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Long-term influence of alternative forest management treatments on total ecosystem and wood product carbon storage

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Abstract: Developing strategies for reducing atmospheric CO_2 is one of the foremost challenges facing natural resource professionals today. The goal of this study was to evaluate total ecosystem and harvested wood product carbon (C) stocks among alternative forest management treatments (selection cutting, shelterwood cutting, commercial clearcutting, and no management) in mixed-species stands in central Maine, USA. These treatments were initiated in the 1950s and have been maintained since, and ecosystem C pools were measured in 2012. When compared across managed treatments, the commercial clearcut had the lowest total ecosystem C stocks by 21%, on average ($P < 0.05$), while the selection and shelterwood treatments had similar total ecosystem C stocks. Including the C stored in harvested wood products did not influence observed differences in C storage among treatments. Total ecosystem C stocks in the reference stand were 247.0 ± 17.7 Mg·ha^{-1} (mean ± SD) compared with 161.7 ± 31.3 Mg·ha^{-1} in the managed stands (171.2 ± 31.7 Mg·ha^{-1} with products C). This study highlights the impacts of long-term forest management treatments on C storage and indicates that the timing of harvests and the species and sizes of trees removed influence C stored in harvested wood products.

Key words: carbon stocks, forest products, forest soils, coarse fragments, site quality.

Résumé : Le développement de stratégies visant à réduire le CO_2 atmosphérique est un des principaux défis que doivent relever aujourd'hui les professionnels des ressources naturelles. Le but de cette étude consistait à estimer les stocks totaux de carbone (C) emmagasinés dans l'écosystème et les produits forestiers récoltés dans des peuplements mixtes soumis à différents traitements d'aménagement forestier (coupe de jardinage, coupe progressive, coupe à blanc commerciale et aucun traitement) dans le centre du Maine, aux États-Unis. Ces traitements ont débuté dans les années 1950 et ont été maintenus depuis. Les réservoirs de C dans l'écosystème ont été mesurés en 2012. Parmi les traitements d'aménagement, les stocks de C les plus faibles, de 21 % en moyenne ($P < 0{,}05$), étaient associés à la coupe à blanc commerciale tandis que les stocks totaux de C dans l'écosystème étaient similaires pour la coupe de jardinage et la coupe progressive. Inclure le C emmagasiné dans les produits forestiers récoltés n'a pas influencé les différences observées entre les traitements dans le stockage du C. Les stocks totaux de C dans l'écosystème atteignaient 247,0 ± 17,7 Mg·ha^{-1} (moyenne ± écart-type) dans le peuplement témoin comparativement à 161,7 ± 31,3 Mg·ha^{-1} dans les peuplements aménagés (171,2 ± 31,7 Mg·ha^{-1} incluant le C dans les produits forestiers). Cette étude met en évidence les impacts à long terme des traitements d'aménagement forestier sur le stockage du C et indique que le moment de la récolte ainsi que l'espèce et la taille des arbres récoltés influencent le C emmagasiné dans les produits forestiers récoltés. [Traduit par la Rédaction]

Mots-clés : stocks de carbone, produits forestiers, sols forestiers, fragments grossiers, qualité de station.

Introduction

Concerns about climate change have increased interest in developing forest management strategies to produce a net reduction in atmospheric CO_2 and to make forests more resilient to future climatic conditions and disturbance regimes, while providing ecosystem services to meet society's needs. Most current research suggests that multi-aged forest management systems such as irregular shelterwood and selection systems may maximize carbon (C) storage in forests when compared with more intensive forest management such as clearcutting (D'Amato et al. 2011; Nunery and Keeton 2010; Powers et al. 2011). However, comparisons are complicated as C storage in harvested wood products needs to be considered when evaluating management strategies in which the objective is to maximize C storage (McKinley et al. 2011; Profft et al. 2009; Skog 2008). Consequently, a better understanding of how accounting for C stored in wood products influences comparisons of C storage among management strategies, particularly between managed and unmanaged stands, is needed to identify forest management strategies that are best suited for maximizing C storage.

Numerous studies have found that unmanaged forest stands have higher total ecosystem C stocks compared with managed stands (Chatterjee et al. 2009; Powers et al. 2011). These studies have also found that total ecosystem C stocks do not differ among managed treatments in some forest types. When differences

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among managed treatments were observed, the live-tree C pool had a major influence on total ecosystem C stocks. Model simulation studies have also shown that more intensive management strategies such as clearcutting on short rotations tend to result in less aboveground C storage than strategies that involve partial cutting (Harmon and Marks 2002; Nunery and Keeton 2010). When C stored in harvested wood products is added to total ecosystem C stocks, some managed stands can have C stocks that are similar to unmanaged stands, and the conclusions about the differences in C stocks between managed treatments can be different than when only total ecosystem C stocks are evaluated (Powers et al. 2011). However, comprehensive and long-term studies in which all major ecosystem C pools are measured and compared are relatively rare, particularly in naturally regenerated, mixed-species forests, which are relatively more common on the North American landscape when compared with single-species plantations.

In particular, site quality can affect C pools through its influence on the quantity of vegetation produced and the decomposition rates of organic matter. For instance, tree growth tends to be poorer on coarse-textured soils that contain higher percentages of coarse fragments than on similar soils with lower percentages of coarse fragments (Childs and Flint 1990). In humid climates, this is partially because the soil organic matter can be leached to depths below the rooting zone (Schaetzl and Anderson 2005), which in turn also affects tree growth and C dynamics. In even-aged stands dominated by yellow poplar (*Liriodendron tulipifera* L.), Keyser (2010) used statistical models to show that site index is positively correlated with aboveground C stocks. However, alternative indicators of site quality such as coarse fragments and the depth to the seasonal high water table may be more appropriate than traditional measures (e.g., site index) in multi-aged, mixed-species stands (Skovsgaard and Vanclay 2013). Interestingly, many studies have noted that site quality likely influenced comparisons of total ecosystem C stocks among treatments (Chatterjee et al. 2009; Powers et al. 2011), but indicators of site quality were not actually included in their assessment.

