerating the development of late-successional structure may offer particular potential for this type of multi-functional forestry.

How to best manage forests for carbon storage is actively debated among researchers (Harmon 2001, Fahey et al. 2010, Birdsey and Pan 2015). Some suggest management scenarios with increased growth rates yield greater levels of carbon sequestration (Birdsey et al. 2006), while others propose limited or passive management techniques to maximize structural complexity and carbon storage, promoting maintenance of old-growth forests for maximum carbon uptake (e.g. Krankina and Harmon 1994, Luyssaert et al. 2008). In northern Minnesota for example, extended rotations are used to accelerate the advancement of diameter classes to larger size classes comparable to old-growth stands (Silver et al. 2013). The re-allocation of basal area to larger size classes, legacy tree retention, the addition of variable horizontal density (small canopy gaps), and elevating coarse woody debris amounts all function to promote old-growth/late-successional stand development. Low-intensity treatments with increased post-harvest residual basal areas, longer rotations, and fewer entry cycles are likely to increase carbon storage potential over the long term (Gustafsson et al. 2012, Palik et al. 2014). Alternatively, some argue intensified and expanded management will elevate carbon sequestration potential by increasing growth rates and carbon sequestered in harvested wood products, for instance through shorter rotations and more frequent entries (Malmsheimer et al. 2008). While the effectiveness of intensified management as a
carbon management strategy remains under debate (McKinley et al. 2011), it is clear that shorter rotations and intensified harvesting generally produce less complex stand structures, and if applied broadly enough, reduce the availability of late-successional habitats at the landscape scale (Gronewold et al. 2012). Less intensive management focused on promoting structural complexity may provide an alternative, contributing to climate mitigation through enhanced carbon storage while providing late-successional habitats (see for example Smith et al. 2008, Dove and Keeton 2015).

Rapidly developing voluntary and compliance carbon markets are providing a financial incentive for forest carbon projects that generate greenhouse gas emissions offsets (Russell-Roy et al. 2014, Kerchner and Keeton 2015). This is encouraging broader adoption of forest management techniques that stock carbon across larger scales (Hoover and Heath 2011). Carbon sequestration in established forests offsets 30% of global CO$_2$ emissions (Pan et al. 2011), with the potential to increase gross terrestrial C uptake by ~2 Pg C annually (Birdsey and Pan 2015). A combination of silvicultural approaches can elevate carbon storage potential at the landscape level while also providing opportunities for timber harvest and other co-benefits (Schwenk et al. 2012). For example, irregular shelterwoods and selection systems maintain carbon stores in large trees and, when combined with thinning treatments, increase spatial heterogeneity and structural complexity (D’Amato et al. 2011). Reducing harvest intensities and increasing post-harvest residual basal areas has been found to be an effective mechanism at increasing carbon stores in northern Minnesota (Gunn et al. 2011).

This paper adds to several previous investigations of responses to structural complexity enhancement (Angers et al. 2005, Dyer et al. 2010, Silver et al. 2013), while
relatively few studies have explored carbon storage potential and structural retention. Prior research has focused on harvest effects on stand structure (Keeton 2006) and elements of late-successional biodiversity, including herpetofauna (McKenny et al. 2006), herbaceous plant communities (Smith et al. 2008), and fungal response (Dove and Keeton 2015). Here we report on aboveground carbon pools, explicitly addressing the question of how structural complexity enhancement affects carbon storage and fluxes in aboveground pools in northern hardwood-conifer forests. Will structural complexity enhancement (SCE) silvicultural treatments enhance carbon storage and fluxes over conventional selection systems? Is active management able to accelerate biomass development above the baseline that would have occurred without treatment? Answering these questions will help inform efforts to integrate carbon forestry and old-growth silviculture in both the northern forest region and beyond (e.g. Bauhus et al. 2009). We hypothesize that 10 years post-treatment: 1) additions to aboveground carbon will be greater under SCE compared to conventional selection treatments and relative to modeled growth potential without treatment (treatment effects); and 2) carbon accumulation rates will correlate positively with site productivity (treatment vs. site variability).

2.4. Methods

2.4.1. Study area

Study sites for this project are located within the Mount Mansfield State Forest (MMSF, 44°30'23.03"N; 72°50'11.24"W) and the Jericho Research Forest (JRF, 44°26’43.70”N; 72°59’44.15”W) in Vermont, USA (Figure 1). The Mount Mansfield
study area falls within the central portion of the Green Mountains, Vermont with elevations ranging from 470 to 660 meters and Peru stony loam soils. Located at the foothills of the Green Mountains with elevations from 200 to 250 meters, soils at the Jericho study site are primarily Adams and Windsor loams sands or sandy loams. Supplementary live tree inventory data from the Forest Ecosystem Research Design Area (FERDA) experiment in New York, USA was also used to complement existing data in this study. The FERDA experiment contains two study sites, Keese Mill and VIC (Visitor Interpretive Center) (44°25'59.6"N 74°20'36.4"W), adjacent to Paul Smith’s College in Franklin County, New York. Elevations at the FERDA sites ranged from 500 to 540 meters and soils are Adams-Colton and Becket-Tunbridge-Skerry complex, rocky and well drained.

Forests in the Vermont study areas are comprised of mature, 70-100 year old northern hardwood-conifer species. Dominant overstory species include *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), *Betula alleghaniensis* (yellow birch) and *Tsuga canadensis* (eastern hemlock). There are minor components of *Picea rubens* (red spruce) at the MMSF study area and *Acer rubrum* (red maple) and *Quercus rubra* (red oak) in the dominant canopy at the JRF study area. Over the course of the 20th century, there were four to six recorded management entries in the study areas post-establishment (Hannah 1999), resulting in multi-aged forest structure confirmed through pre-treatment tree coring as reported in Keeton (2006). Dominant overstory species at the FERDA study area include *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), *Betula alleghaniensis* (yellow birch), with minor components of *Acer rubrum*
(red maple) and *Picea rubens* (red spruce). The FERDA sites were used extensively for agriculture until the 1900s and have been partially harvested at least once.

### 2.4.2. Silvicultural treatments

This long-term project employs a before-after-control-impact (BACI) experimental design (Krebs 1999), with structural metrics compared pre- and post-harvest and between silvicultural treatments. Initiated in 2001, with treatments implemented in 2003, this project presents a unique opportunity to assess over 10 years of post-treatment response data.

