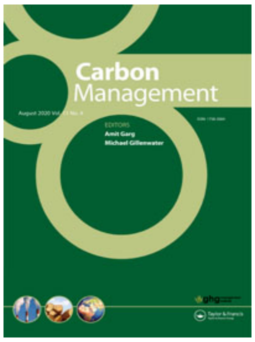

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Strategies for enhancing long-term carbon sequestration in mixed-species, naturally regenerated Northern temperate forests

Joshua J. Puhlick[a], Aaron R. Weiskittel[a,b], Laura S. Kenefic[c], Christopher W. Woodall[d] and Ivan J. Fernandez[a,e]

[a]School of Forest Resources, University of Maine, Orono, ME, USA; [b]Center for Research on Sustainable Forests, University of Maine, Orono, ME, USA; [c]Northern Research Station, Northern Forest Science and Applications, USDA Forest Service, Bradley, ME, USA; [d]Northern Research Station, Forest Inventory and Analysis, USDA Forest Service, Durham, USA; [e]Climate Change Institute, University of Maine, Orono, ME, USA

ABSTRACT
We compared long-term C sequestration in the pools of aboveground portions of live trees, dead wood, and harvested wood products among highly contrasting forest management scenarios on a rotation (30-100 years) and 100-year basis. Average annual net change in C (AAC) and the cumulative sum of net changes in C were calculated using 65 years of data from permanent plots representing contrasting approaches to managing mixed-species stands dominated by shade-tolerant coniferous species on the Penobscot Experimental Forest in Maine, USA. Simulations of tree growth and mortality were used to estimate C pools to 100 years. On a rotation basis and for all pools combined, scenarios with selection cutting had greater AAC than those with shelterwood cutting followed by thinning or with diameter-limit cutting ($p < 0.05$). For combined pools, the cumulative sum of net changes in C for the unmanaged, selection, and guiding diameter-limit stands was positive for most of the study period. Our results suggest that strategies that maintain overstory stocking levels necessary to regenerate desired species and promote the development of sawlog-sized trees can enhance long-term C sequestration in mixed-species, naturally regenerated northern temperate forests.

KEYWORDS
Carbon storage; carbon stocks; carbon accumulation; silviculture; rotation

Introduction

The future status of terrestrial C, especially with regard to forests, is coming under increasing focus as it relates to the global C cycle and climate change. Although forests can actively sequester C from the atmosphere, they also present a risk of C emission through degradation, land-use conversion, or other disturbance events such as wildfire [1, 2]. Refining our understanding of forest C trajectories, especially in the context of various approaches to management (e.g. silvicultural and/or land-use strategies), will be paramount to objectively identifying pathways to mitigating increasing atmospheric CO_2 [3, 4]. Beyond policy concerns, using silvicultural strategies to mitigate increases in atmospheric CO_2 is also an important objective of many forest landowners and is being embraced by multiple ownerships across spatial and governance scales (e.g. towns to states). Managing forests to sequester C from the atmosphere offers a level of synergy as C management can concomitantly provide additional ecosystem services such as biodiversity maintenance and habitat provision [5, 6].

There are a number of forests with no recent timber harvesting (e.g. old-growth and/or reserved forest land) that store vast amounts of C with expectations of continued C sequestration due to healthy stand structures and/or species compositions, or even their protected status [7–9]. Perhaps equally important, numerous privately owned forests, degraded forests, and/or forests lacking optimal structures and/or species compositions for future net C sequestration may benefit from silvicultural activities that enhance C sequestration rates at times in concert with production of harvested wood products with long residence times [10]. Given the losses of early seral forests and habitat associated with strategies to maximize forest C stocks (i.e. undisturbed and/or unmanaged forests), understanding the C balance consequences of various forest management strategies

CONTACT Joshua J. Puhlick joshua.puhlick@maine.edu School of Forest Resources, University of Maine, 5755 Nutting Hall, Orono, ME, 04469, USA

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geared toward rehabilitating degraded forests and/or improving delivery of ecosystem services in forests (water, wildlife, or forest products) in the face of global change will be vital [11–13]. Unfortunately, there are relatively few studies comparing silvicultural strategies for sequestering C that are based on long-term empirical data, particularly in naturally regenerated, mixed-species forests. Identifying the types of strategies that can be used to sequester the most net C over various time scales is needed to inform policy and management actions, especially given the role of forests in the global C cycle.

Disturbance, species composition, and site quality influence C stocks and rates of C sequestration over time [9]. Timber harvesting reduces live tree C stocks through transfer of C to harvested wood products or dead wood pools, but can increase the C sequestration rate of the forest through the establishment and growth of new cohorts of trees and growth on residual trees. Residual trees in lower canopy positions that are free of disease or damage and able to respond to release have the potential to sequester additional amounts of C. When regenerating stands, retaining some upper canopy trees of species that are fast-growing and windfirm as reserve trees could also contribute to stand-level C sequestration rates [9, 14]. Natural disturbances and timber harvesting also result in transfers of C from the live tree pool to other terrestrial pools and the atmosphere (i.e. decay or combustion) with the frequency and severity of these disturbances influencing the magnitude of transfers over time [15, 16]. Silvicultural strategies that promote large-sized trees have been shown to increase combined forest and product C stocks partially because products derived from sawlog-sized trees are retained over long periods of time [17, 18]. Finally, while there can be greater C sequestration on highly productive sites, species composition and disturbance events also influence C trajectories [9].

While knowledge about differences in C stocks among forest management scenarios at any one point in time is informative [17–19], knowledge about rates of C sequestration are often equally or more meaningful for informing policy and planning decisions. For example, policy makers interested in mitigating climate change often require information on the amount of C that can be accumulated in forests over various timeframes – usually on the order of decades. Most studies of C sequestration use data from even-aged stands containing relatively few species [10, 20, 21]. In a study by Bradford and Kastendick [21], young (< 60 years old), unmanaged red pine (*Pinus resinosa* Aiton) and aspen (*Populus* spp.) stands of clearcut origin had higher rates of forest C sequestration than older stands with similar species and stand histories. For a southern Appalachian red spruce (*Picea rubens* Sarg.) - Fraser fir (*Abies fraseri* Pursh.) forest, Moore *et al.* [10] found that even-aged and uneven-aged silvicultural scenarios maintained positive values of average annual change in aboveground C sequestration over a 100-year period.

Additional studies of C sequestration that include naturally regenerated stands with diverse species mixtures and high structural diversity are also needed to inform policy and planning decisions. Forest management alternatives such as the guiding diameter-limit approach, which is best known for its use in pine stands of the southern USA [22–24], could also be evaluated for effectiveness in meeting C objectives in other regions. The guiding diameter-limit approach allows some long-lived species to reach sawlog size and offers landowners the flexibility of cutting trees below diameter limits if trees are expected to die, and retaining trees above diameter limits to protect the stand from winds and to retain seed sources [25].The cumulative sum of net changes in C stocks has also proven useful for visually depicting trends in C accumulation or loss over time and could further aid in decision-making processes [26].

In the northeastern USA, there have been several studies using simulations of tree growth to calculate C stocks over time. Schwenk *et al.* [6] found that silvicultural approaches with less frequent harvesting and greater structural retention had the greatest mean aboveground live tree C stocks over a 100-year period. Their simulation study of C stocks in northern hardwood stands in Vermont included four prescriptions: clearcut, shelterwood, single-tree selection, and no management. In a similar study by Carpentier *et al.* [5], intensive forest management resulted in a weak multi-criteria decision analysis (MCDA) utility value for C storage in aboveground live trees and dead wood compared to a no management scenario. The C storage value for an ecosystem management scenario was similar to both the no management and intensive management scenarios. These 70-year simulation results were the same for northern hardwood stands, shade-intolerant hardwood stands, and white spruce (*Picea glauca* (Moench) Voss) plantations in New York. In another study,

Table 1. Description of forest management scenarios used to model C stocks over a 100-year period.

Scenario	Description
Unmanaged	No cutting.
Selection	Single-tree selection cutting. Three separate scenarios involved cutting on 5-, 10-, and 20-year cycles.
Uniform shelterwood with two-stage overstory removal	Two overstory removal cuttings using the shelterwood method of regeneration. The new cohort of trees was commercially thinned twice and then the stand was regenerated using a one-cut shelterwood approach.
Uniform shelterwood with three-stage overstory removal	Two separate scenarios, both involved three removal cuttings using the shelterwood method of regeneration. The first scenario was followed by precommercial and commercial thinning and then clearcut and planted to spruce. The second scenario involved no treatments after the three removal cuts.
Diameter-limit	Two separate scenarios. The first with fixed diameter limits for desired species. The second with guiding diameter limits; diameter limits were increased above those used for fixed diameter-limit scenario and there was flexibility for leaving trees above and below the diameter limits.
Commercial clearcut	Most or all of the merchantable trees of desired species were cut twice, once in the 1950s and again in the 1980s.

Lutz *et al.* [27] found that tree growth rates, annual C storage in aboveground pools, and albedo had the strongest influence on optimal rotation length, which averaged 94 years for diverse forest types in New Hampshire. These past studies have clearly identified the complex interactions between management and C storage, but have been primarily simulation-based with limited incorporation of long-term data, which may limit their overall inference.

Given the growing need to better understand the C balance implications of various forest management scenarios, the goal of our study was to use 65 years of empirical data and simulations of tree growth and mortality from a long-term silvicultural study in Maine, USA, to refine our understanding of forest C dynamics. Our first objective was to compare average annual net C sequestration (AAC as in Moore *et al.* [10]; Mg ha^{-1} yr^{-1}) in the pools of aboveground portions of live trees, dead wood, and harvested wood products among contrasting forest management scenarios on a rotation (30-100 years) and 100-year basis. Our second objective was to evaluate trends in the cumulative sum of net changes in C stocks over time by stand and forest management scenario. Finally, we sought to integrate the findings from the preceding objectives into a more holistic understanding of the benefits and risks associated with using silvicultural techniques to enhance C storage in Acadian forests with refined recommendations for optimal strategies and future research.