The overall goal of this study was to evaluate C stocks in a mixed-species forest across several contrasting long-term forest management treatments that have been maintained and monitored since the 1950s on the Penobscot Experimental Forest in central Maine, USA. Our specific objectives were to (*i*) test for differences in the average C stocks of individual and combined ecosystem pools among the forest management treatments, after making adjustments to treatment means to account for potential differences in site quality among stands, (*ii*) evaluate differences in average total ecosystem C stocks (on-site C storage) plus C stored in harvested wood products, and (*iii*) assess the relative contribution of individual ecosystem pools to total ecosystem C storage. We also examined the potential of the managed treatments to have C stocks similar to those of the unmanaged reference stand after accounting for C storage in harvested wood products. The working hypothesis was that the unmanaged reference stand would have the highest C storage even after accounting for harvested wood products but that important and significant differences would be detected among the alternative forest management treatments examined.

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), and is within the Acadian Forest, a transitional zone between the eastern North American broadleaf and boreal forests (Halliday 1937). Mean temperatures in February and July are –7.1 °C and 20.0 °C, respectively, mean annual precipitation is 107 cm, and the terrain is generally flat. Tree species composition is diverse and includes balsam fir (*Abies balsamea* (L.) Mill), red spruce (*Picea rubens* Sarg.), 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 (*Populus* spp.). Since the 1950s, the 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 (Sendak et al. 2003). Each treatment was assigned to two experimental units (stands) ranging from 7 to 18 ha in size.

For the present study, C pools were measured in stands managed according to three prescriptions (single-tree selection cutting on a 5-year cycle, three-stage uniform shelterwood cutting, and commercial clearcutting) and an unmanaged reference stand. The selection stands had been cut 11 times prior to our sampling in 2012; residual structural goals were defined using the BDq method to specify target residual basal area, maximum diameter, and distribution of trees among size classes (e.g., Guldin (1991)). The shelterwood stands were regenerated over a period of 17 years, with final overstory removal in the 1970s, and no management has since taken place. The commercial clearcut stands had been harvested twice since the PEF was established in 1950, once in the 1950s and again in the 1980s. The commercial clearcut treatment is a form of exploitive cutting in which the most valuable trees were removed from the stand, leaving many small-diameter and poor-quality trees. This treatment is different from clearcutting as a regeneration method in silviculture in which all trees are cut and a new cohort of trees is established after the cutting of older trees. The reference stand was not part of the original USDA Forest Service study design but was later added because no harvesting had occurred in the stand since the late 1800s (Brissette and Kenefic 2014). Detailed descriptions and timings of each treatment and stand are presented in Sendak et al. (2003) and Brissette and Kenefic (2014). The timing of harvests within replicates was not synchronized within a given number of years (Sendak et al. 2003), which contributes to between-stand variation.

Our measurements of C pools in 2012 were timely because the shelterwood and commercial clearcut stands have attributes that suggest harvesting could now be conducted in these stands (Table 1). For instance, the shelterwood stands had high stem densities and small tree diameters with high height to diameter ratios indicating that regenerating these stands with one of the common regeneration methods (e.g., seed tree cutting leaving eastern white pines coupled with site preparation until a new cohort of trees becomes established) would be more appropriate than thinning, which could result in the windthrow of residual trees. The commercial clearcut stands could be harvested for a third time since the 1950s, which would emulate repeated heavy partial harvesting every 30 years. This makes these treatments comparable from the standpoint that they are at the end of their harvest intervals. In the reference and selection stands, C storage may be relatively constant over time, with fluctuations resulting from the frequency and severity of natural disturbances.

Before 1950, repeated partial cutting and forest fires of unknown frequency and severity occurred across the PEF (Kenefic and Brissette 2014). 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 was largely eastern hemlock, balsam fir, red spruce, hardwoods (mostly red maple (*Acer rubrum* L.)), and other softwoods (mostly northern white cedar) (Olson and Wagner 2010; Sendak et al. 2003). Eastern white pine was a minor component of the stands (<10% of total basal area), except in the reference stand (20% of total basal area). The stands were irregularly uneven aged, with relatively low stem density in the larger size classes (Kenefic and Brissette 2014; Sendak et al. 2003). Since the 1950s, stem-only harvesting (tree tops and branches cut from the tree bole and left on site) has been primarily conducted during the winter months. Most stands were harvested using chainsaws and rubber-tired skidders, but horse

Table 1. Mean (standard deviation) and range of forest attributes associated with permanent plots by treatment.

Attribute	Treatment			
	Reference (N = 4)	Selection (N = 10)	Shelterwood (N = 10)	Clearcut (N = 10)
Tree density (trees·ha^{-1})	831 (282)	2613 (2082)	7959 (3231)	6083 (2400)
	531–1149	507–6783	3897–15229	3286–11354
QMD (cm)	29.7 (5.2)	15.1 (6.3)	8.9 (1.7)	7.9 (1.0)
	23.0–34.0	8.3–27.5	6.9–11.7	5.7–9.1
Total basal area (m^2·ha^{-1})	54.0 (7.0)	30.4 (6.3)	46.0 (8.6)	28.0 (6.3)
	47.7–60.5	20.6–42.1	33.7–65.3	21.2–38.9
Conifer basal area (% of total basal area)	91.1 (4.0)	89.7 (8.4)	85.5 (14.1)	43.0 (23.3)
	86.7–96.4	72.1–100	51.6–97.9	18.3–79.1
Depth to water table* (cm)	45 (15)	34 (17)	38 (11)	29 (10)
	30–64	0–51	15–53	13–43
Cartographic DTW (cm)	87 (81)	143 (120)	71 (59)	125 (100)
	4–198	9–373	6–187	21–284
Coarse fragments (%)	40.6 (14.3)	35.5 (16.9)	29.6 (17.4)	35.8 (14.5)
	23.5–58.6	15.8–66.8	2.3–72.5	18.8–64.1

Note: Data are from measurements of trees ≥ 1.3 cm diameter at breast height and soil properties on plots where ecosystem C pools were measured in 2012. N, the number of plots; QMD, quadratic mean diameter; DTW, depth-to-water.