Pre-treatment data were collected in 2001 and 2002, treatments introduced to the MMSF and JRF study sites in 2003, and 10 years of post-treatment response data evaluated in 2013. The three experimental manipulations included two conventional uneven-aged treatments (single-tree and group selection) modified to enhance post-harvest structural retention, and a SCE treatment designed to enhance late-successional forest structure. Treatments were implemented across 2 ha units in a randomized block design, separated by a minimum 50 m buffer (Fig. 4). Each MMSF and JRF treatment unit contains 5 randomly placed permanent sample plots that are 0.10 ha in size; plots thus cover 25% of each treatment unit’s total area. An important element of the SCE treatment was the target diameter distribution, which was based on a rotated sigmoid form (Goff and West 1975, O’Hara 1998). In selecting this distribution over a negative exponential or “reverse J” form, the objective was to allocate more growing space and basal area to larger size classes, thereby promoting development of both late-
successional/old-growth structure and biomass accumulation over time. The rotated sigmoid exponential distribution was achieved through the application of a non-constant q-factor in each diameter size class (see Table 2 for details). Target residual basal area, in this case a desired future condition, was set at 34 m$^2$ ha$^{-1}$ and max diameter at breast height (dbh) to 90 cm, indicative of late-successional structure. Late-successional structure was further enhanced through crown release around larger trees, and silvicultural creation of coarse woody debris, small canopy gaps (0.02 ha mean size), standing dead trees, and tip-up mounds (see Keeton 2006). Conventional uneven-aged treatments included single-tree and group selection harvests, with target residual basal areas of 18.4 m$^2$ ha$^{-1}$. Single-tree and group selection treatments had the same BDq prescriptions (Table 2), though applied in dispersed or aggregated pattern respectively. Group selection cutting patches averaged 0.05 ha in size, with nine groups per treatment unit. Groups were well distributed but placed to release desired advanced regeneration; there was light retention of large dead trees and mature beech exhibiting resistance to bark disease (*Nectria coccinea* var. *faginata*) within some groups.

Supplementary conventional (single-tree and group selection) and control treatment live tree data were used from the FERDA project, initiated in 1998 and harvested in 2000, with replications at Keese Mill and VIC sites. FERDA treatment units are 2 ha with 8 permanent plots per unit, 0.04 in size. FERDA single-tree and group selection treatment replications matched MMSF and JRF, with similar target post-harvest residual basal areas (18.4 m$^2$ ha$^{-1}$), BDq, and selection patch sizes (0.05 ha). We selected FERDA replications for use in this study with pre-treatment basal areas most comparable
to the JRF and MMSF study sites. There were additional treatment types tested in the FERDA project, data from which were not used in this project.

Each conventional treatment was replicated twice at the MMSF and JRF study sites (across a total of 4 units), and twice at each FERDA site (Keese Mill and VIC). The SCE treatment was replicated two times at the MMSF and two times at the JRF. There are two un-harvested control units at Mount Mansfield, two at Jericho, and two controls used from the FERDA project.

2.4.3. Field inventory

The field inventory data used in this study focused on measurements needed for aboveground biomass estimations. Within each plot (MMSF and JRF sites) we measured, identified, recorded, and permanently tagged all live and standing dead trees ≥ 5 centimeters diameter at breast height (dbh) and > 1.37 m tall. We recorded decay class (1-9) for all standing dead trees following Sollins et al. (1987) and measured standing dead heights using an Impulse 200 laser range finder (Laser Technology, Englewood, Colorado, USA). Downed log volume by decay class (1-5) (Sollins et al. 1987) was estimated following the line-intercept method (Shivers and Borders 1996) for all downed logs >1 m in length and ≥10 cm diameter along two 31.62 m center transects bisecting each plot. Diameter-at-intersect, species, and decay class for each log along the center transects were recorded. For regeneration estimates, we tallied seedlings by species within a 1 m belt along each center transect nested inside each permanent plot. In the FERDA plots, all live and standing dead trees ≥ 2.54 cm dbh were inventoried and
permanently tagged but downed wood was not inventoried.

**2.5. Data processing and analysis**

**2.5.1. Stand-structural metrics**

We compared MMSF and JRF field inventory data collected in 2013 with inventory data from 2003 (first year post-harvest) and 2001 (pre-harvest and the year of project initiation) to assess differences in levels of carbon storage pre- and post-harvest and between treatments. A comparable period pre- and post-harvest was used for the FERDA live tree data. We input all field inventory data (pre- and post-harvest) into the Northeast Ecosystem Management Decision Model (NED-3) (Twery and Thomasa 2014) to generate stand structural metrics. These included live, dead, and total tree basal area, stem density, aboveground biomass, live tree quadratic mean diameter (QMD) and percent hardwood (Table 3). Slope and aspect were averaged for each treatment unit and site indexes were determined from pre-harvest tree core and height information (MMSF and JRF) and from the Natural Resources Conservation Service soil survey (FERDA).

**2.5.2. Biomass and carbon quantification**

To quantify live tree and standing dead carbon during each pre- and post-harvest inventory year studied, we first estimated live and dead tree biomass using Jenkins et al. (2003) group-specific allometric equations embedded in NED-3. Live tree carbon was calculated by dividing the mean biomass for each treatment unit by two. Biomass calculations are the same for both live and dead trees in NED using the Jenkins et al.
(2003) equations. Consequently, to determine standing dead tree biomass and carbon content, we made deductions to the allometrically derived estimates following the CARB (California Air Resources Board) carbon inventory protocol (Climate Action Reserve 2014). Adjustments reflected the amount of biomass missing (e.g. from breakage, decay, disease, etc.) from each dead tree when compared to its living counterpart. Deductions were determined by calculating the difference between the measured standing dead tree height compared to the pre-treatment inventoried live tree height for the same stem. For missing live tree heights, we used regression equations determined by diameter-species relationships using existing tree inventory data. We then applied a density reduction factor following Harmon et al. (2011) correlating with measured decay class to all adjusted standing dead biomass values. Mean standing dead carbon for each unit was calculated using the final adjusted biomass values for individual standing dead trees divided by two. Downed log carbon content was determined following Harmon et al. (2008). Inventoried downed log volumes were adjusted by species specific gravities for each decay class (1-5). Adjusted volumes were then transformed to biomass and adjusted by carbon content by decay class. Species were assigned proportionate to the mean overstory basal area per treatment unit for all unknown species.