Materials and methods

Study site and experimental design

The 1619-ha Penobscot Experimental Forest (PEF) is located in central Maine, USA (44°52′N, 68°38′W; mean elevation of 43 m). The PEF is within the Acadian Forest, which is an ecotone between the eastern North American broadleaf and boreal forests [28]. Tree species composition is diverse and includes balsam fir (*Abies balsamea* (L.) Mill), red spruce, eastern hemlock (*Tsuga canadensis* (L.) Carrière), northern white-cedar (*Thuja occidentalis* L.), and eastern white pine (*Pinus strobus* L.), in mixture with maples (*Acer* spp.), birches (*Betula* spp.), and aspens. Since the 1950s, the United States Department of Agriculture (USDA) Forest Service has maintained studies on the PEF to investigate the influence of silvicultural treatments and exploitative cuttings on stand composition, structure, growth, and yield [29]. Each of 10 treatments evaluated in this study (Table 1) was assigned to two experimental units (stands) ranging from 7 to 18 ha in size for a total of 20 stands. Each stand contains permanent plots with a nested design with 0.08-, 0.02-, and 0.008-ha circular plots sharing the same center (see Figure 4 in Waskiewicz *et al.* [30]). Table S1 lists the number of plots in each stand that were used to estimate C stocks and sequestration. Trees $\geq$ 11.4 cm diameter at breast height (dbh; 1.37 m) are measured on the entire 0.08-ha plot, trees $\geq$ 6.4 cm are measured on the 0.02-ha plot, and trees $\geq$ 1.3 cm are measured on the 0.008-ha plot. The plot design reduces time allocated to measuring small trees; for example, trees ranging from 1.3 to 6.3 cm dbh are only measured on the 0.008-ha plot. Plot locations were randomly selected using a systemic grid with a random start [30].

Before 1950, repeated partial cutting and forest fires of unknown frequency and severity occurred across the PEF [31]. Commercial harvesting began in the late 1700s and continued until the late 1800s. When the USDA Forest Service silvicultural experiment began in the 1950s, tree species composition in the stands used for this study included eastern hemlock, balsam fir, red spruce, hardwoods, and other softwoods [29, 32]. The stands

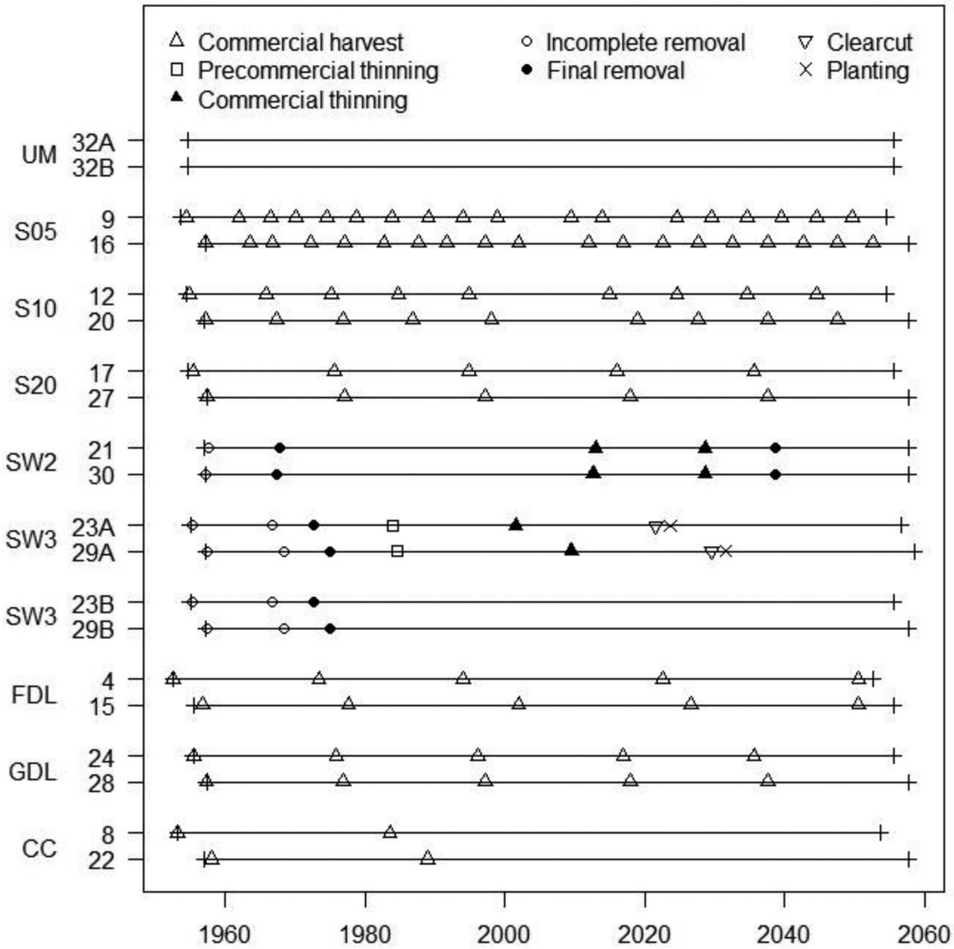

Figure 1. **Timelines of scenarios by stand showing management activities over a 100-year period. UM = unmanaged; S10 = selection cutting on a 10-year cycle; see Table 3 for other scenario codes.**

were irregularly uneven-aged, with relatively low stem density in the larger size classes [29, 31]. The majority of plots within stands used for this study occurred on soils derived from till; exceptions were two stands with plots that occurred on soils derived from glaciomarine sediments. Soils that occupied upland positions included loamy-skeletal, isotic, frigid Lithic Haplorthods (Thorndike series); coarse-loamy, isotic, frigid Oxyaquic Haplorthods (Plaisted series); and coarse-loamy, isotic, frigid Aquic Haplorthods (Howland series) [33]. Soils derived from till that occupied lower positions included loamy, mixed, active, acid, frigid, shallow Aeric Endoaquepts (Monarda series); and loamy, mixed, superactive, nonacid, frigid, shallow Histic Humaquepts (Burnham series). Soils derived from glaciomarine sediments included fine, illitic, frigid Aquic Dystric Eutrudepts (Buxton series); fine, illitic, nonacid, frigid Aeric Epiaquepts (Lamoine series); and fine, illitic, nonacid, frigid Typic Epiaquepts (Scantic series).

For the present study, C stocks were calculated for stands managed according to nine prescriptions and two unmanaged reference stands (Table 1). For the selection stands, residual structural goals were defined using the BDq method to specify target residual basal area, maximum diameter, and distribution of trees among size classes [34, 35]. In the uniform shelterwood with two-stage overstory removal stands, advance regeneration was present when the removal of the overwood began in the 1950s (Figure 1). During the final removal of the overwood approximately 10 years later, submerchantable trees (<16.5 cm dbh) and some larger trees for which there was no local market were not removed; no additional activities were conducted until commercial thinning in 2012. The uniform shelterwood with three-stage overstory removal stands were regenerated over a period of 17 years, with final removal of all trees $\geq$ 6.4 cm dbh in the 1970s. In the early 1980s, the new cohort of trees was precommercially thinned in one half of each stand; spruce were favored and about 1668 crop trees ha^{-1} were left [29]. For the fixed and guiding diameter-limit treatments, all merchantable trees of desired species above prescribed diameter limits were removed [35]. The guiding diameter-limit approach is an alternative to fixed-diameter limit cutting and is best known for its use in pine stands of the southern USA [22–24]. In the commercial clearcut stands, most or all of the merchantable trees were removed without explicit attention to regeneration. For the fixed diameter-limit and commercial clearcut stands, cuttings were repeated when the volume of merchantable trees was at least equal to that removed in the first cut. Guiding diameter-limit cutting was conducted every 20 years. The reference stands have not been harvested since the late 1800s, but have experienced more recent partial natural disturbances [9]. Detailed descriptions and timings of each treatment and stand are presented in Sendak *et al.* [29] and Brissette and Kenefic [34].

Summarization of historical data

Our methods required that we estimate C in the aboveground components of live trees, dead wood, and harvested wood products since the inception of the forest management treatments at the PEF. For plots with tree mortality records dating back to the 1950s, we tallied the number of live trees and trees that had been harvested or died due to non-harvest mortality agents; the records were from Kenefic *et al.* [35] and more recent inventories to 2019. The Forest Service measured live trees on permanent plots every 5 years (every 10 years starting in 2000) and before and after harvest; trees that had died since the previous inventory were recorded as harvest or non-harvest mortality.

For each inventory, aboveground C in live trees was estimated with regional biomass equations [36] and species-specific C concentrations by Lamlom and Savidge [37]. For non-harvest mortality, bole and branch C above the stump was estimated with the Young *et al.* [36] equations and C concentrations by Lamlom and Savidge [37]. These methods were also used to estimate C in the tops and branches of trees killed during harvest, plus the boles of trees < 11.4 cm dbh that were killed during harvest. Then, species-specific downed coarse woody debris (CWD) decay rates for eastern USA forests and the study area's climate regime [38] were used to estimate dead wood C stocks from non-harvest mortality and harvest residues for each inventory; this methodology assumes that dead wood was incorporated into the downed CWD pool immediately after death. The estimated dead wood C stocks are conservative because they are based on recruited dead wood (i.e. not from trees that died before the 1950s or portions of trees that were cut and left on-site before the 1950s, or from annual and episodic inputs from live trees).

For harvest mortality, the volume in sawlogs and pulpwood was determined using regional species-specific taper equations [39] and local merchantability standards [18]. Then, the amount of wood biomass in each product was calculated using equations from Miles and Smith [40] and C concentration estimates by Lamlom and Savidge [37] were used to calculate C stocks. Finally, the amount of C in wood products and landfills for each inventory was estimated using residence times for hardwoods and softwoods, and for pulpwood and sawlogs from Smith *et al.* [41]. Prior to 1989, non-sawlog, hardwood material was utilized as fuelwood and was assumed to be combusted at time of harvest.