*Depth to redoximorphic features was used as an indicator of depth to water table.

logging and cut-to-length harvesters with forwarders were also used over time (Sendak et al. 2003).

Each stand had a system of 8 to 21 permanent plots (PSPs) for measuring trees and other forest attributes. For this study, we measured C pools at five PSPs in each replicate of the selection, shelterwood, and commercial clearcut treatments for a total of 30 PSPs. We also measured C pools at four PSPs in the reference stand. The PSPs for this study were selected in a random, stratified process, which is described in detail by Puhlick et al. (2016*a*). Briefly, PSPs were stratified according to the proportion of major soil types on glacial till within each stand. The soils series that occur in each treatment are also described by Puhlick et al. (2016*a*). The PSPs consisted of a nested design with 0.08, 0.02, and 0.008 ha circular plots sharing the same plot center. Trees ≥ 11.4 cm diameter at breast height (dbh; 1.37 m) were measured on the entire 0.08 ha plot, trees ≥ 6.4 cm dbh were measured on the 0.02 ha plot, and trees ≥ 1.3 cm dbh were measured on the 0.008 ha plot.

Data collection

Trees and shrubs ≥ 1.3 cm dbh were measured on PSPs in accordance with the USDA Forest Service nested-plot design. Trees and shrubs < 1.3 cm dbh were measured on three 0.0013 ha plots (radius = 2.07 m) established 4 m from PSP center at 0°, 90°, and 270° magnetic north. Species and dbh were recorded for trees ≥ 0.3 cm dbh, and species and height were recorded for trees < 0.3 cm dbh. These measurements were used to calculate live-tree and shrub ovendry biomass using “complete tree” allometric regression equations (Young et al. 1980). These predicted biomass values included aboveground and belowground portions of trees and shrubs excluding fine roots (Young and Carpenter 1967). Biomass was converted to C content using species-specific C concentration estimates (Lamlom and Savidge 2003).

For each PSP, herbaceous vegetation was clipped and collected from a 0.25 m^2 quadrat. Bryophytes were collected separately from other herbaceous vegetation because they were used to develop a function for predicting bryophyte mass from bryophyte cover (Puhlick et al. 2016*b*). In the laboratory, samples were ovendried at 65 °C to a constant mass, weighed, and ground to 0.85 mm using a Thomas-Wiley laboratory mill. Subsamples were analyzed for total C (TC) by combustion analysis at 1350 °C using a LECO CN-2000 analyzer (LECO Corp.). For the non-bryophyte samples, C content was calculated by multiplying the sample’s ovendry mass by its TC estimate. For bryophytes, approximately 30 measurements of bryophyte cover were taken along transects established on each PSP (Puhlick et al. 2016*b*). A robust average of bryophyte mass was derived using these measurements and the bryophyte cover function noted above. An average TC estimate from the bryophyte samples was then used to determine bryophyte C content.

Fine woody debris (FWD) was measured along three line transects per PSP according to methods developed by Brown (1974). For each transect, we recorded the number of woody pieces at the point of intersection with the sampling plane having diameters of <0.64, 0.64–2.53, and 2.54–7.61 cm within the first 1, 2, and 4 m of the transect, respectively. For each size class, ovendry biomass was calculated using formulas developed by Brown (1974) for the Northern Region of the USDA Forest Service. These values were summed to derive a total FWD biomass estimate for each PSP. An average TC estimate from samples of FWD buried within the O_i horizon was used to derive FWD C content.

Downed woody debris (DWD) and stumps were measured on the 0.02 ha plots. The volume of each DWD piece was calculated using the conic–paraboloid formula (Fraver et al. 2007). For the portion of stumps > 15 cm from the root collar, volume was calculated using the formula for a cylinder; volume in the lower portion of stumps was included in estimates of belowground C. DWD and stump biomass were calculated using nondecayed species-specific wood and bark specific gravity, average bark volume as a percentage of wood volume (Miles and Smith 2009), and a decay class reduction factor (Harmon et al. 2011). Then, biomass to C conversion factors developed by Harmon et al. (2008) were used to estimate C content. The C contents for individual DWD pieces and stumps were summed, and expansion factors were used to derive per hectare values for each PSP.

Snags were measured on PSPs in accordance with the USDA Forest Service nested-plot design. For broken snags, methods developed by Russell and Weiskittel (2012) were used to determine top diameter. Volume was calculated by (*i*) dividing the snag into 100 sections of equal length, (*ii*) determining the large- and small-end diameters of each section using taper equations developed by Li et al. (2012), (*iii*) using Smalian’s formula to calculate the volume of each section, and (*iv*) summing the section volumes (Husch et al. 2003). Only the volume above the stump was calculated, and biomass and C content were determined using the same methods as for DWD.