2.5.3. Carbon responses to treatments

Carbon response trends were evaluated first using mean absolute values for each pool (live tree, standing dead, downed log) by treatment. For all carbon response comparisons, single-tree and group selection treatments were grouped into a
“conventional” uneven-aged treatment following Keeton (2006). There was no significant difference in stand structural responses for each treatment type, supporting this grouping (see Table 2).

For the second carbon quantification assessing post-harvest carbon storage in each treatment relative to untreated or “baseline” conditions within each unit, we calculated percentage differences between post-harvest and baseline carbon values for all measured pools within treatments. This determined how near to the un-harvested or “baseline” condition each treatment returned 10-years post-harvest. We chose the percentage difference metric as a standardized comparison normalizing relative difference between harvested and baseline values across the range of inherent site variability. Percentage differences were calculated following Littlefield and Keeton (2012), modified from Westerling et al. (2006). Percentage differences were calculated as follows:

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

where \( V_H \) is equal to a post-harvest carbon value, and \( V_B \) is equal to a baseline carbon value (see below for “baseline” carbon definitions). Using the above formula, we compared carbon storage in each pool 10 years post-harvest against baseline values specific to each treatment unit. In this analysis, a zero (0) percentage difference indicates no difference from the baseline conditions; a negative (-) percentage difference indicates below the baseline; and a positive (+) percentage difference indicates above or surpassed the baseline conditions. Therefore, for post-harvest-baseline carbon pool comparisons, percentage differences that are closer to 0/above 0 indicate greater C storage potential.
Carbon flux for each pool was defined as the amount of C lost or gained over the 10-year interval post-harvest (Mg ha\(^{-1}\) yr\(^{-1}\)) (Harmon 2001, Russell et al. 2014). These were calculated by determining the difference between mean carbon the year immediately post-harvest and mean carbon 10 years post-harvest and dividing by 10 (the time span of comparison).

2.5.4. Modeling no-management scenarios to produce baseline conditions for each treatment unit

For the live tree carbon pool, we simulated baseline conditions for comparison to post-harvest data using growth and yielding to project stand development in each unit. We did this by projecting 10 years of growth using pre-treatment data and assuming no treatment or management. This provided a baseline for normalizing measured (i.e. empirical) carbon responses against the inherent growth and carbon accumulation potential specific to each unit, for instance related to differences in site productivity, initial stocking, and stand composition and quality. The northeastern variant of the Forest Vegetation Simulator (NE-FVS) was selected for this purpose because of its wide use in a variety of forest management (Crookston and Dixon 2005) and carbon offset applications (Kerchner and Keeton 2015). NE-FVS is a distance-independent and individual tree-based growth and yield model suitable for both even and uneven-aged stands. Regional validation studies of NE-FVS have shown accurate volume and biomass projections in northern hardwood forests, within 10-15% when simulating forest growth (Yaussy 2000). However, a limitation is that FVS has been shown to have known inaccuracies estimating
large, live tree growth in northeastern U.S. late-successional and old-growth forests (Gunn et al. 2014, MacLean et al. 2014). In our study this limitation is acceptable in that the resulting growth projections are conservative, for only a 10-year time interval. Our FVS projections allowed us to test our first hypothesis regarding treatment effects.

Stand level growth simulations in FVS are known to be sensitive to regeneration inputs (Ray et al. 2009). Therefore, we evaluated growth sensitivity in our projections by modeling three different regeneration input scenarios: inventoried regeneration densities, adjusted inventoried regeneration densities (by one order of magnitude), and no regeneration (Table 4). We found that there was 5-10% variability in growth projections between the different regeneration scenarios. With increasing regeneration, density-dependent mortality in overstory trees increased due to model behavior, producing more variation in live tree biomass development and basal area amounts. We chose the “no regeneration” scenario for our final FVS no-management baseline projections to maintain consistency in forest growth projections.

The no-management baseline CWM (standing dead and downed wood) carbon pools were assumed to be equivalent to the pre-harvest values; changes in the CWM pools were also compared against the controls, as were the live tree pool. We did not model CWM development because recruitment into this pool was unlikely to have changed significantly over the 10-year time interval (Woodall 2010, Russell et al. 2014).

2.5.5. Statistical analyses

To explore our first hypothesis (treatment effects), we tested for statistically significant differences in carbon responses between treatments by pool, and comparing
the empirical values 10 years post-harvest to the no-management baseline. For this purpose we employed one-way ANOVA tests and post-hoc Tukey-Kramer multiple comparisons. Statistical comparisons of means by treatment and pool were conducted in JMP Pro 11 (SAS Institute Inc. 2013). Shapiro-Wilk tests for normality confirmed normal distribution of data (alpha = 0.05) and one-way ANOVAs and Tukey-Kramer HSD (honest significant difference) post-hoc mean comparisons tested for significant differences in carbon pool means pre- and post-harvest. Homogeneity of variance was tested using $F$-tests.

To test our second hypothesis (treatment vs. site variability), we evaluated the relative influence of multiple independent variables (e.g., treatment type, site productivity, location, and other site characteristics) on the dependent variables (percentage difference carbon per pool). This consisted of Classification And Regression Tree (CART) analyses (Breiman et al. 1984) conducted in S-plus 8.2 (TIBCO Software 2010). CART is a robust non-parametric technique that accommodates both categorical and continuous variables (Littlefield and Keeton 2012). A tree hierarchically ranks the predictive power of multiple independent variables by repeatedly splitting dependent variables into more homogenous groups based on combinations of independent or explanatory variables, which can explain variation within partitioned values of the dependent variable (De'ath and Fabricius 2000). We used a robust set of predictor variables (n/2) representative of site variability (percent hardwood, slope, aspect, location) (Table 5). Cost-complexity pruning was used to remove insignificant nodes ($\alpha = 0.05$).
2.6. Results

2.6.1. Carbon responses post-treatment

Our results support the first hypothesis, that SCE carbon amounts and fluxes 10-years post harvest would be greatest relative to pre-harvest or no-management baseline values when compared to conventional treatments. Comparisons of treatments pre- to post-harvest indicate greatest amounts of biomass development (carbon storage) (Fig. 5) and greatest carbon fluxes (Table 7) in structural complexity enhancement treatments as compared to conventional treatments. Percentage differences (Table 6, Fig. 7) show the greatest increases occurred in post-harvest SCE carbon relative to pre-harvest levels.