Simulated C stocks

While empirical data were used to estimate past C stocks, our objective was to compare C sequestration among scenarios over the course of rotations and over 100 years. We used recent inventory data to model C sequestration over these time periods, with simulations of additional silvicultural treatments and tree growth and mortality as needed. An evaluation of C sequestration on a rotation basis is important because it allows for comparison between uneven-aged stands in which stocking remains high over time and even-aged stands in which stocking is temporally variable due to large reductions in live tree C stocks at the time of stand regeneration. In the shelterwood stands on the PEF, the rotation length is the time between the initiation of the new cohort in the 1950s and the removal of that cohort once target tree sizes for pulpwood or sawtimber production have been reached (Figure 1). Based on previous work in these stands, shelterwood rotation lengths of approximately 65 years for the scenario with three-stage overstory removal and precommercial thinning and 80 years for the scenario with two-stage overstory removal and no precommercial thinning were used for simulation [42]. For the commercial clearcut stands, the rotation is the time between the first and second cuts (i.e. 30 years) because of the low volume remaining after the 1980s cutting [12, 29]. We did not simulate additional cuttings in these stands, though silvicultural rehabilitation or repeated commercial clearcutting are management alternatives [11–13]. In uneven-aged stands, an

Table 2. Model fit statistics for mixed-effects models of average annual net change in C that contained forest management treatment as a fixed effect and stand as a random effect (b_i) on a rotation and 100-year basis.

C pool	Marginal R^2	Conditional R^2	Residual SE (Mg ha^{-1})	b_i SE (Mg ha^{-1})
Rotation				
Live trees	0.275	0.323	0.255	0.093
Dead wood	0.477	0.477	0.059	< 0.001
Wood products	0.507	0.621	0.055	0.037
All C pools	0.360	0.360	0.243	< 0.001
100 years				
Live trees	0.670	0.731	0.255	0.127
Dead wood	0.717	0.729	0.060	0.011
Wood products	0.732	0.791	0.055	0.028
All C pools	0.735	0.768	0.246	0.099

SE, standard error.

overstory removal does not occur but the minimum amount of time required for a newly regenerated tree to reach the target maximum diameter can be regarded as the rotation [43, 44]. Tree age-size relationships in the PEF selection stands indicate that this is 100 years [44]. A similar rotation age was used for the guiding and fixed diameter-limit scenarios, with slight variation (<10 years) due to differences in periodicity of harvests. A rotation length of 100 years was used for the unmanaged reference stands. Finally, we modeled C sequestration over a period of 100 years for all stands to make comparisons on a time frame that is commonly used for C accounting purposes.

The most recent inventories of live trees ≥ 1.3 cm dbh and tree regeneration were used to simulate future growth and mortality using a locally calibrated growth and yield model – the Acadian variant of the USDA Forest Service, Forest Vegetation Simulator (FVS-ACD) [45]. We also used FVS-Online, which is the online interface to the FVS modeling system. For each stand, the site index was determined using methodologies developed by Seymour and Fajvan [46] for uneven-aged stands, a site classification system by Briggs [47], or the height of dominant trees within a stand and stand age [48] (Table S1). For simulations of selection and diameter-limit cutting, we used the BDq targets and species-specific diameter limits outlined in Kenefic *et al.* [35]. Table S2 includes keywords that were used in simulations. Tree growth and mortality were predicted on a yearly basis and C stocks were computed as described for the historical data. Then, a stock change approach described by Puhlick *et al.* [9] was used to calculate the average annual net change in C stocks for time periods between inventories: (C stocks in time 2 – C stocks in time 1)/time between inventories in years. For each permanent plot, AAC was derived by summing the net change in C stocks for each inventory period and dividing the sum by the total timespan of measurements for the rotation or 100 years. The denominators of these equations were computed using values that included the month and year of inventory: year + (month/12); with January = 1, February = 2, etc.

For each permanent plot, the amount of regeneration used in FVS was limited to 4,942 trees ha^{-1} based on recommendations by Ray *et al.* [49] for mixed-species stands of the region. Each permanent plot contained 3-4, 0.0004- or 0.0013-ha plots (radius = 1.13 or 2.07 m, respectively) for measuring tree regeneration [18, 35]. When the observed number of seedlings exceeded 4,942 trees ha^{-1} on a given regeneration plot (after applying an appropriate expansion factor to individual trees), each tree species was allocated a proportion of maximum number of trees supplied to FVS (i.e. 4,942 trees ha^{-1}). Specifically, for each species, the number of seedlings within size classes defined by Waskiewicz *et al.* [30] was multiplied by a weighted value, with more weight given to trees in the larger size classes. The values for each size class were then summed and divided by a corresponding value for all species. Finally, the number of regeneration plots associated with a given permanent plot was divided by the number of trees computed for each regeneration plot. For each species, the average height of seedlings was used in FVS.

Data analysis

Mixed effects modeling was used to evaluate the influence of forest management scenario and depth to redoximorphic features in the soil on average annual net C sequestration in the aboveground components of live trees and recruited dead wood and wood products. For each permanent plot, depth to redoximorphic features were measured by Olson *et al.* [50]. Separate models of average annual net C sequestration were developed for individual pools (i.e. live trees, dead wood, and wood products) and all pools

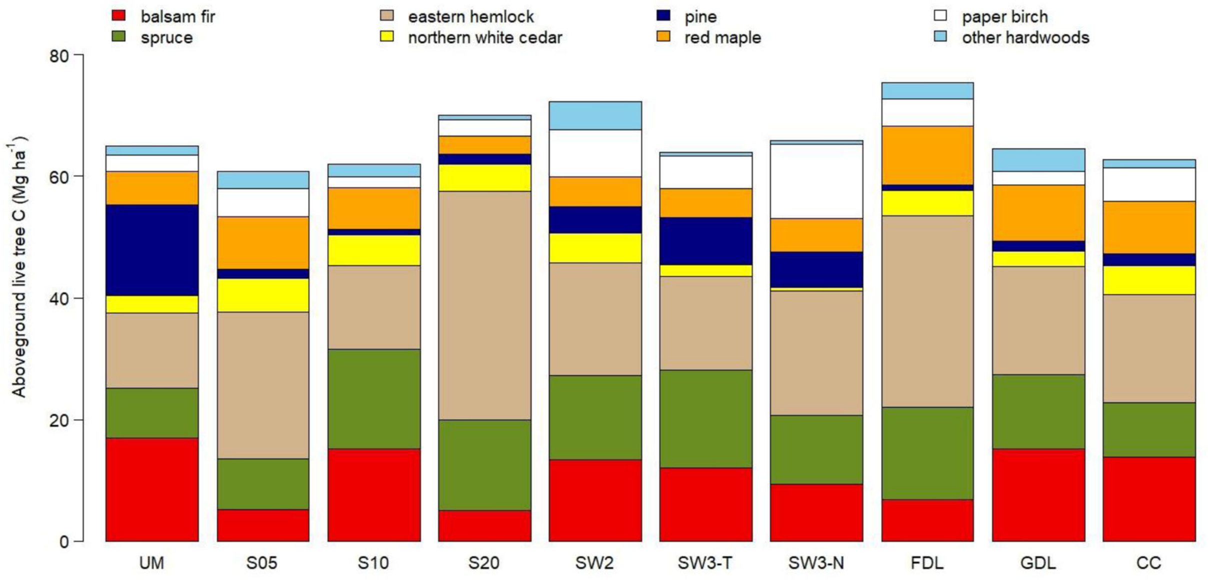

Figure 2. Average C stocks (Mg ha^{-1}) at the beginning of experiment in the 1950s by species and forest management scenario. The mean values are the overall means (i.e. the mean values for each stand were used to compute the overall mean for each scenario). See Figure 1 and Table 3 for scenario codes.

combined. In addition, separate models were also developed for C sequestration over the course of a rotation and for 100 years. For the unmanaged and selection cutting on a 10-year cycle scenarios, one stand occurred on soils derived from till and one stand occurred on soils derived from glaciomarine sediments. Hence, these scenarios were not included in our statistical analysis because differences in soil properties between soils derived from till and glaciomarine sediments, such as soil pH and nutrient concentrations, can influence C dynamics [9]. For the other scenarios, only plots occurring on till were used in the present study. Stand was used as a random effect to account for the nested structure of the data and potential correlation between observations from the same stand. Likelihood ratio tests were used to determine the optimal models in terms of fixed effects. The lme function in the nlme package [51] in R [52] was used to fit the linear mixed-effects models. Least-squares (LS) means and pairwise comparisons were calculated using the lsmeans and cld functions in the lsmeans [53] and multcompView [54] packages, respectively, in R. For the pairwise comparisons, differences between C stock LS means were considered significant if $p < 0.05$ after applying a Tukey's honest significant difference multiplicity adjustment.

Results

Before the initiation of forest management treatments in the 1950s, aboveground live tree C stocks by forest management scenario were 66.2 ± 4.8 Mg ha^{-1} (mean ± SD) and ranged from 60.8 to 75.4 Mg ha^{-1} (Figure 2). Most stands had a higher proportion of softwood C stocks than hardwood C stocks (Figure S1). At the end of the rotations, aboveground live tree C stocks were 87.1 ± 24.0 Mg ha^{-1} and ranged from 59.8 to 143.1 Mg ha^{-1} (Figure 2). At the end of the 100-year period, aboveground live tree C stocks were 88.6 ± 32.6 Mg ha^{-1} and ranged from 37.5 to 143.1 Mg ha^{-1} (Figure 2). At the end of the rotations and the 100-year period, C stocks are shown by component (i.e. live trees, dead wood, and wood products), stand, and forest management scenario in Figure S2 (Figure 3).