On the same transects that were used to measure bryophyte cover, organic (O) horizon depth was also measured. The pedotransfer function developed by Puhlick et al. (2016*b*) was used to predict O horizon C content at these locations, and an average was derived for each PSP. These values were then reduced by the average percentage of coarse root C content in the O horizon for a given stand (Puhlick et al. 2016*b*). This adjustment was made because coarse root C content was included in the live-tree and shrub C content estimate. Mineral soil samples were collected from beneath the surface O horizon to a depth of 1 m below the top of the mineral soil using an impact-driven soil corer (Puhlick et al. 2016*a*) with an internal diameter of 5.1 cm. For each PSP, the mineral soil was sampled at one location with the corer. Fine earth fraction (<2 mm) and coarse charcoal were included in our estimate of mineral soil C content.

The amount of C stored in the stumps and root systems of trees that were harvested or had died due to nonharvest mortality agents was estimated using records of tree mortality (Puhlick 2015). Combined stump and root biomass at time of tree death was calculated using biomass equations developed by Young et al. (1980), and a negative exponential function was used to determine C storage. An annual decomposition rate constant (k) of 0.046 developed for Norway spruce (*Picea abies* (L.) Karst.) (Melin et al. 2009) was used in the function due to limited species-specific decomposition rate constants in this region for the combined stump and coarse root system portion of trees. A C concentration estimate of 50% was used to derive C content of stumps and root systems.

A production approach based on methods by Smith et al. (2006) was used to estimate C storage in harvested wood products and landfills. Trees that were harvested from PSPs were determined from USDA Forest Service inventories conducted immediately before and after harvest (Puhlick 2015). For individual trees, the volume in sawlogs and pulpwood was determined using regional species-specific taper equations (Li et al. 2012) and local merchantability standards (Supplementary Table S1[1]). For each harvest, the amount of wood biomass in each product was calculated using equations from Miles and Smith (2009), and C concentration estimates by Lamlom and Savidge (2003) were used to calculate C content. Finally, C storage in wood products and landfills was estimated using residence time data from Smith et al. (2006) (for examples, see Supplementary Table S2[1]). Prior to 1989, nonsawlog, hardwood material was utilized as fuelwood and was assumed to be combusted at the time of harvest. We did not consider emissions during harvest, transport, manufacturing of products, or combustion for energy in our calculations as we were primarily interested in quantifying pools of stored C rather than conducting a full life-cycle analysis.

Several indicators of site quality were also measured on PSPs. For each PSP, a soil pit was excavated to measure depth to redoximorphic features and drainage class, which was determined following the Maine Association of Professional Soil Scientists (2002) guidelines. Average cartographic depth-to-water, which is based on elevation, flow channels, and wetlands (Murphy et al. 2011; White et al. 2012), was derived from a raster data set of 1 m resolution (UNB Forest Watershed Research Center 2014) using values within each PSP. This metric represents a wetness index that can be related to drainage condition. The relative volume of coarse fragments in the mineral soil was calculated as the estimated volume of coarse fragments and ledge within the soil core volume sampled divided by the total volume of the soil core. One soil core was collected 3 m outside of each PSP to avoid influence on other long-term studies.

Data analysis

Mixed-effects modeling was used to evaluate the influence of treatment and soil properties on the C stocks of seven individual pools: (1) overstory live trees and shrubs ≥ 1.3 cm dbh, including aboveground and belowground components but excluding fine roots; (2) understory tree and shrub regeneration and herbaceous plants; (3) CWD, including DWD and the portions of snags and stumps 15 cm above the root collar; (4) stump–root systems of harvested trees and snags, including the portions of stumps < 15 cm and their roots; (5) forest floor, including FWD but not coarse roots; (6) mineral soil, including fine earth fractions and coarse charcoal; and (7) harvested wood product C stored in products and landfills. We also evaluated the C stocks of four aggregated pools: (1) total ecosystem (on-site pools), (2) total ecosystem plus C stored in harvested wood products, (3) aboveground (live trees and shrubs above a 15 cm stump, tree and shrub regeneration above the root collar, herbaceous plants, and CWD), and (4) belowground (live trees and shrubs below a 15 cm stump, tree and shrub regeneration below the root collar, stump–root systems of harvested trees and snags, forest floor, and mineral soil). Although there are two reference stands on the PEF, only one of these stands occurs on glacial till and was examined in this study. Because the reference was not replicated on glacial till, we only used data from the managed treatments (selection, shelterwood, and commercial clearcut) in our statistical analysis.

Treatment, depth to redoximorphic features, cartographic depth-to-water, drainage class, and the relative volume of coarse fragments in the mineral soil were evaluated for inclusion in the models as fixed effects. "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. Logarithmic transformations were applied to understory ($\log_{10}(x + 0.1) + 1$), CWD ($\log_{10}(x + 1)$), and forest floor ($\log_{10}x$) C stocks to linearize the relationship between these response variables and the explanatory variables. Likelihood ratio tests were used to determine the optimal models in terms of fixed effects. The lme function in the nlme package (Pinheiro et al. 2014) in R (R Core Team 2014) 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 (Lenth 2014) and multcompView (Graves et al. 2012) 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 honestly significant difference multiplicity adjustment.

Results

Average basal area was 54.0 m²·ha⁻¹ in the unmanaged reference stand compared with 34.8 m²·ha⁻¹ in the managed stands, and the average size (diameter) of trees varied by forest management treatment (Table 1). Although data from the reference stand were not included in our statistical analysis, the reference stand had, on average, greater overstory live-tree and shrub and CWD C stocks than the managed treatments (Table 2). These C pools influenced total ecosystem C, which was also notably higher in the reference stand (Table 2). For the managed stands, total ecosystem C was 161.7 ± 31.3 Mg·ha⁻¹ (mean ± SD). Even when C stored in harvested wood products was added to total ecosystem C, mean total ecosystem + products C was numerically greater in the reference stand (Fig. 1). For the managed stands, total ecosystem + products C stocks were 171.2 ± 31.7 Mg·ha⁻¹.