Mean SCE standing dead and downed log carbon post-harvest (2013) was greater in SCE treatment units than conventional and controls (Fig. 5). Live tree and total C was significantly greater in controls than conventional units 10 years post-harvest \( (P = 0.004) \) and was also greater in SCE units than conventional units. Mean SCE standing dead carbon 10 years post-harvest measured 3.67 Mg ha\(^{-1}\) compared to 2.03 Mg ha\(^{-1}\) and 3.26 Mg ha\(^{-1}\) in conventional and control treatments, respectively. Mean SCE downed log carbon measured 9.00 Mg ha\(^{-1}\) in SCE treatments compared to a conventional mean of 4.14 Mg ha\(^{-1}\) and 4.80 Mg ha\(^{-1}\) for controls. Post-harvest mean live tree carbon was 98.22 Mg ha\(^{-1}\) in SCE treatments compared to 77.17 Mg ha\(^{-1}\) and 112.85 Mg ha\(^{-1}\) in conventional and control treatments. Total carbon in SCE treatments was 110.89 Mg ha\(^{-1}\), 83.34 Mg ha\(^{-1}\) in conventional treatments, and 120.91 Mg ha\(^{-1}\) in control treatments. Limited significance in C differences between treatments for each year can be attributed
to site variability factors including DCWM decay rates, percent hardwood/conifer basal areas, site index values, and greater initial inputs of dead wood to DCWM pools.

Relative to conventional treatments, SCE carbon fluxes were either greater or comparable in live tree, standing dead, and downed log pools, which also supported our first hypothesis (Table 7). Mean live tree C flux measured 1.27 Mg ha\(^{-1}\) yr\(^{-1}\) in the SCE units compared to 1.19 Mg ha\(^{-1}\) yr\(^{-1}\) in the conventional units and 1.30 Mg ha\(^{-1}\) yr\(^{-1}\) in the control units. Standing dead C fluxes measured -0.24 Mg ha\(^{-1}\) yr\(^{-1}\) in SCE treatments, 0.25 Mg ha\(^{-1}\) yr\(^{-1}\) in conventional treatments, and -0.05 Mg ha\(^{-1}\) yr\(^{-1}\) in controls. SCE downed log pools demonstrated the greatest difference in fluxes compared to other treatments, measuring -0.72 Mg ha\(^{-1}\) yr\(^{-1}\) compared to -0.33 and -0.05 Mg ha\(^{-1}\) yr\(^{-1}\) in conventional and control treatments, respectively (\(P < 0.05\)).

Percentage differences between post-harvest and no-management baseline carbon for each pool were lowest in SCE treatments relative to conventional treatments, supporting our first hypothesis that SCE treatments will result in C levels closest to untreated or manipulated stand development (Table 6, Fig. 7). Percentage differences were below the baseline (negative) in all treatments in the live tree pool, measuring -17.45% in SCE units and -42.81% in conventional units. Standing dead SCE carbon was again closest to the baseline, with a -65.70% difference compared to -90.20% in conventional units. Downed log carbon under SCE surpassed the baseline with a measured 32.86% increase, yet in conventional units was still below, with a 40.02% decrease.
2.6.2. Effects of site variability on biomass development (carbon storage)

It is evident from our CART results that treatment type is most influential on carbon storage across all pools, but that variability in site conditions interacted with treatment in determining carbon response in most situations, supporting our second hypothesis (treatment vs. effect). Treatment type explained variations in percentage differences in carbon storage at the first and sometimes secondary splits of all trees (Fig. 3). Individual pools demonstrated different responses in carbon storage due to variations in site conditions, demonstrated by relative ranking of secondary predictor variables. Five predictor variables were selected for the final CART models: treatment, aspect, slope, site index, and percent hardwood (percent of hardwood basal area) (Table 5).

The live tree carbon CART model (Fig. 5A) primary split (most influential predictive variable) was split between conventional treatments and SCE and control treatments. Carbon storage potential increased moving from conventional treatments to control and SCE treatments. Conventionally treated areas were additionally influenced by aspect (at the secondary split), with the percentage difference carbon increasing in negative value (less post-harvest carbon relative to reference carbon) as site orientation moved to the northwest. Percent hardwood and treatment were selected as partitioning points for variance within controls and SCE treatments, with percentage difference increasing in positive value (greater carbon storage) with increase in percent hardwood and from SCE to control treatments.

In both coarse woody material models (Fig. 5B and C), there is a stronger influence of site variation on carbon storage, as indicated by the selection of slope, site index, percent hardwood, and location as predictor variables in the final models.
Treatment was selected as the most important predictor of percentage difference between post-harvest and reference carbon in both models. In the standing dead model (Fig. 5B) the primary node was split between SCE and conventional treatments and controls. Carbon storage potential was greatest in controls and lowest in SCE and conventional treatments. Slope was selected as a secondary predictor for SCE and conventional treatments, with slopes less than 29° having less post-harvest than reference carbon, or a greater *negative* percentage difference. As slopes increased, percentage differences in CWM carbon decreased. Location was also ranked as secondary predictor variable for standing dead carbon in control treatments, with a greater percentage difference at the Mansfield site (higher amounts of standing dead carbon post-harvest than pre-harvest). Percentage difference for downed log carbon was greatest in SCE treatments, with the CART model (Fig. 5C) split between control and conventional treatments and SCE treatments. A secondary predictor of SCE-treated sites was site index, with the percentage difference for carbon increasing with decreasing site productivity. Percent hardwood and treatment were selected as partitioning points for variance among control and conventional treatments.

### 2.7. Discussion

Carbon stocking in aboveground biomass pools in northern hardwood forests increases with silvicultural prescriptions which aim to retain structure, increase horizontal and vertical complexity, and elevate coarse woody material. Of the treatments tested in this study, the SCE treatment resulted in aboveground carbon storage levels closest to un-
harvested or no-management conditions. Additionally, after a decade this treatment maintained and developed greater amounts of carbon storage than the other selection systems tested, likely as a result of elevated post-harvest structural retention and other the silvicultural techniques employed in the SCE treatment (see Table 2 for prescription details). We also found site variability to have an important secondary effect on the amount and rate of carbon accumulation in each pool, with carbon storage potential generally increasing with site conditions favoring better growth response to silvicultural treatment, as indicated by our CART models.