While the unmanaged and selection cutting on a 10-year cycle scenarios were not used in statistical models, AAC in the combined live tree, dead wood, and wood product pools on a rotation basis was quantitatively similar among the unmanaged, all selection cutting, and uniform shelterwood with three-stage overstory removal followed by no thinning scenarios (Figure 4). On a 100-year basis, AAC of the unmanaged and selection cutting scenarios was quantitatively similar to the commercial clearcut scenario that was allowed to recover after two commercial harvests in those stands (Figure 5). For the unmanaged and selection cutting on a 10-year cycle scenarios, AAC in the combined live tree, dead wood, and wood product pools was 1.095 ± 0.171 and 1.015 ± 0.334 Mg ha^{-1} yr^{-1}, respectively. AAC was quantitatively similar between the till and glaciomarine sediment stands of these two scenarios. For the unmanaged scenario, the live tree pool sequestered the most C, while C sequestered in dead wood and wood

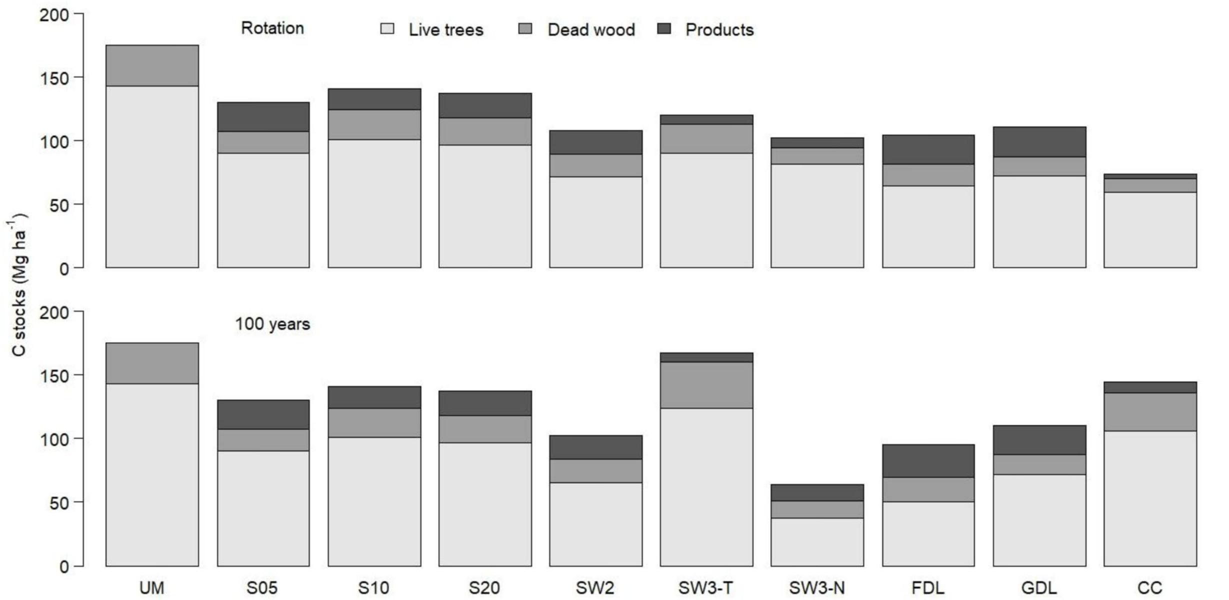

Figure 3. Average C stocks (Mg ha^{-1}) at the end of the rotation and 100-year period by live tree, dead wood, and wood product pools and forest management scenario. The mean values are the overall means (i.e. the mean values for each stand were used to compute the overall mean for each scenario). See Figure 1 and Table 3 for scenario codes.

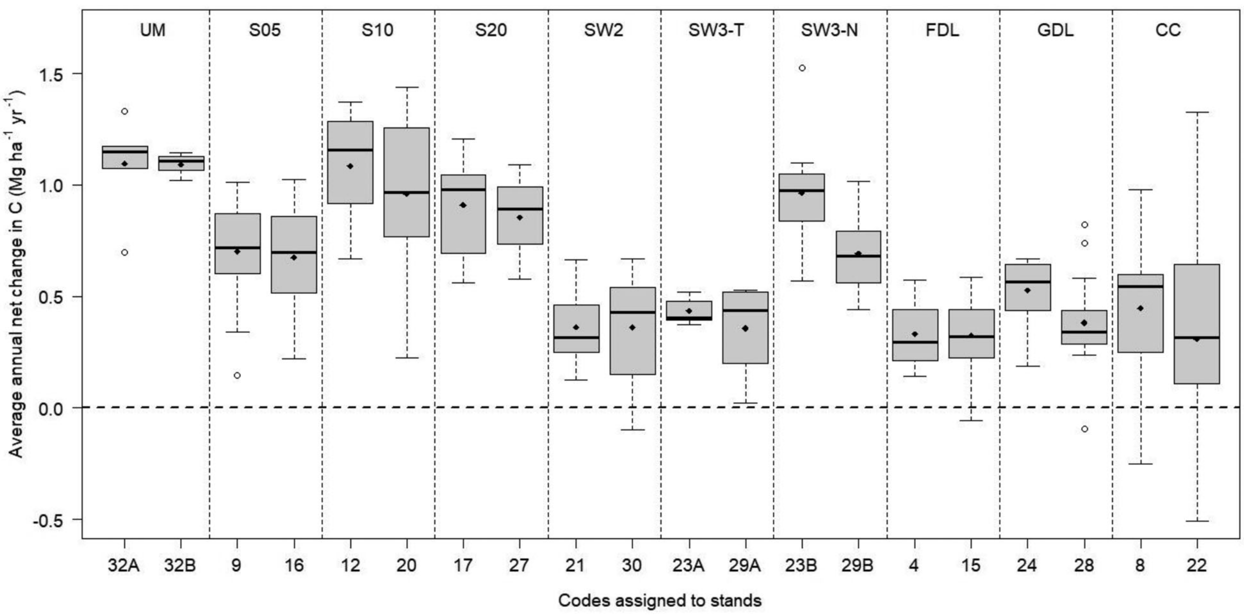

Figure 4. Average annual net change in C (Mg ha^{-1} yr^{-1}) for the combined live tree, dead wood, and wood product pools on a rotation basis. The horizontal line and black dot in each box are the median and mean, respectively. The boxes define the hinge (25-75% quartile, and the line is 1.5 times the hinge), and points outside the hinge are represented as dots. The mean value in each box is the stand-level mean (i.e. computed from plot values of average annual net change in C for a given stand) and the length of the box and lines show variation among plot values. See Figure 1 and Table 3 for scenario codes.

products accounted for a greater percentage of the overall C sequestration for the selection scenarios (Figure 6, Figure S3, and Figure S4).

The best models of AAC for the combined live tree, dead wood, and wood product pools included forest management scenario as a statistically significant fixed effect ($p < 0.05$). On a rotation and 100-year basis, the forest management scenario effect explained 36 and 74% of the variation in AAC, respectively (Table 2). On a rotation and 100-year basis, variation in AAC between stands with the same treatment accounted for < 1 and 14% of the components of variance, respectively. On a rotation basis, pairwise comparisons indicated that selection cutting and uniform shelterwood cutting with three-stage overstory removal followed by no thinning scenarios had greater AAC than other shelterwood and diameter-limit cutting scenarios ($p < 0.05$). AAC was similar between the selection cutting on a 5-year cycle

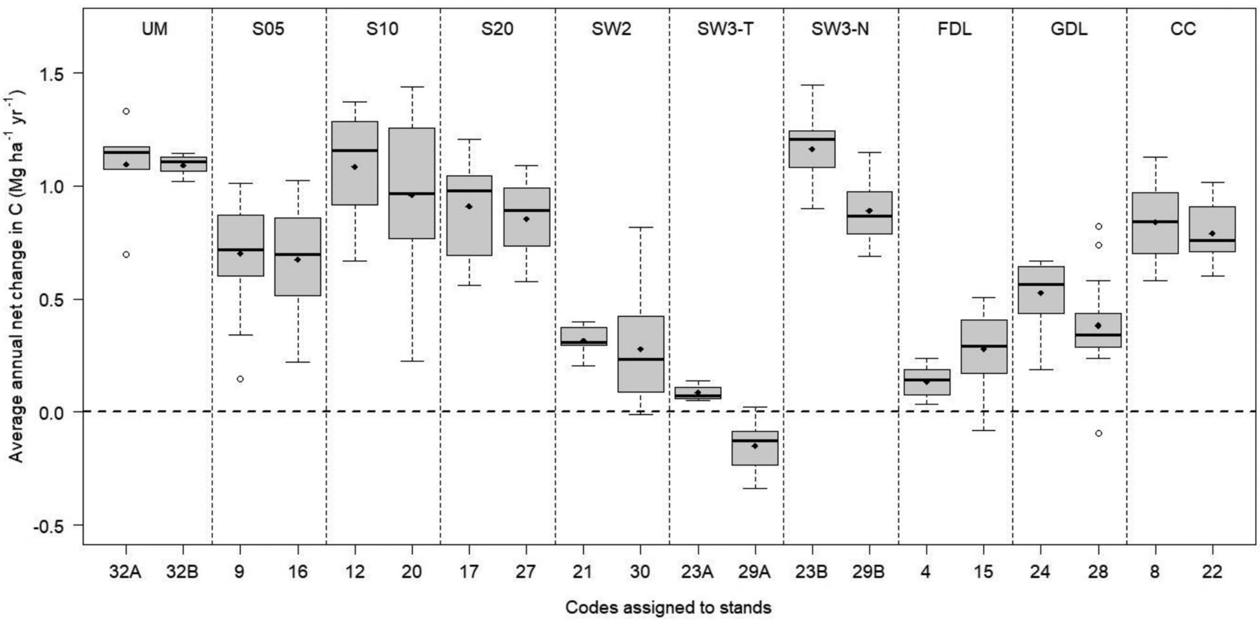

Figure 5. Average annual net change in C (Mg ha^{-1} yr^{-1}) for the combined live tree, dead wood, and wood product pools on a 100-year basis. The horizontal line and black dot in each box are the median and mean, respectively. The boxes define the hinge (25-75% quartile, and the line is 1.5 times the hinge), and points outside the hinge are represented as dots. The mean value in each box is the stand-level mean (i.e. computed from plot values of average annual net change in C for a given stand) and the length of the box and lines show variation among plot values. See Figure 1 and Table 3 for scenario codes.

and commercial clearcut scenarios (Table 3). On a 100-year basis, selection cutting, uniform shelterwood with three-stage overstory removal followed by no thinning, and commercial clearcut scenarios had greater AAC than the uniform shelterwood with three-stage overstory removal followed by thinning and the fixed diameter-limit cutting scenarios. AAC was similar among the guiding diameter-limit cutting, selection cutting, uniform shelterwood with three-stage overstory removal followed by no thinning, and commercial clearcutting scenarios. Likelihood ratio tests indicated that depth to redoximorphic features did not have a statistically significant effect on AAC.