For the selection, shelterwood, and commercial clearcut treatments, C in wood harvested from 1950 to 2012 was 38.8 ± 8.3, 38.1 ±

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2016-0193.

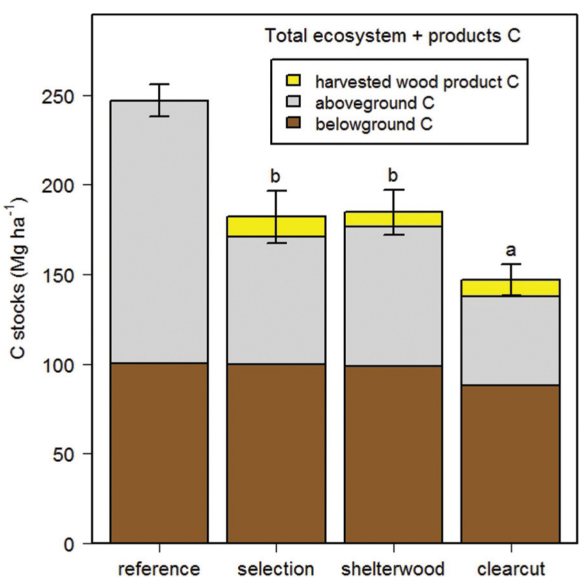
Table 2. The observed mean (standard deviation) and range of C stocks (Mg·ha^{-1}) on permanent plots by C pool and treatment.

	Treatment			
C pool	Reference (N = 4)	Selection (N = 10)	Shelterwood (N = 10)	Clearcut (N = 10)
Individual C pools				
Overstory*	168.6 (18.5)	84.5 (18.1)	93.2 (17.9)	60.3 (14.2)
	152.4–187.3	56.9–111.2	63.8–130.8	47.0–88.5
Understory	0.23 (0.18)	0.95 (0.51)	0.21 (0.12)	0.36 (0.16)
	0.02–0.43	0.42–1.86	0.04–0.48	0.10–0.66
CWD	13.0 (6.2)	3.3 (2.0)	3.8 (2.2)	1.8 (1.1)
	6.8–20.2	0.6–7.1	1.2–6.7	0.5–4.2
Stump–root systems	2.9 (1.4)	6.5 (1.9)	4.6 (1.2)	6.8 (1.6)
	1.9–4.9	3.8–10.3	3.1–7.0	3.8–8.8
Forest floor	16.9 (3.7)	27.8 (5.4)	23.7 (3.3)	22.1 (2.2)
	12.4–20.3	18.8–36.0	18.9–28.3	18.8–25.6
Mineral soil	45.3 (12.9)	47.7 (21.5)	51.1 (14.6)	46.2 (14.2)
	36.8–64.3	16.9–83.8	21.5–73.4	24.5–70.1
Harvested wood products	—	11.4 (3.0)	7.8 (4.3)	9.3 (2.5)
	—	7.3–18.0	1.8–13.8	5.3–12.6
Aggregated C pools				
Aboveground	146.5 (20.2)	70.9 (13.3)	77.9 (16.2)	49.7 (11.2)
	128.7–168.7	48.8–90.3	51.8–110.4	39.9–71.5
Belowground	100.4 (6.6)	99.9 (22.7)	98.8 (16.8)	87.8 (14.1)
	96.2–110.3	70.4–134.2	66.4–118.9	63.0–113.6
Total ecosystem	247.0 (17.7)	170.8 (33.5)	176.7 (25.6)	137.6 (19.6)
	226.8–267.3	132.5–218.0	142.0–229.3	103.6–169.4
Total ecosystem + products	247.0 (17.7)	182.2 (32.5)	184.5 (28.5)	146.9 (19.4)
	226.8–267.3	142.9–226.3	147.5–243.2	113.6–178.1

Note: N is the number of plots.

*Includes aboveground and belowground portions of live trees and shrubs except for fine roots.

Fig. 1. Mean and standard error of total ecosystem C plus C stored in harvested wood products (Mg·ha^{-1}). Different letters indicate significantly different least-squares means at the average relative volume of coarse fragments in the mineral soil (33.6%). Note that the reference was not included in pairwise comparisons tests. [This figure is available in colour online.]



14.0, and 38.0 ± 5.3 Mg·ha^{-1}, respectively. As noted previously, the commercial clearcut treatment as exploitive extraction was different from clearcutting as regeneration method in silviculture. The average stock of C in wood harvested from the managed stands ranged from 34.4 to 41.8 Mg·ha^{-1}. For C in wood harvested from 1950 to 2012, there were no statistical differences in C stocks among the managed treatments. For the selection, shelterwood, and commercial clearcut treatments, the average wood product C remaining in products or landfills in 2012 was estimated to be 29%, 20%, and 24%, respectively.

The best models of overstory, aboveground, total ecosystem, and total ecosystem + products C stocks included a forest management treatment effect and the relative volume of coarse fragments in the mineral soil as statistically significant fixed effects (P < 0.05) (Table 3). The overall models explained between 44% and 54% of the original variation in C stocks, while variation in C stocks between stands in which the same treatment was applied accounted for between <1 and 3.6% of the observed variance (Table 3). The relative volume of coarse fragments in the mineral soil was negatively correlated with these C stocks and explained much of the variation in C stocks between stands within treatments (Supplementary Table S3[1]). Also, pairwise comparisons indicated that the selection and shelterwood stands had higher C stocks than the commercial clearcut stands (P < 0.05), and C stocks were similar between the selection and shelterwood stands (Table 4). Depth to redoximorphic features, cartographic depth-to-water, and drainage class did not have significant influence on these C stocks.