2.7.1. Carbon responses to old-growth structure enhancement

Pre- and post-harvest measured carbon outcomes

Absolute carbon 10 years-post harvest was greater in SCE units in all pools relative to conventional treatments. This can be attributed, in part, to a higher post-harvest target residual basal area in SCE units during treatment and also to elevated CWM inputs for enhanced structural retention. SCE absolute carbon values were comparable to or above published regional values for C stocks, and for some pools close to regional old-growth/late-successional amounts. The USDA Forest Service (2015) recently reported mature northern hardwood mean live tree C to be between 60 and 80 Mg ha\(^{-1}\), standing dead C between 2 and 4 Mg ha\(^{-1}\), and downed log C between 6 and 9 Mg ha\(^{-1}\). Other studies specific to northern New England report comparable values (Keeton et al. 2011). Bradford et al. (2011) found northern New Hampshire mature hardwood forests (maximum age of 120 years) to contain 96 Mg ha\(^{-1}\) live tree C and 18 Mg ha\(^{-1}\) C in coarse woody material. Whitman and Hagan (2007) reported higher levels
in mature northern hardwood forests in Maine, 113 Mg ha\(^{-1}\) live tree C, 10 Mg ha\(^{-1}\) standing dead C, and 12 Mg ha\(^{-1}\) downed log C. Aboveground carbon amounts from our study were comparable to regional values, with SCE live tree C measuring 98.22 Mg ha\(^{-1}\), standing dead at 3.67 Mg ha\(^{-1}\), and downed log at 9.00 Mg ha\(^{-1}\). Regional old-growth northern hardwood C stocking has been reported at 116-141 Mg ha\(^{-1}\) live tree C, 8-22 Mg ha\(^{-1}\) standing dead C, and 12-18 Mg ha\(^{-1}\) downed log (Goodburn and Lorimer 1998, Fisk et al. 2002, Whitman and Hagan 2007, Bradford et al. 2010, Keeton et al. 2011, Hoover et al. 2012, Gunn et al. 2014, McGarvey et al. 2015). Carbon stocking in SCE treatments 10 years post-harvest was at the upper threshold or above regional mean values, and in some cases approaching regional old-growth stocking levels, indicating the effectiveness of this treatment type in promoting late-successional/old-growth C stocking levels and structure.

*Management vs. no-management effects on carbon accumulation*

When comparing measured carbon outcomes from treated units with no-harvest baselines utilizing percentage differences, SCE percentage differences for all pools were closest to or above the no-harvest baseline relative to conventional treatments. This is consistent with literature predicting accelerated biomass development and recovery of late-successional characteristics following treatments similar to structural complexity enhancement (Bauhus et al. 2009). Management scenarios involving no-treatment have consistently shown the greatest total long-term carbon storage, accounting for both in-situ forest carbon and the life cycle of wood products (Harmon 2001, Fahey et al. 2010,
Nunery and Keeton 2010). However, in our study the contrast with no management was lowest across all carbon pools under SCE as compared to the conventional treatments. This finding suggests great potential for low-intensity silvicultural techniques as carbon forestry approaches in the northern hardwood region, assuming regeneration and other management objectives are met, which of course will vary tremendously by site and ownership (Schwenk et al. 2012).

The response of DCWM in this study was particularly promising toward the integration of management for late-successional habitats with carbon storage. Ten years post-harvest, downed log carbon under SCE was significantly higher than the no-harvest baseline and the control units. In addition to providing important habitat (McGee et al. 1999, McKenny et al. 2006, Dove and Keeton 2015) and riparian functions (Keeton et al. 2007b, Warren et al. 2009), our results suggest structural complexity approaches have the potential to store significant amounts of carbon in downed woody material, as well.

*Carbon flux variations by pool and treatment*

Carbon fluxes were greatest in the live tree and downed log pools following the SCE treatment. These results indicate both a high level of C sequestration (uptake) from accelerated tree growth in response to harvest, as well as C loss through decay. The latter is likely due to the large input of silviculturally created coarse woody material. Our coarse woody material flux rates are comparable to regional published estimates (Russell et al. 2013, Bradford et al. 2010, Gunn et al. 2014). However, we note the difficulty in accurately measuring CWM flux rates due to the combined effects of density, volume, and/or biomass depletion in addition to losses from heterotrophic respiration (Forrester et
Additionally, CWM flux is usually greatest within the first 10 years post-harvest. Live tree and total C flux rates for all treatments were greater than (Nunery and Keeton 2010, Gunn et al. 2014) or comparable to regional estimates (Bradford et al. 2010), with SCE live tree flux measuring higher than conventional treatments. While the conventional treatments also showed elevated levels of tree growth, we found that SCE achieved similar or greater growth responses in overstory trees. This is an important finding relative to the potential for low-intensity treatments of this type to maintain both complex stand structures and to elevate carbon sequestration (see, for example, Bauhus et al. 2009). While our study does not provide a basis for determining a mechanism for the elevated uptake rates, it is possible this was due to crown release of dominant trees as well as variable canopy openness (or gapiness), both of which were explicit objectives of SCE.

Comparisons of empirical data with modeled forest stand development

This study provided the unique opportunity to compare empirical data with prior projected outcomes. Using previous results from replications tested in this study, Keeton (2006) projected aboveground biomass development in SCE treatments to be 91.4% of that projected under no-treatment potential 50 years post-harvest. Results from this study 10 years post-harvest are already comparable to these projections, with SCE total C at 84.1% of no-treatment potential. Projections for 50 years post-harvest biomass production (in the live tree pool) in conventional treatments were 79.1% of no treatment potential (Keeton 2006). We measured biomass development following conventional
treatments at 55% of no-treatment potential. It is evident from our results that FVS significantly underestimated biomass development in the Keeton (2006) projections. This is consistent with the findings of MacLean et al. (2014) who found that uncalibrated regional FVS tended to under-predict carbon for FIA plots across the northeastern United States. Our findings are contrary to Gunn et al. (2014), however, who found FVS to overestimate carbons stocks in both late-successional and old-growth northeastern forests. Finally, total post-harvest aboveground carbon for conventional treatments measured in this study was nearly equal to (<1% difference) comparable treatments projected by Nunery and Keeton (2010). SCE total carbon measured 10 years post-harvest was only 7.89% below that of 10-year projections for no-management scenarios modeled by Nunery and Keeton (2010). These differences in FVS projected outcomes for northeastern tree growth and C stocking suggest a need to improve model calibration and accuracy, particularly given the wide acceptance of FVS by forest carbon markets (Kerchner and Keeton 2015). Additionally, the effects of natural disturbances, invasive species (e.g. beech bark disease), and climate change (e.g. changes in species distributions) on forest stand development also need to be considered when projecting future forest conditions (Seidl et al. 2014).