For the unharvested, selection, and guiding diameter-limit stands, the cumulative sum of net changes in C stocks for combined live tree, dead wood, and wood product pools was positive for most of the 100-year period evaluated in this study (Figure 7). For one of the unmanaged stands (stand 32 A), tree mortality at the beginning of the 100-year period led to an initial loss of C in live trees, but with a corresponding increase in dead wood C accumulation. Despite this initial decrease, C accumulated in combined pools consistently increased over time in both unmanaged stands. In stands where forest management activities occurred, C accumulated in wood products generally increased over time. This was best exemplified by the selection and guiding diameter-limit stands. For all of the shelterwood stands with thinning, the cumulative sum of net changes in C stocks for combined pools was negative for about the first 40 years of the study, but was positive by the end of the rotation periods. For stands regenerated with uniform shelterwood cutting with three-stage overstory removal and no thinning thereafter, C accumulation approached levels comparable to the unmanaged stands by 100 years. For stands where commercial clearcutting occurred in the 1950s and again in the 1980s, C accumulation reached levels about half that of unmanaged stands when allowed to recover after harvests.

Discussion

Our findings indicate that maintaining portions of a landscape as reserves (i.e. no timber management) combined with additional forested landscapes where selection cutting or similar forms of multi-aged silviculture could be practiced could enhance C sequestration compared to other forest management alternatives. Multi-aged silvicultural systems, such as selection and irregular shelterwood systems, can provide the additional benefit of increasing resiliency by maintaining structural and compositional complexity that can reduce C emission risk in some forest types [55]. For the combined live tree, dead wood, and harvested wood product pools, AAC was quantitatively similar among the unmanaged and all of the selection cutting scenarios. In the selection cutting

Table 3. Least-squares (LS) mean (standard error) average annual net change in C (AAC, Mg ha^{-1} yr^{-1}) by forest management scenario and C pool on a rotation and 100-year basis. S05 = selection cutting on a 5-year cycle; S20 = selection cutting on a 20-year cycle; SW2 = uniform shelterwood with two-stage overstory removal; SW3 = uniform shelterwood with three-stage overstory removal; T = thinning; N = no thinning; FDL = fixed diameter-limit cutting; GDL = guiding diameter-limit cutting; CC = commercial clearcut.

Scenario	C pools Live trees	Dead wood	Wood products	All C pools
Rotation				
S05	0.292 (0.080) ab	0.168 (0.010) ab	0.225 (0.028) a	0.685 (0.043) bc
S20	0.271 (0.088) ab	0.211 (0.021) abc	0.194 (0.029) a	0.891 (0.077) c
SW2	− 0.010 (0.087) ab	0.218 (0.013) ac	0.228 (0.027) a	0.362 (0.058) a
SW3-T	0.233 (0.076) ab	0.187 (0.013) ab	0.119 (0.026) a	0.394 (0.038) a
SW3-N	0.399 (0.100) b	0.335 (0.015) d	0.105 (0.028) a	0.844 (0.068) c
FDL	− 0.109 (0.076) a	0.173 (0.009) ab	0.225 (0.028) a	0.328 (0.037) a
GDL	0.070 (0.078) ab	0.153 (0.007) b	0.232 (0.027) a	0.439 (0.044) a
CC	− 0.071 (0.118) ab	0.320 (0.026) cd	0.138 (0.028) a	0.395 (0.078) ab
100 years				
S05	0.293 (0.101) bcd	0.168 (0.013) a	0.225 (0.022) cd	0.687 (0.083) cde
S20	0.269 (0.108) abcd	0.211 (0.022) ab	0.194 (0.024) bcd	0.887 (0.107) de
SW2	− 0.069 (0.105) acd	0.182 (0.011) a	0.181 (0.021) abcd	0.295 (0.089) abc
SW3-T	− 0.280 (0.092) a	0.136 (0.013) a	0.127 (0.021) abd	− 0.034 (0.074) b
SW3-N	0.597 (0.100) b	0.368 (0.013) c	0.067 (0.021) a	1.032 (0.082) e
FDL	− 0.242 (0.095) ad	0.184 (0.013) a	0.259 (0.022) c	0.210 (0.078) ab
GDL	0.072 (0.099) abcd	0.153 (0.011) a	0.232 (0.022) cd	0.450 (0.082) acd
CC	0.430 (0.095) bc	0.300 (0.013) bc	0.084 (0.021) ab	0.816 (0.076) de

Note: Different letters indicate significant differences between LS mean AAC among treatments at $p < 0.05$.

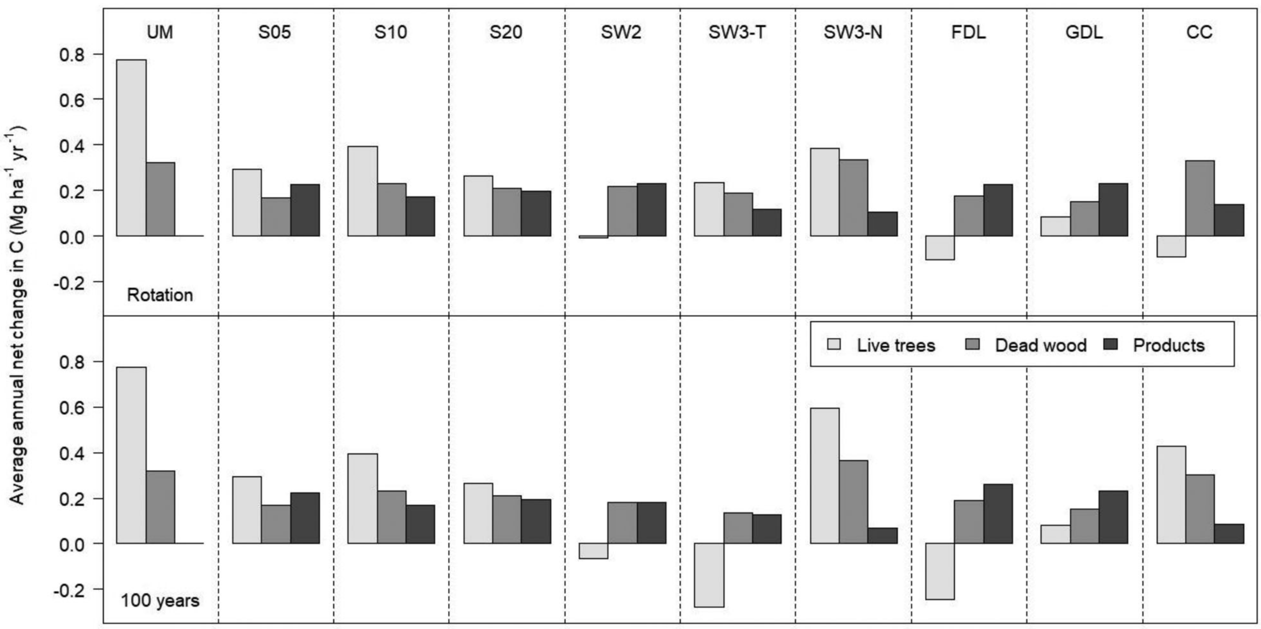

Figure 6. Mean average annual net change in C (Mg ha^{-1} yr^{-1}) for the live tree, dead wood, and wood product pools on a rotation and 100-year basis by forest management treatment. The mean values are the overall means (i.e. the mean values for each stand were used to compute the overall mean for each treatment). See Figure 1 and Table 3 for scenario codes.

scenarios, C in live trees was periodically transferred to the harvested wood product and dead wood pools due to timber harvesting. Some of this transferred C was initially emitted during the manufacturing of products and the remaining C was stored in products or landfills for various time periods depending on species and product categories. Selection cutting also promoted the growth of large diameter trees with resulting products from those trees having long residence times. At the same time, new cohorts of trees were periodically established and relatively high sequestration rates in these trees contributed to overall C sequestration. By the end of the 100-year study period, the selection stands also sequestered amounts of C in the aboveground portions of live trees similar to that of the unmanaged stands. These findings indicate that structurally complex forests managed for products with long residence times can sequester C at levels similar to those of unmanaged forests.