The optimal model of understory C stocks included just a forest management treatment effect (P < 0.05), which explained 53% of the original variation in understory C stocks, and variation in C stocks between stands in which the same treatment was applied accounted for <1% of the observed variance. On average, the selection stands had higher understory C stocks than the shelterwood and commercial clearcut stands (P < 0.001 and P = 0.001), and understory C stocks were similar between the shelterwood and commercial clearcut stands (P = 0.515). The soil properties evaluated in this study did not have significant influence on understory, forest floor, stump–root system, or belowground C stocks.

Table 3. Model fit statistics for mixed-effects models of C pools that contained treatment (a_i) and the relative volume of coarse fragments in the mineral soil (CF; %, 0–100) as fixed effects and "stand" as a random effect (b_i).

C pool	Model of C stocks (Mg·ha⁻¹)	a_i (SE) Selection	Shelterwood	Clearcut	Slope SE	Marginal R^2	Conditional R^2	Residual SE (Mg·ha⁻¹)	b_i SE (Mg·ha⁻¹)
Overstory*	a_i – 0.394(CF) + b_i	98.5 (8.5)	104.9 (7.7)	74.4 (7.6)	0.185	0.523	0.540	15.586	3.028
Aboveground	a_i – 0.339(CF) + b_i	82.9 (6.7)	88.0 (5.9)	61.9 (5.8)	0.151	0.548	0.551	12.760	1.032
Total ecosystem	a_i – 0.706(CF) + b_i	195.8 (13.1)	197.6 (11.5)	162.9 (11.4)	0.290	0.444	0.454	24.514	3.137
Total ecosystem + products	a_i – 0.733(CF) + b_i	208.2 (13.1)	206.2 (11.3)	173.2 (11.2)	0.295	0.438	0.438	25.062	0.003

Note: TEC, total ecosystem C; SE, standard error.

*Includes aboveground and belowground portions of live trees and shrubs except for fine roots.

Table 4. Least-squares (LS) mean (standard error) C stocks (Mg·ha⁻¹) at the mean relative volume of coarse fragments in the mineral soil (33.6%) by C pool and treatment.

C pool	Treatment: Selection (N = 10)	Shelterwood (N = 10)	Clearcut (N = 10)
Overstory*	85.3 (5.4)b	91.6 (5.4)b	61.2 (5.4)a
Aboveground	71.5 (4.1)b	76.6 (4.1)b	50.5 (4.1)a
Total ecosystem	172.1 (8.1)b	173.9 (8.1)b	139.1 (8.1)a
Total ecosystem + products	183.5 (7.9)b	181.6 (8.0)b	148.5 (8.0)a

Note: Different letters indicate significant differences between LS mean C stocks among treatments at P < 0.05. N is the number of plots.

*Includes aboveground and belowground portions of live trees and shrubs except for fine roots.

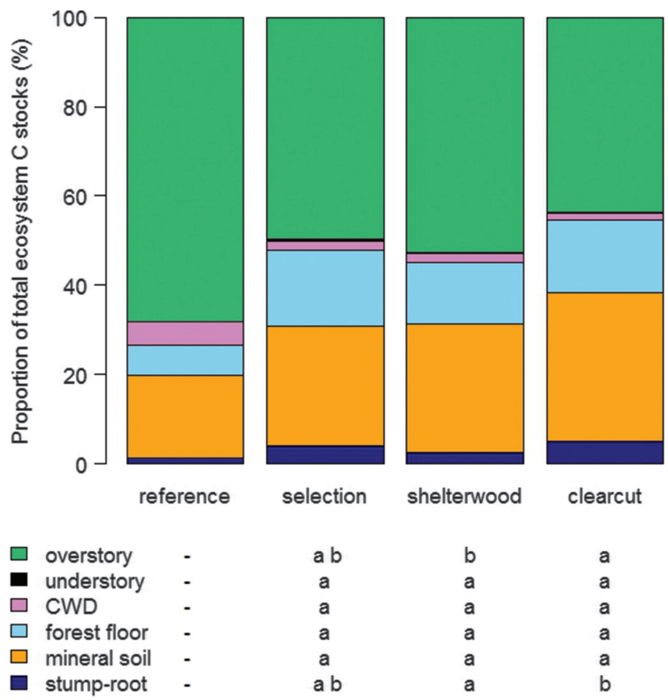
For forest floor, stump–root system, and belowground C stocks, likelihood ratio tests indicated that forest management treatment effect was not significant (P = 0.117, 0.081, and 0.302, respectively), and stand-level variation accounted for 46%, 31%, and 17% of the observed variance, respectively. For CWD C stocks, there was a weak interaction between treatment effect and depth to redoximorphic features (L = 5.741, P = 0.057). Also, there was an interaction between treatment effect and the relative volume of coarse fragments in the mineral soil (L = 7.141, P = 0.028) for mineral soil C stocks. In these models, stand-level variation accounted for 46% and 29% of the observed variance, respectively. The results suggested that there were no statistical differences in mean CWD or mineral soil C among the replicated treatments.

In the managed stands, the average relative contributions of the overstory, understory, CWD, forest floor, mineral soil, and stump–root system C stocks to total ecosystem C were 48.6%, 0.2%, 1.9%, 15.7%, 29.7%, and 3.9%, respectively (Fig. 2). The relative contribution of individual C stocks to total ecosystem C differed among treatments for the overstory and stump–root system C stocks (P < 0.05) but was not statistically different among treatments for other C stocks. Pairwise comparisons indicated that the shelterwood treatment had a higher proportion of overstory C than the commercial clearcut treatment (P = 0.005), and the proportion of overstory C was similar between the selection and shelterwood treatments (P = 0.508) and the selection and commercial clearcut treatments (P = 0.101). Pairwise comparisons also indicated that the shelterwood treatment had a lower proportion of stump–root system C than the commercial clearcut treatment (P = 0.010), and the proportion of stump–root system C was similar between the selection and shelterwood treatments (P = 0.117) and the selection and commercial clearcut treatments (P = 0.616).