*Site variability effects on carbon storage potential*

Our CART models were consistent in showing treatment type to have the greatest influence on carbon stocking in all aboveground pools measured. Model results also demonstrated the effect of site variability on C in pools. Disparity in carbon storage potential in all pools as a result of differences in site conditions were explained in CART
results (Fig. 5), suggesting a relationship between alterations in site conditions and biomass development/carbon storage similar to those described by Littlefield and Keeton (2012) and Nunery and Keeton (2010). It can generally be assumed that C storage potential was directly affected by aspects of site variability, such as percent hardwood, productivity, and slope, which was most clearly evident in the live tree and standing dead CART models (Fig. 5A and C).

2.7.2. Implications for forest carbon management

Multi-functional forest management practices promoting the development of stand structural complexity and associated late-successional habitat characteristics (Keeton 2006, Bauhus et al. 2009) are likely to provide important carbon storage co-benefits based on the results of this study. Disturbance-based management (Seymour et al. 2002, Franklin et al. 2007) promoting legacy tree retention, inputs to coarse woody debris pools, increased vertical and horizontal heterogeneity, and elevated biomass levels are options for maximizing C storage potential (Franklin and Pelt 2004, Gustafsson et al. 2012). These provide important co-benefits in terms of habitat function and biodiversity conservation targeted at the full array of temperate forest species, including those associated with late-successional habitats (Lindenmayer et al. 2000, Keith et al. 2009). The re-allocation of diameter distributions to larger size classes supports the growth of large trees, an important element of late-successional forest structure. Recent research (Stephenson et al. 2014) analyzing 403 tropical and temperate trees species indicates that tree growth rate increases continuously with size, as does C sequestration and storage for
most trees. Large trees, previously assumed to slow in both productivity and growth rate (Weiner and Thomas 2001, Meinzer et al. 2011), function as long-term carbon sinks (Carey et al. 2001). These findings further support the significance of structural retention as a co-benefit to forest carbon storage.

As the debate continues surrounding forest management for climate mitigation, solutions meeting a multitude of management objectives are preferable to promote maximum ecosystem-level resiliency (Millar et al. 2007). Prescriptions that focus on enhancing forest biomass and structure are thought to have the most positive effects on increasing carbon uptake and storage (Ducey et al. 2013). U.S. forests currently offset approximately 16% of anthropogenic CO\(_2\) emissions, but this has the potential to decline as a result of land conversions and lack of management (EPA 2012, Joyce et al. 2014). In the 1990s, nearly 20% of global carbon dioxide emissions were from changes in land use and land management, mostly through deforestation (Hassan et al. 2005). While passive or no-management options have been found to yield the greatest carbon uptake benefit (Nunery and Keeton 2010), we suggest the consideration of structural retention treatments to continue to enhance C storage. Multiple studies (Angers et al. 2005, Schwartz et al. 2005, Dyer et al. 2010, Gronewold et al. 2012, Chen et al. 2015) have revealed the effectiveness of managing for elevated structure, including legacy retention, horizontal variability, and increased coarse woody material inputs.

2.7.3. Conclusions

A more widespread adoption of silvicultural practices with a focus on structural complexity enhancement, biomass development, ecosystem function, and diversity in
species composition stands to promote resilience to climate change and also address the issue of global decline in biodiversity and carbon stocks (Lindenmayer et al. 2012). As our research has suggested, silvicultural treatments that enhance structure and carbon storage offer a variety of ecosystem services and management tools for landowners at multiple scales. Global carbon markets, temperature and precipitation alterations, and shifts in disturbance frequencies and intensities are increasing the necessity for landowners and forest managers to be prepared with a suite of management alternatives. These include the modification of harvests to increase retention and rotation length, in addition to the emulation of natural disturbance regimes. Silvicultural treatments evaluated in this study present alternative forest management options that can assist with climate mitigation, structural enhancement, and ecosystem function.

2.8. Acknowledgements

This research was supported by grants from the USDA McIntire-Stennis Forest Research Program and the USDA Forest Service. The authors are particularly grateful to the University of Vermont Carbon Dynamics Lab for their support and input throughout the course of this project and to all field crews who provided field inventory assistance. Insightful reviews and feedback were provided by Shelly Rayback and Gillian Galford. Alan Howard provided critical assistance with statistical analyses and Mark Twery with NED-3 and the FERDA data set. Additionally, we would like to thank Gerald Smith with the Natural Resources Conservation Service for providing soils and site index information for the FERDA project.
Table 2: Silvicultural prescription details for experimental treatment manipulations at the MMSF, JRF, and FERDA study areas. Listed in the table is the target BDq for each treatment. The BDq is equal to 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).

<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 prescription</th>
</tr>
</thead>
<tbody>
<tr>
<td>SINGLE-TREE SEL.</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 SEL.</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></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Vertically differentiated canopy</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Increased horizontal complexity</td>
<td></td>
</tr>
<tr>
<td>SCE</td>
<td>34</td>
<td>90</td>
<td>2.0/1.1/1.3</td>
<td>Re-allocation of basal area to larger size class</td>
<td>Rotated sigmoid diameter dist.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>High max d and target basal area</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Retention of trees &gt;60 cm dbh</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Single-tree sel. with target diameter dist.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Growth acceleration of larger trees</td>
<td>Release advance regeneration</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Elevated coarse woody material inputs for</td>
<td>Tree girdling/felling and leaving trees</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>added structure</td>
<td></td>
</tr>
</tbody>
</table>
Table 3: Site characteristics of experimental treatment units located in the Mansfield and Jericho study areas and for supplementary data from the Forest Ecosystem Research and Demonstration Area (VIC and Keese Mill sites). SCE = structural complexity enhancement; VIC = Visitor Interpretive Center.