While we found that selection cutting can enhance C sequestration compared to other forest management alternatives, selection cutting in North America has been mostly practiced on

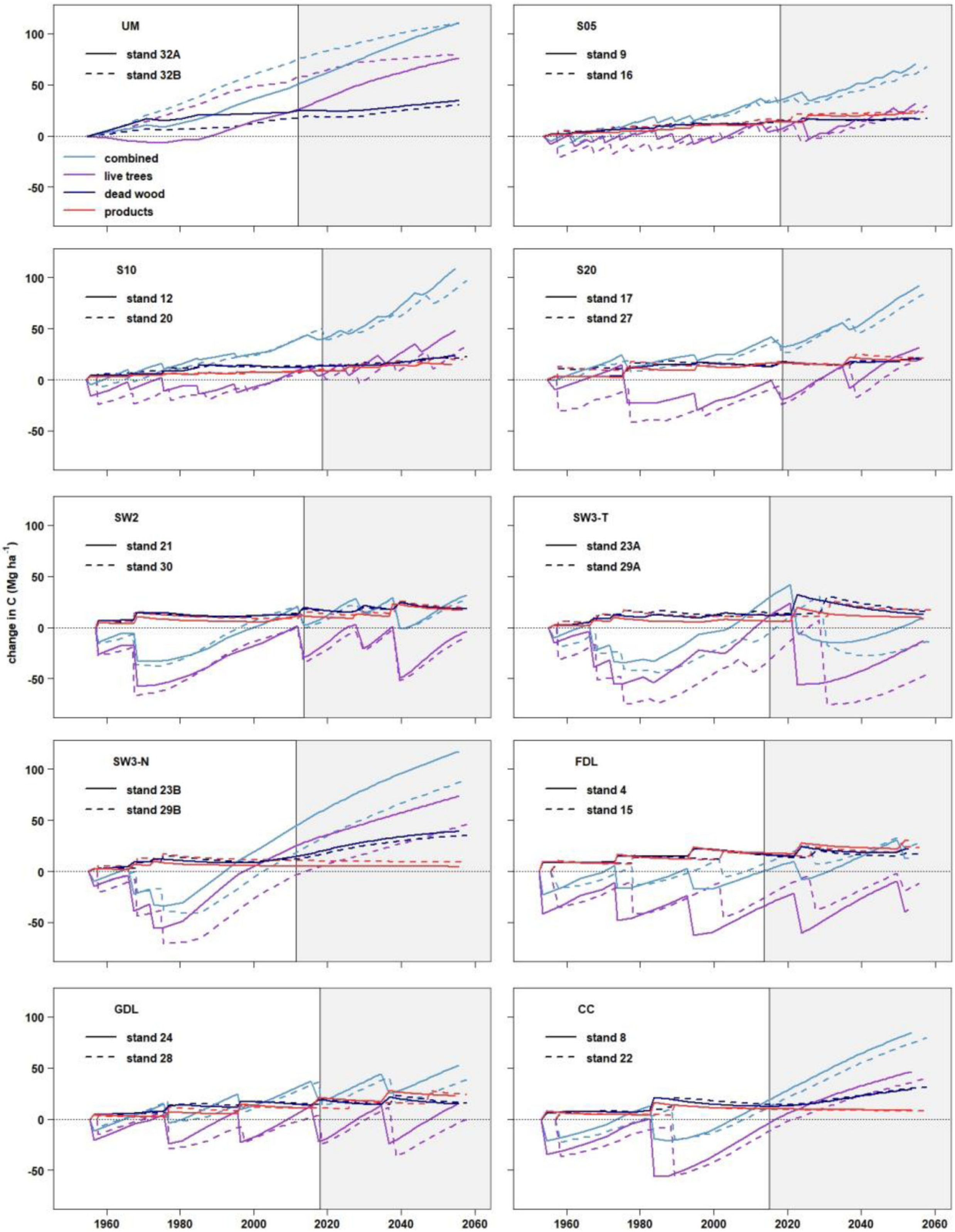

Figure 7. Cumulative sum of net changes in C stocks (Mg ha^{-1}) over 100-year period by stand and forest management scenario. Gray shading indicates the portion of the 100-year period that involved estimating C stocks from simulations of tree growth and mortality; the starting dates involving simulations is approximate because these dates often varied by stand within scenario (see Figure 1). Net changes in C stocks between inventories can be positive (C accumulation) or negative (C loss). See Figure 1 and Table 3 for scenario codes.

experimental forests in the USA and Canada. However, silvicultural systems that promote similar stand conditions could be utilized to sequester comparable amounts of C. The selection stands on the PEF have a high degree of structural and species diversity [32, 56], which are comparable to some forms of irregular shelterwood or gap-based approaches [57–59]. Despite the similarity in AAC between the selection cutting on a 5-year cutting cycle and commercial clearcut scenarios on a rotation basis, commercial clearcutting led to an abundance of non-merchantable species and poor-quality trees [12, 13]. These post-harvest conditions could limit the future potential for C sequestration in live trees and harvested wood products. Finally, selection cutting on a longer cycle (e.g. 20 years) could be an alternative for landowners who desire to sequester C and ensure that harvesting operations are economically feasible for logging contractors.

On a rotation basis, the shelterwood scenarios that included thinning sequestered less C than the selection scenarios. However, over multiple rotations, C accumulated in wood products from the shelterwood stands could dampen the overall loss of C when regenerating stands. In our study, there was evidence of this after the first rotation in the shelterwood stands (Figure 7). Also, the timing of commercial thinning and amount of biomass removed influence C dynamics. In this study, an early commercial thinning entry with a 40% basal area reduction was simulated. Thinning stands to low densities can accomplish goals such as promoting growth on individual trees so that they reach certain product classes sooner [60]. However, there is a greater initial live tree C loss and early thinning of pulpwood-sized trees generate products that have short residence times. We also found that open stand conditions post-thinning caused a bottleneck for desired shade-tolerant conifer tree regeneration. Many sprouting hardwoods (e.g. red maple (*Acer rubrum* L.) and aspen) and balsam fir became quickly established after thinning, and the low stocking of overstory trees after thinning precluded use of the uniform shelterwood method with three stages of overstory removal.

On both a rotation and 100-year basis, the fixed diameter-limit cutting scenario sequestered less C than the selection cutting scenarios. However, the guiding diameter-limit cutting and selection cutting scenarios sequestered similar amounts of C (Table 3). In terms of structure and species composition, the guiding diameter-limit stands have been shown to be more similar to selection stands than the fixed diameter-limit stands [61, 62]. While the focus of the guiding diameter-limit approach is on tree removal and not residual stand condition, it could be an alternative to selection cutting for some landowners. The guiding diameter-limit approach allows some long-lived species to reach sawlog size, and products derived from sawlog-sized trees have the potential to store C for long periods of time. The guiding diameter-limit approach also offers landowners the flexibility of cutting trees below diameter limits if trees are expected to die, and retaining trees above diameter limits to protect the stand from winds and retain seed sources [25]. Retaining large trees of fast-growing species has the additional benefit of enhancing stand-level C sequestration.

Our results were similar to those of other studies that simulated C stocks over long periods of time. For example, the average annual C stocks reported by Schwenk *et al.* [6] were quantitatively greater for their selection cutting scenario than shelterwood cutting or clearcut scenarios. However, it is important to consider that their simulations were conducted with data from northern hardwood stands and our inventory data were from conifer-dominated, mixed-species stands. On a 70-year and single-management basis (i.e. one forest management scenario applied to a given stand of a certain forest type), Carpentier *et al.* [5] found that C stock MCDA utility values were statistically similar for intensive and ecosystem management scenarios. Their ecosystem management treatments varied by forest type, but for northern hardwoods was single-tree selection cutting on a 20-year cutting cycle. In contrast, our study showed that AAC was greater for selection cutting on a 20-year cutting cycle than for diameter-limit or commercial clearcut scenarios. Again, differences in species composition, time periods considered, and metrics used to compare scenarios need to be considered when making comparisons among studies. For example, some forest types dominated by species with faster growth rates (e.g. aspen and eastern white pine) could have higher C sequestration rates than forest types dominated by species with slower growth rates or that are prone to disease (e.g. American beech (*Fagus grandifolia* Ehrh.)).

Our simulated C stocks at the end of rotations were similar to those of studies that were based on long-term measurements of forest and wood product pools. For example, mean live tree C stocks for the uniform shelterwood with two-stage overstory removal followed by commercial thinning and the uniform shelterwood with three-stage overstory removal followed by precommercial and commercial thinning scenarios (71.7 and 89.9 Mg ha^{-1}, respectively) were similar to C stocks following thinning treatments to various levels of basal area in red pine stands (approximately 60 to 80 Mg ha^{-1}) [17]. For these scenarios, wood product C stocks were also similar between studies (7.3 to 18.6 Mg ha^{-1} for our study and approximately 8 to 18 Mg ha^{-1} for the study by Powers *et al.* [17]). Also, after more than five decades of single-tree selection cutting in northern hardwoods, Powers *et al.* [17] found that live tree C stocks were approximately 70 to 90 Mg ha^{-1}. In our study, C stocks averaged 90.4 to 101.1 after 100 years of single-tree selection on various cutting cycles. However, it is important to note that the study by Powers *et al.* [17] included live tree C in belowground portions of trees and our study only included aboveground C. Also, for the scenarios involving thinning, the method of thinning (e.g. thinning from below), residual basal areas, and timing of thinning can influence C stocks over the course of a rotation [63].

Our analysis has several limitations and should be considered within the context of the PEF. First, the initial stand conditions of the forest permitted the use of a variety of treatment alternatives. Across many other forested landscapes, some stands have poor stocking of desired species, contain submerchantable trees, or have other attributes that limit management options [64–66]. When comparing C sequestration among forest management treatments, starting conditions can also influence estimates of C sequestration and the ranking of different treatments with regard to C objectives. For example, estimates of AAC could be different if starting from a well-stocked forest, cutover stand conditions, or clearcutting followed by tree planting. Second, dead wood and harvested wood product C stocks before the 1950s were not included in our estimates of C sequestration. In forests managed for wood products, C stored in dead wood and products from previous rotations would contribute to the overall sequestration of C in consecutive rotations [67]. However, repetitive harvesting can also result in accelerated decomposition of dead wood or its incorporation into belowground pools [68]. These impacts depend on the amount of the stand area disturbed by machinery, biomass removed, and frequency of harvests [69, 70]. Our results are also based on past merchantability standards, which will likely change in the future. For example, many mills are beginning to accept smaller diameter sawlogs which could influence the amount of wood extracted from forests and C stored in products. For scenarios involving diameter-limit cutting, decreasing diameter limits for certain species could result in more trees being cut and less material being left on site in the tops of trees, but more wood being stored in products. Finally, our projected C stocks do not account for major disturbances such as the hemlock woolly adelgid (*Adelges tsugae*) or eastern spruce budworm (*Choristoneura fumiferana*), and do not consider alternative climate and atmospheric CO_2 trajectories.