Discussion

Average total ecosystem C storage differed among selection, shelterwood, and commercial clearcut treatments that were initiated nearly 60 years before our study was conducted on the PEF. However, it is important to consider that our inference concerning a forest management treatment effect was limited to two stands per treatment due to the study design established in 1950.

Fig. 2. Carbon storage in ecosystem pools expressed as a proportion of total ecosystem C stocks following nearly 60 years of management on the Penobscot Experimental Forest in Maine, USA. Different letters indicate significantly different least-squares means. Note that the reference was not included in pairwise comparisons tests, and the overstory C pool includes the aboveground and belowground portions of live trees and shrubs expect for fine roots. CWD, coarse woody debris. [This figure is available in colour online.]



Future strategies for addressing this constraint on the PEF include grouping stands with similar harvesting intensities and frequencies to potentially achieve better inference about C storage between broad categories of forest management treatments. For the specific treatments evaluated in this study, our findings indicate that certain practices such as selection cutting and shelterwoods may be better alternatives for maximizing total ecosystem C storage than commercial clearcutting. In this study, the commercial clearcut treatment involved the cutting of the most valuable trees, leaving many small-diameter and poor-quality trees. Hence, caution should be used when comparing our results with those of C storage in stands that were clearcut with the intention of establishing a new cohort of trees after all of the older trees were cut.

Also, average total ecosystem C stocks were 247.0 Mg·ha⁻¹ in the unmanaged reference stand compared with 161.7 Mg·ha⁻¹ in the managed stands. The average total ecosystem C stocks of the reference stand were similar to those reported for a 133-year-old aspen-dominated stand (approximately 230 Mg·ha⁻¹) (Bradford and Kastendick 2010) and for unmanaged northern hardwood stands (224 Mg·ha^{-1}) (Powers et al. 2011) in the North American Great Lakes region. In another study, Fahey et al. (2005) found that total ecosystem C stocks in a second-growth hardwood forest at Hubbard Brook in New Hampshire were 296 Mg·ha^{-1}. However, it is important to note differences among studies in the depth of soil sampling. For example, in this study, we sampled mineral soils to a depth of 1 m, whereas the previously mentioned studies sampled mineral soils to a depth of 30 cm (North American Great Lakes studies) or to the bottom of the B horizon (Hubbard Brook).

Our finding that commercial clearcutting results in less live-tree C storage, over the long term, than management treatments involving light, partial cutting is consistent with results from other studies (Nunery and Keeton 2010; Powers et al. 2011). In the commercial clearcut stands, most of the merchantable trees of good quality were cut, while poor-quality trees were often left uncut. High-graded stands such as the commercial clearcut stands on the PEF are common across the Acadian Forest region, which implies that C storage in live-tree biomass could be enhanced through the use of selection or shelterwood cutting as opposed to commercial clearcutting. Furthermore, the magnitude of the live-tree and shrub C pool was primarily responsible for differences in total ecosystem C stocks among treatments, which has also been found in other studies (Chatterjee et al. 2009; Mund and Schulze 2006; Powers et al. 2011). Specifically, the removal of many merchantable trees in the commercial clearcut stands during the 1980s partially explains the lower observed total ecosystem C storage compared with the other managed treatments. Also, while deadwood additions have been relatively similar among the managed stands since the 1950s (Puhlick et al. 2016*c*), the minimal amount of large-diameter trees that could be incorporated into deadwood pools in the commercial clearcut stands may result in lower total ecosystem C storage over time compared with other treatments.

Accounting for C storage in harvested wood products did not change our conclusions about differences in total C stocks between the replicated treatments. However, the high variability in harvested wood product C stocks between stands in which the same treatment was applied should be considered when interpreting our results. This variability is partially due to the timing of harvests and the species and sizes of trees harvested within stands. For instance, the timing of the second commercial clearcut influenced whether small-sized hardwood pieces were used for fuelwood or pulpwood. For the shelterwood treatment, a similar amount of total wood was harvested from each stand, but a higher proportion of softwood sawlogs were harvested from one stand (stand 29B). Because harvests in shelterwood stands occurred before the 1980s, the high amount of pulpwood-sized hardwood pieces in stand 23B were utilized as fuelwood and assumed to be combusted at the time of harvest. For the selection stands, the large amount of C remaining in wood products that were derived from recent harvests compensated for the lower amount of wood harvested during each stand entry compared with the other treatments.

The relative volume of coarse fragments in the mineral soil was negatively correlated with live-tree and shrub C stocks. A high percentage of coarse fragments in the mineral soil may limit biomass production, and hence C storage in live vegetation, by reducing the volume of the mineral soil fine earth fraction that could reduce the available nutrient supply (Childs and Flint 1990; Poesen and Lavee 1994). However, this assumes that the concentrations of available nutrients such as N, P, and Ca in the fine fraction of the mineral soil are not significantly influenced by coarse fragment content. This may not always be the case. For example, some studies have shown that C and essential nutrients become more concentrated in the fine fraction of the mineral soil as coarse fragment content increases (Childs and Flint 1990; Schaetzl 1991). However, in humid climates, coarse fragments increase the percolation rates of water through the mineral soil, resulting in the possibility that C and nutrients may be more likely to be leached to depths below the rooting zone (Schaetzl and Anderson 2005). This could partially explain the lack of correlation between the relative volume of coarse fragments in the mineral soil and mineral soil C concentration at our study site (Puhlick et al. 2016*a*). Nutrient and water availability were not evaluated.