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Unit</th>
<th>Silvicultural treatment</th>
<th>Site index</th>
<th>Slope (%)</th>
<th>Aspect (degrees)</th>
<th>Percent hardwood</th>
<th>Initial basal area (total) (m² ha⁻¹)</th>
<th>Initial stem density (total) (trees ha⁻¹)</th>
<th>Initial QMD* (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mansfield</td>
<td>Vermont</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>Vermont</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>Vermont</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>Vermont</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>24.0</td>
</tr>
<tr>
<td>Mansfield</td>
<td>Vermont</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>Vermont</td>
<td>6</td>
<td>Group sel.</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>Vermont</td>
<td>7</td>
<td>Group sel.</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>Vermont</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>Vermont</td>
<td>1</td>
<td>Control</td>
<td>60</td>
<td>27.1</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>Vermont</td>
<td>2</td>
<td>SCE</td>
<td>60</td>
<td>27.8</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>Vermont</td>
<td>3</td>
<td>SCE</td>
<td>60</td>
<td>42.6</td>
<td>147</td>
<td>54.77</td>
<td>44.0</td>
<td>1034</td>
<td>23.3</td>
</tr>
<tr>
<td>Jericho</td>
<td>Vermont</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>
<tr>
<td>VIC</td>
<td>New York</td>
<td>4</td>
<td>Single-tree</td>
<td>60</td>
<td>1.0</td>
<td>10</td>
<td>87.57</td>
<td>28.6</td>
<td>837</td>
<td>20.8</td>
</tr>
<tr>
<td>VIC</td>
<td>New York</td>
<td>5</td>
<td>Group sel.</td>
<td>60</td>
<td>1.0</td>
<td>345</td>
<td>79.09</td>
<td>23.8</td>
<td>1059</td>
<td>16.9</td>
</tr>
<tr>
<td>VIC</td>
<td>New York</td>
<td>9</td>
<td>Group sel.</td>
<td>60</td>
<td>5.0</td>
<td>278</td>
<td>91.03</td>
<td>30.9</td>
<td>762</td>
<td>22.7</td>
</tr>
<tr>
<td>Keese Mill</td>
<td>New York</td>
<td>11</td>
<td>Single-tree</td>
<td>60</td>
<td>3.0</td>
<td>278</td>
<td>90.45</td>
<td>39.4</td>
<td>822</td>
<td>24.7</td>
</tr>
<tr>
<td>Keese Mill</td>
<td>New York</td>
<td>12</td>
<td>Control</td>
<td>60</td>
<td>5.0</td>
<td>278</td>
<td>91.22</td>
<td>26.0</td>
<td>1147</td>
<td>17.0</td>
</tr>
<tr>
<td>Keese Mill</td>
<td>New York</td>
<td>13</td>
<td>Control</td>
<td>60</td>
<td>3.0</td>
<td>278</td>
<td>85.06</td>
<td>29.0</td>
<td>1044</td>
<td>18.8</td>
</tr>
</tbody>
</table>

*Site index values determined by the height of the dominant species at 50 years of age, which was sugar maple for all sites.
Table 4: FVS model validation comparing post-harvest inventory data to FVS 10-year post-harvest projections. FVS Input 1 was with no regeneration, FVS Input 2 used actual regeneration densities from 2003 field inventories, and FVS Input 3 used adjusted 2003 regeneration densities by one order of magnitude. SCE = Structural Complexity Enhancement; STS = Single-Tree Selection; GS = Group Selection

<table>
<thead>
<tr>
<th>Location</th>
<th>Treatment</th>
<th>Unit</th>
<th>BASAL AREA (m² ha⁻¹)</th>
<th>ABOVEGROUND BIOMASS (Mg ha⁻¹)</th>
<th>TOTAL REGEN. DENS. (seed ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>2003 Inventory</td>
<td>2013 Inventory</td>
<td>FVS Input 1</td>
</tr>
<tr>
<td>Mansfield</td>
<td>Control</td>
<td>1</td>
<td>33.7</td>
<td>36.3</td>
<td>35.8</td>
</tr>
<tr>
<td>Mansfield</td>
<td>SCE</td>
<td>2</td>
<td>20.4</td>
<td>24.0</td>
<td>23.2</td>
</tr>
<tr>
<td>Mansfield</td>
<td>SCE</td>
<td>3</td>
<td>20.1</td>
<td>24.4</td>
<td>23.2</td>
</tr>
<tr>
<td>Mansfield</td>
<td>STS</td>
<td>4</td>
<td>19.1</td>
<td>20.0</td>
<td>22.2</td>
</tr>
<tr>
<td>Mansfield</td>
<td>STS</td>
<td>5</td>
<td>15.9</td>
<td>21.4</td>
<td>18.2</td>
</tr>
<tr>
<td>Mansfield</td>
<td>GS</td>
<td>6</td>
<td>19.0</td>
<td>24.0</td>
<td>22.4</td>
</tr>
<tr>
<td>Mansfield</td>
<td>GS</td>
<td>7</td>
<td>11.2</td>
<td>15.6</td>
<td>13.8</td>
</tr>
<tr>
<td>Mansfield</td>
<td>Control</td>
<td>8</td>
<td>25.7</td>
<td>30.9</td>
<td>29.2</td>
</tr>
<tr>
<td>Jericho</td>
<td>Control</td>
<td>1</td>
<td>32.0</td>
<td>36.6</td>
<td>36.1</td>
</tr>
<tr>
<td>Jericho</td>
<td>SCE</td>
<td>2</td>
<td>23.9</td>
<td>29.8</td>
<td>28.2</td>
</tr>
<tr>
<td>Jericho</td>
<td>SCE</td>
<td>3</td>
<td>32.1</td>
<td>31.0</td>
<td>37.4</td>
</tr>
<tr>
<td>Jericho</td>
<td>Control</td>
<td>4</td>
<td>28.3</td>
<td>31.9</td>
<td>32.6</td>
</tr>
</tbody>
</table>

SCE = Structural Complexity Enhancement; STS = Single-Tree Selection; GS = Group Selection
Table 5: Description of variables used in CART analyses. All variables are independent except for the first listed variable, carbon (N = numeric, C = categorical).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type</th>
<th>Values</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Difference carbon</td>
<td>N</td>
<td>−70 &lt; x &lt; 70</td>
<td>% difference carbon between 10 years post-harvest and reference carbon amounts calculated for each aboveground pool (Littlefield and Keeton 2012)</td>
</tr>
<tr>
<td>Treatment</td>
<td>C</td>
<td>A-D</td>
<td>A (Structural Complexity Enhancement), B (Single-Tree Selection), C (Group Selection), D (Control)</td>
</tr>
<tr>
<td>Location</td>
<td>C</td>
<td>A-D</td>
<td>A (Mount Mansfield State Forest, VT), B (Jericho Research Forest, VT), C (VIC, NY), D (Keese Mill, NY)</td>
</tr>
<tr>
<td>Aspect</td>
<td>N</td>
<td>0 &lt; x &lt; 345</td>
<td>Aspect (degrees) of individual treatment units</td>
</tr>
<tr>
<td>Slope</td>
<td>N</td>
<td>0-43</td>
<td>Slope (percent steepness) of individual treatment units</td>
</tr>
<tr>
<td>Percent hardwood</td>
<td>N</td>
<td>53 &lt; x &lt; 100</td>
<td>Percent overstory species hardwood of each treatment unit, calculated as a percentage of total basal area</td>
</tr>
<tr>
<td>Site index</td>
<td>N</td>
<td>55 &lt; x &lt; 70</td>
<td>Site index of dominant tree at age 50 for each unit</td>
</tr>
</tbody>
</table>
Table 6: Mean carbon values and percentage differences for post-harvest carbon means (by aboveground pool) compared to reference carbon means for each silvicultural treatment (Littlefield and Keeton 2012). One-way ANOVA and Tukey-Kramer post-hoc analysis results are listed ($\alpha = 0.05$). SCE = Structural Complexity Enhancement; Conventional = Single-Tree + Group Selection. Degrees of freedom = 2.