Future studies that compare the influence of altered disturbance and climatic regimes on C sequestration would be informative. For example, the risk of C emissions due the hemlock woolly adelgid could be compared between forests managed and not managed for timber products. When forests have conditions that make them prone to severe disturbances, forest management that results in C being sequestered in products may minimize the risk of overall long-term C emissions compared to no timber management scenarios. While this may be true for forests prone to high-intensity wildfires in which fuels are combusted, there is less certainty about C trajectories for forests subject to disturbances that result in large transfers of C to the dead wood pool. On a landscape scale, such analyses could incorporate the temporal and spatial aspects of disturbance under alternative climate and atmospheric CO_2 trajectories. Other studies of C sequestration are needed for cutover and unhealthy forests (e.g. forests effected by disease), and could be compared to scenarios with the rehabilitation or restoration of those forests.

Our findings indicate that modeling the C consequences associated with alternative thinning entry times and biomass removals would be useful for planning and policy decisions. As noted by Mika and Keeton [71], modeling C sequestration over consecutive rotations would also be informative, especially in regard to wood product C stocks. However, given the urgency of mitigating climate change over the short-term (i.e. decades), studies involving shorter time periods (e.g. single rotations for scenarios involving stands regenerated with the shelterwood method followed by thinning) and with a higher level of certainty are important. In our study, commercial thinning to low densities caused a bottleneck for tree regeneration of desired species and limited regeneration methods to clearcutting and planting, or releasing the regeneration that was present and conducting a cleaning and fill planting. Generally, site conditions on the PEF are not considered desirable for this type of intensive management due to poor drainage and low soil fertility, but such methods – including the C sequestration advantages and disadvantages of artificial versus natural regeneration systems – should be further considered in future analyses of this type.

The sequestration of C in soils and the benefits of other ecosystem services, which were not evaluated in this study, also merit consideration. For managed stands on the PEF, Puhlick *et al.* [18] found that the average relative contribution of belowground C pools to total ecosystem C was over 50% for mineral soils to a depth of 1 m. Management strategies that could enhance C sequestration in this large C pool include retaining sections of cut trees on the forest floor to be incorporated into the soil, and maintaining species mixtures to increase the resiliency of the forest to disturbances and climate change thereby avoiding high decomposition rates of soil C [72, 73]. Forest management that promotes mixtures of conifers and hardwoods can also make forests less susceptible to the eastern spruce budworm and perhaps reduce the risk of C emissions [74]. Forest management strategies that create early successional habitat for certain wildlife species could also reduce C emission risk if unhealthy or degraded areas of the landscape were strategically regenerated. In short, the development and application of management strategies that incorporate C, forest resiliency, and other ecosystem objectives (maintaining or enhancing biodiversity, etc.) allow forest managers to adapt to rapidly changing conditions, while trying to minimize both short- and long-term risk.

Conclusion

Comparisons of C sequestration among contrasting forest management scenarios over various timeframes and for different forest types are needed to inform planning and policy decisions related to mitigating climate change. On a rotation basis, we found that scenarios with selection cutting had greater AAC for combined live tree, dead wood, and wood product pools than those with shelterwood cutting followed by thinning or with diameter-limit cutting ($p < 0.05$). For unmanaged, selection, and guiding diameter-limit stands, the cumulative sum of net changes in C stocks for combined live tree, dead wood, and wood product pools was positive for most of the study period. This suggests that these strategies may be appropriate when objectives are to accumulate C across a range of time (e.g. 30-100 years). Overall, our results indicate that strategies that maintain overstory stocking levels necessary to regenerate desired species and promote the development of sawlog-sized trees can enhance long-term C sequestration in forests with similar species composition and soils. At the landscape-scale, an approach involving multiple forest management strategies could be implemented to reduce risks associated with homogenous forest conditions.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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References

1. Earles JM, North MP, Hurteau MD. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. Ecol Appl. 2014;24(4):732–740. doi:10.1890/13-1860.1.
2. Hicke JA, Meddens AJH, Allen CD, et al. Carbon stocks of trees killed by bark beetles and wildfire in the western United States. Environ Res Lett. 2013;8(3):8.
3. Puhlick J, Woodall C, Weiskittel A. Implications of land-use change on forest carbon stocks in the eastern United States. Environ Res Lett. 2017;12(2):13.
4. Woodall CW, Walters BF, Coulston JW, et al. Monitoring network confirms land use change is a substantial component of the forest carbon sink in the eastern United States. Sci Rep. 2015;5(1):17028. doi:10.1038/srep17028.
5. Carpentier S, Filotas E, Handa IT, et al. Trade-offs between timber production, carbon stocking and habitat quality when managing woodlots for multiple ecosystem services. Envir Conserv. 2017;44(1):14–23. doi:10.1017/S0376892916000357.
6. Schwenk WS, Donovan TM, Keeton WS, et al. Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision

analysis. Ecol Appl. 2012;22(5):1612–1627. doi:10.1890/11-0864.1.
7. Carey EV, Sala A, Keane R, et al. Are old forests underestimated as global carbon sinks?. Glob Change Biol. 2001;7(4):339–344. doi:10.1046/j.1365-2486.2001.00418.x.
8. Luyssaert S, Schulze ED, Borner A, et al. Old-growth forests as global carbon sinks. Nature. 2008;455(7210):213–215. doi:10.1038/nature07276.
9. Puhlick JJ, Fraver S, Fernandez IJ, et al. Site quality, disturbance, and vegetation effects on carbon storage and accumulation in old, mixed-species stands in central Maine, USA. Nat Areas J. 2019;39(4):429–441. doi:10.3375/043.039.0406.
10. Moore PT, DeRose JR, Long JN, et al. Using silviculture to influence carbon sequestration in southern Appalachian spruce-fir forests. Forests. 2012;3(2):300–316. doi:10.3390/f3020300.
11. Kenefic LS. Selective cutting, rehabilitation, and alternatives for forests of northeastern North America and elsewhere. J For. 2014;112(3):259–260. doi:10.5849/jof.13-036.
12. Kenefic LS, Bataineh M, Wilson JS, et al. Silvicultural rehabilitation of cutover mixedwood stands. J For. 2014;112(3):261–271. doi:10.5849/jof.13-033.
13. Puhlick JJ, Kuehne C, Kenefic LS. Crop tree growth response and quality after silvicultural rehabilitation of cutover stands. Can J for Res. 2018;49:670–679.
14. Teets A, Fraver S, Weiskittel AR, et al. Quantifying climate-growth relationships at the stand level in a mature mixed-species conifer forest. Glob Chang Biol. 2018;24(8):3587–3602. doi:10.1111/gcb.14120.
15. Puhlick JJ, Weiskittel AR, Fraver S, et al. Assessing the role of natural disturbance and forest management on dead wood dynamics in mixed-species stands of central Maine, USA. Can J for Res. 2016;46(9):1092–1102. doi:10.1139/cjfr-2016-0177.
16. Spies TA, Turner MG. Dynamic forest mosaics. In: Hunter ML, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge (UK): Cambridge University Press; 1999. p. 95–160.
17. Powers M, Kolka R, Palik B, et al. Long-term management impacts on carbon storage in Lake States forests. For Ecol Manag. 2011;262(3):424–431. doi:10.1016/j.foreco.2011.04.008.
18. Puhlick JJ, Weiskittel AR, Fernandez IJ, et al. Long-term influence of alternative forest management treatments on total ecosystem and wood product carbon storage. Can J for Res. 2016;46(11):1404–1412. doi:10.1139/cjfr-2016-0193.
19. Chatterjee A, Vance GF, Tinker DB. Carbon pools of managed and unmanaged stands of ponderosa and lodgepole pine forests in Wyoming. Can J for Res. 2009;39(10):1893–1900. doi:10.1139/X09-112.
20. Alban DH, Perala DA. Carbon storage in Lake States aspen ecosystems. Can J for Res. 1992;22(8):1107–1110. doi:10.1139/x92-146.
21. Bradford JB, Kastendick DN. Age-related patterns of forest complexity and carbon storage in pine and aspen-birch ecosystems of northern Minnesota, USA. Can J for Res. 2010;40(3):401–409. doi:10.1139/X10-002.
22. Guldin JM. Experience with the selection method in pine stands in the southern United States, with implications for future application. Forestry. 2011;84(5):539–546. doi:10.1093/forestry/cpr035.
23. Guldin JM, Baker JB. Uneven-aged silviculture, southern style. J For. 1998;96(7):22–26.
24. Reynolds RR, Baker JB, Ku TT. Four decades of selection management on the Crossett farm forestry forties. Fayetteville, AR: University of Arkansas, Arkansas Agricultural Experiment Station; 1984. (Bulletin 872).
25. Miller GW, Smith HC. A practical alternative to single-tree selection?. North J Appl For. 1993;10(1):32–38. doi:10.1093/njaf/10.1.32.
26. Dugan AJ, Birdsey R, Healey SP, et al. Forest sector carbon analyses support land management planning and projects: assessing the influence of anthropogenic and natural factors. Clim Change. 2017;144(2):207–220. doi:10.1007/s10584-017-2038-5.
27. Lutz DA, Burakowski EA, Murphy MB, et al. Trade-offs between three forest ecosystem services across the state of New Hampshire, USA: timber, carbon, and albedo. Ecol Appl. 2016;26(1):146–161. doi:10.1890/14-2207.
28. Halliday W. A forest classification for Canada. Ottawa, Ontario: Canadian Forest Service; 1937. (Bull. 89).
29. Sendak PE, Brissette JC, Frank RM. Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest. Can J for Res. 2003;33(11):2116–2128. doi:10.1139/x03-140.
30. Waskiewicz JD, Kenefic LS, Rogers NS, et al. Sampling and measurement protocols for long-term silvicultural studies on the Penobscot Experimental Forest. Newtown Square, PA: USDA For. Serv.; 2015. (NRS-147).
31. Kenefic LS, Brissette JC. History of the Penobscot Experimental Forest, 1950-2010. In Kenefic LS, Brissette JC, editors. Penobscot Experimental Forest: 60 years of research and demonstration in Maine, 1950-2010; NRS-P-123. Newtown Square, PA: USDA For. Serv.; 2014.
32. Olson MG, Wagner RG. Long-term compositional dynamics of Acadian mixedwood stands under different silvicultural regimes. Can J for Res. 2010;40(10):1993–2002. doi:10.1139/X10-145.
33. Natural Resources Conservation Service. Natural Resources Conservation Service Southern Penobscot County Soil Map. Version 11, Feb 15, 2012. 2012 [cited. http://www.nrcs.usda.gov/wps/portal/nrcs/surveylist/soils/survey/state/?stateId=ME.
34. Brissette JC, Kenefic LS. Centerpiece of research on the Penobscot Experimental Forest: the US Forest Service long-term silvicultural study. In: Kenefic LS, Brissette JC, editors. Penobscot Experimental Forest: 60 years of research and demonstration in Maine, 1950-2010. Newtown Square, PA: USDA For. Serv.; 2014. NRS-P-123.
35. Kenefic LS, Rogers NS, Puhlick JJ, et al. Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest. 2nd Edition. 2015. In:

USDA For. Serv. Research Data Archive. Available from: 10.2737/RDS-2012-0008-2.

36. Young HE, Ribe JH, Wainwright K. Weight tables for tree and shrub species in Maine. Orono, ME: University of Maine, Life Sciences and Agriculture Experiment Station; 1980. (Misc. Rep. 230).
37. Lamlom SH, Savidge RA. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenerg. 2003; 25(4):381–388. doi:10.1016/S0961-9534(03)00033-3.
38. Russell MB, Woodall CW, Fraver S, et al. Residence times and decay rates of downed woody debris biomass/carbon in eastern US forests. Ecosystems. 2014; 17(5):765–777. doi:10.1007/s10021-014-9757-5.
39. Li R, Weiskittel A, Dick AR, et al. Regional stem taper equations for eleven conifer species in the Acadian Region of North America: Development and assessment. N J App For. 2012;29(1):5–14. doi:10.5849/njaf.10-037.
40. Miles PD, Smith WB. Specific gravity and other properties of wood and bark for 156 tree species found in North America. Newtown Square, PA: USDA For. Serv.; 2009. (NRS-38).
41. Smith JE, Heath LS, Skog KE, et al. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. Newtown Square, PA: USDA For. Serv.; 2006. (NE-343).
42. Seymour RS, Meyer SR, Wagner RG. The Cooperative Forestry Research Unit Commercial Thinning Research Network: 9-year results. Newtown Square, PA: USDA For. Serv.; 2014. (Kenefic LS, Brissette JC, editors. Penobscot Experimental Forest: 60 years of research and demonstration in Maine., 1950-2010; NRS-P-123).
43. Bauhus J, McElhinny CM, Alcorn P. Stand structure and tree growth in uneven-aged spotted gum (Corymbia maculata) forests: some implications for management. Forestry. 2002;75(4):451–456. doi:10.1093/forestry/75.4.451.
44. Seymour RS, Kenefic LS. Balance and sustainability in multiaged stands - A northern conifer case study. J For. 1998;96(7):12–17.
45. Weiskittel A, Kershaw J, Crookston N, et al. The Acadian Variant of the Forest Vegetation Simulator: Continued development and evaluation. In: Keyser, CE, Keyser, TL. editors. Proceedings of the 2017 Forest Vegetation Simulator (FVS) e-Conference. e-Gen. Tech. Rep. SRS-224. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 2017.
46. Seymour RS, Fajvan MA. Influence of prior growth suppression and soil on red spruce site index. North J Appl For. 2001;18(2):55–62. doi:10.1093/njaf/18.2.55.
47. Briggs RD. Site Classification Field Guide. Orono, ME: Cooperative Forestry Research Unit; 1994. (Technical Note 6).
48. Wilson DS, Seymour RS, Maguire DA. Density management diagram for northeastern red spruce and balsam fir forests. North J Appl For. 1999;16(1):48–56. doi:10.1093/njaf/16.1.48.
49. Ray DG, Saunders MR, Seymour RS. Recent changes to the Northeast variant of the Forest Vegetation Simulator and some basic strategies for improving model outputs. North J Appl For. 2009;26(1):31–34. doi:10.1093/njaf/26.1.31.
50. Olson E, Kenefic LS, Dibble AC, et al. Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: Influence of site, silviculture, and land use history. J Torrey Bot Soc. 2011;138(4):453–464. doi:10.3159/TORREY-D-10-00019.1.
51. Pinheiro JC, Bates DM, DebRoy S, et al. nlme: Linear and nonlinear mixed effects models. 2014. http://CRAN.R-project.org/package=nlme.
52. R Development Core Team. R: A language and environment for statistical computing. 2014.
53. Lenth RV. lsmeans: Least-squares means. 2014. http://CRAN.R-project.org/package=lsmeans.
54. Graves S, Piepho HP, Selzer L, et al. multcompView: Visualizations of paired comparisons. 2012. http://CRAN.R-project.org/package=multcompView.
55. D'Amato AW, Bradford JB, Fraver S, et al. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. For Ecol Manag. 2011;262(5):803–816. doi:10.1016/j.foreco.2011.05.014.
56. Saunders MR, Wagner RG. Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems. Can J for Res. 2008;38(3):498–517. doi:10.1139/X07-155.
57. Arseneault JE, Saunders MR, Seymour RS, et al. First decadal response to treatment in a disturbance-based silviculture experiment in Maine. For Ecol Manag. 2011;262(3):404–412. doi:10.1016/j.foreco.2011.04.006.
58. D'Amato AW, Catanzaro PF, Fletcher LS. Early Regeneration and Structural Responses to Patch Selection and Structural Retention in Second-Growth Northern Hardwoods. For Sci. 2015;61(1):183–189. doi:10.5849/forsci.13-180.
59. Raymond P, Bedard S, Roy V, et al. The Irregular Shelterwood System: Review, Classification, and Potential Application to Forests Affected by Partial Disturbances. J For. 2009;107(8):405–413.
60. Pelletier G, Pitt DG. Silvicultural responses of two spruce plantations to midrotation commercial thinning in New Brunswick. Can J for Res. 2008;38(4):851–867. doi:10.1139/X07-173.
61. Kenefic LS, Brissette JC, Sendak PE. The effects of alternative diameter-limit cutting treatments: Some findings from a long-term northern conifer experiment. In: Ward JS, editor. Proceedings of the 84th Annual Winter Meeting of the New England Society of American Foresters. Newtown Square, PA: USDA For. Serv.; 2004. NE-314).
62. Granstrom M. Northern Conifer Forest Management: Silvicultural, Economic, and Ecological Outcomes From 65 Years of Study [Master's thesis]. Orono (ME): University of Maine; 2019.
63. Hoover C, Stout S. The carbon consequences of thinning techniques: Stand structure makes a difference. J For. 2007;105(5):266–270.

64. Bédard S, Guillemette F, Raymond P, et al. Rehabilitation of northern hardwood stands using multicohort silvicultural scenarios in Quebec. J For. 2014;112(3):276–286. doi:10.5849/jof.13-035.
65. Kelty MJ, D'Amato AW. Historical prespective on diameter-limit cutting in northeastern forests. 2005. In: Kenefic LS, Nyland RD, editors. Proceedings of the conference on diameter-limit cutting in northeastern forests. NE-342.
66. Nyland RD. Exploitation and greed in eastern hardwood forests: Will foresters get another chance?. J For. 1992;90(1):33–37.
67. Mika AM, Keeton WS. Net carbon fluxes at stand and landscape scales from wood bioenergy harvests in the US Northeast. Glob Change Biol Bioenergy. 2014; 7(3):438–454
68. Bradford JB, Fraver S, Milo AM, et al. Effects of multiple interacting disturbances and salvage logging on forest carbon stocks. For Ecol Manag. 2012;267: 209–214. doi:10.1016/j.foreco.2011.12.010.
69. Stokland JN, Siitonen J, Jonsson BG. Biodiversity in dead wood. Cambridge, UK: Cambridge University Press; 2012.
70. Vanderwel MC, Malcolm JR, Smith SM. An integrated model for snag and downed woody debris decay class transitions. For Ecol Manag. 2006;234(1-3): 48–59. doi:10.1016/j.foreco.2006.06.020.
71. Mika AM, Keeton WS. Factors contributing to carbon fluxes from bioenergy harvests in the U.S. Northeast: an analysis using field data. GCB Bioenergy. 2013;5(3):290–305. doi:10.1111/j.1757-1707.2012.01183.x.
72. Jandl R, Lindner M, Vesterdal L, et al. How strongly can forest management influence soil carbon sequestration?. Geoderma. 2007;137(3-4):253–268. doi:10.1016/j.geoderma.2006.09.003.
73. Kabrick JM, Clark KL, D'Amato AW, et al. Managing hardwood-softwood mixtures for future forests in eastern North America: Assessing suitability to projected climate change. J For. 2017;115(3):190–201. doi:10.5849/jof.2016-024.
74. Su Q, MacLean DA, Needham TD. The influence of hardwood content on balsam fir defoliation by spruce budworm. Can J for Res. 1996;26(9): 1620–1628. doi:10.1139/x26-182.