<table>
<thead>
<tr>
<th>Aboveground carbon pool</th>
<th>Post-harvest mean</th>
<th>Reference mean</th>
<th>% difference</th>
<th>$F$</th>
<th>Significance ($P$)</th>
<th>Tukey Kramer HSD</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live tree carbon (Mg ha$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SCE</td>
<td>98.22</td>
<td>119.15</td>
<td>-17.45%</td>
<td>11.00</td>
<td>0.001</td>
<td>Control &gt; Conv.</td>
<td>0.001</td>
</tr>
<tr>
<td>Conventional</td>
<td>77.17</td>
<td>120.08</td>
<td>-42.81%</td>
<td></td>
<td>SCE &gt; Conv.</td>
<td></td>
<td>0.050</td>
</tr>
<tr>
<td>Control</td>
<td>112.85</td>
<td>115.19</td>
<td>-3.21%</td>
<td></td>
<td>Control &gt; SCE</td>
<td></td>
<td>0.374</td>
</tr>
<tr>
<td>Standing dead tree carbon (Mg ha$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SCE</td>
<td>3.67</td>
<td>6.31</td>
<td>-65.70%</td>
<td>8.83</td>
<td>0.008</td>
<td>Control &gt; Conv.</td>
<td>0.009</td>
</tr>
<tr>
<td>Conventional</td>
<td>2.03</td>
<td>6.06</td>
<td>-90.20%</td>
<td></td>
<td>Control &gt; SCE</td>
<td></td>
<td>0.023</td>
</tr>
<tr>
<td>Control</td>
<td>3.26</td>
<td>1.85</td>
<td>68.13%</td>
<td></td>
<td>SCE &gt; Conv.</td>
<td></td>
<td>0.821</td>
</tr>
<tr>
<td>Downed log carbon (Mg ha$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SCE</td>
<td>9.00</td>
<td>6.34</td>
<td>32.86%</td>
<td>11.94</td>
<td>0.003</td>
<td>SCE &gt; Control</td>
<td>0.003</td>
</tr>
<tr>
<td>Conventional</td>
<td>4.14</td>
<td>5.28</td>
<td>-19.36%</td>
<td></td>
<td>SCE &gt; Conv.</td>
<td></td>
<td>0.020</td>
</tr>
<tr>
<td>Control</td>
<td>4.80</td>
<td>7.08</td>
<td>-40.02%</td>
<td></td>
<td>Conv. &gt; Control</td>
<td></td>
<td>0.408</td>
</tr>
<tr>
<td>Total carbon (Mg ha$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SCE</td>
<td>110.88</td>
<td>131.80</td>
<td>-15.90%</td>
<td>9.54</td>
<td>0.006</td>
<td>Control &gt; Conv.</td>
<td>0.005</td>
</tr>
<tr>
<td>Conventional</td>
<td>80.36</td>
<td>126.44</td>
<td>-44.94%</td>
<td></td>
<td>SCE &gt; Conv.</td>
<td></td>
<td>0.062</td>
</tr>
<tr>
<td>Control</td>
<td>131.88</td>
<td>128.12</td>
<td>2.46%</td>
<td></td>
<td>SCE &gt; Conv.</td>
<td></td>
<td>0.265</td>
</tr>
</tbody>
</table>
Table 7: Mean annual C flux per pool and treatment over the 10-year interval post-harvest and significance levels ($\alpha = 0.05$).

Degrees of freedom = 2.

<table>
<thead>
<tr>
<th>Carbon pool</th>
<th>SCE</th>
<th>Conventional</th>
<th>Control</th>
<th>F</th>
<th>Significance ($P$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live tree</td>
<td>1.27 ± 0.65</td>
<td>1.19 ± 0.34</td>
<td>1.30 ± 0.43</td>
<td>0.02</td>
<td>0.983</td>
</tr>
<tr>
<td>Standing dead</td>
<td>−0.24 ± 0.16</td>
<td>−0.25 ± 0.05</td>
<td>0.08 ± 0.03</td>
<td>3.70</td>
<td>0.067</td>
</tr>
<tr>
<td>Downed log</td>
<td>−0.72 ± 0.03</td>
<td>−0.33 ± 0.09</td>
<td>−0.05 ± 0.10</td>
<td>18.07</td>
<td><strong>0.000</strong></td>
</tr>
<tr>
<td>Total C</td>
<td>0.31 ± 0.48</td>
<td>0.45 ± 0.23</td>
<td>1.93 ± 0.31</td>
<td>6.45</td>
<td><strong>0.018</strong></td>
</tr>
</tbody>
</table>
Figure 4: Regional map with locations of the three project study areas: MMSF (A), JRF (B), and FERDA (C). Also shown are treatment unit layout maps the MMSF (A) and JRF (B) 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 5: Carbon pool mean comparisons, pre- (2001) and post-harvest (2003 and 2013) with Tukey-Kramer HSD ANOVA tests (alpha = 0.05). Significant results are reported; Error bars represent one stand error; whiskers are representative the spread of data. (A) Live tree carbon. (B) Standing dead carbon. (C) Downed log carbon. (D) Total carbon. Conventional treatments refer to the combination of single-tree and group selection treatments.
Figure 6: Classification and Regression Tree Analyses showing selected independent variables ranked by predictive strength (top to bottom) for live tree (A), standing dead (B), and downed log (C) percentage difference carbon. The amount of deviance for each variable is proportional to the length of each vertical line. Minimum number of observations required for each split = 2; minimum deviance = 0.05; n = 18 (live tree) and n = 12 (standing dead and downed log).
Figure 7. Percentage differences between post-harvest and baseline carbon compared between treatments and for all pools. Comparisons were made using Tukey-Kramer HSD ANOVA tests (alpha = 0.05). Significant results are reported; error bars represent one stand error.


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