The relative volume of coarse fragments in the mineral soil also explained most of the variation in overstory live-tree and shrub, aboveground, and total ecosystem C stocks between stands in which the same treatment was applied. Stands that had a higher percentage of coarse fragments had lower overstory, aboveground, and total ecosystem C stocks. An exception was for total ecosystem C stocks in the shelterwood stands, but these stands had, on average, similar percentages of coarse fragments (27.7% and 31.5%; Supplementary Table S3[1]). In some instances, the negative relationship between the relative volume of coarse fragments in the mineral soil and total ecosystem C stocks was partially due the mineral soil C pool. This was particularly true of the selection stands, where there was a strong negative correlation between the relative volume of coarse fragments in the mineral soil and mineral soil C stocks.

Overall, our results support the general conclusion made by Childs and Flint (1990) that sites with a lower percentage of coarse fragments tend to be more productive than similar soils with a higher percentage of coarse fragments. However, an important consideration is that our study was conducted on coarse-textured soils derived from glacial till. On fine-textured soils such as those derived from alluvial or marine parent material in Maine, the correlation between the relative volume of coarse fragments in the mineral soil and overstory C stocks may not be significant or could be positive (Childs and Flint 1990; Poesen and Lavee 1994). Hence, caution in interpreting the effects of the percentage of coarse fragments in the mineral soil should be used when working in areas with multiple parent materials and soil types. Our study also suggests that sites with a low percentage of coarse fragments would be favorable for C projects on glacial till and highlights the importance of considering sampling depth in the soil.

Differences in the relative contributions of the overstory and stump–root system C pools to total ecosystem C storage between treatments is likely due to intensity and timing of harvests within stands. The contribution of the overstory live-tree and shrub pool to total ecosystem C storage was higher in the shelterwood treatment than in the commercial clearcut treatment, likely because of the heavy harvests and more recent harvesting in the clearcut stands, which reduced live-tree and shrub biomass. However, the heavy and relatively recent harvests in the clearcut stands are partially responsible for the large contribution of the stump–root system pool to total ecosystem C storage in the clearcut stands. In the selection stands, frequent additions to the stump–root system pool through repeated harvesting are partially responsible for the similar contribution of this pool to total ecosystem C storage as in the commercial clearcut stands.

While our comparisons of C pools among forest management treatments were based on the quantification of stored C, it is also important to consider the influence of emissions during the harvest, transport, and manufacturing of wood products or wood combustion for energy on treatment comparisons. However, empirical data that could be used to calculate emissions are lacking for harvests on the PEF, especially at the plot level. Future studies based on model simulations could account for emissions from obtaining and manufacturing wood products as well as substitution and displacement effects, which could influence which treatment has the greater atmospheric CO_2 mitigation contribution. For example, Perez-Garcia et al. (2005) show that when displacement effects are accounted for, some forest management treatments can have a greater net reduction in atmospheric CO_2 than a protection strategy. Hence, while our study contributes information that can be used to make an assessment of C storage in forests and products, these factors alone do not indicate the net effect on atmospheric CO_2.

Also, studies of live-tree C sequestration since the 1950s on the PEF would be informative, but including emissions from deadwood would be challenging because individual dead trees have only recently been tracked on PSPs (since the 1990s). Furthermore, repeat measurements of other C pools (e.g., the forest floor and mineral soil) were not made over time. Another limitation of this study is that the PEF is just one study site in central Maine with limited replication and high variability, which suggests the need for additional long-term study sites in the region across a wider range of conditions. Despite these constraints, future analysis and projection of aboveground C sequestration at the PEF would improve our understanding of C dynamics in these and related forests. Finally, the ecological consequences of managing forests to reduce atmospheric CO_2 should also be considered when implementing forest management treatments. Certain silvicultural treatments may achieve multiple objectives, including C storage and promoting long-term ecological health and biodiversity, compared with exploitative practices, which have been shown to degrade stand conditions over time (Kenefic and Nyland 2005).

Conclusions

After nearly 60 years of forest management, average total ecosystem C storage was highest in the selection and shelterwood treatments and lowest in the commercial clearcut treatment. Adding C stored in harvested wood products to current total ecosystem C stocks did not change our conclusions about observed differences in C stocks among these treatments. However, there was significant variation in C storage between stands in which the same treatment was applied that may be partially due to the timing of harvests, differences in species composition, the size of trees harvested within stands, and inherent differences in potential productivity. Stands with a higher proportion of soil volume in coarse fragments tended to have lower total ecosystem C stocks, highlighting the importance of this site-quality variable in ecosystem C budgets.

Overall, this study highlights the importance of using certain forest management practices as opposed to commercial clearcutting when objectives include maximizing C storage in forests. This study could serve as a baseline for future measurements of forest ecosystem C pools in this experimental forest, and the data can be used to validate model projections of C storage. This study also highlights the long-term impacts of long-term forest management treatments and demonstrates the continued usefulness of long-term field data. Additional research is needed to better understand the potential interaction between forest management, total ecosystem C pools, and climate across a broader range of forest types and management.

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References

Bradford, J.B., and Kastendick, D.N. 2010. Age-related patterns of forest complexity and carbon storage in pine and aspen–birch ecosystems of northern Minnesota, USA. Can. J. For. Res. **40**(3): 401–409. doi:10.1139/X10-002.

Brissette, J.C., and Kenefic, L.S. 2014. Centerpiece of research on the Penobscot Experimental Forest: the US Forest Service long-term silvicultural study. *In* Penobscot Experimental Forest: 60 years of research and demonstration in Maine, 1950–2010. *Edited by* L.S. Kenefic and J.C. Brissette. USDA Forest Service Gen. Tech. Rep. NRS-P-123.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service Gen. Tech. Rep. INT-16.

Chatterjee, A., Vance, G.F., and Tinker, D.B. 2009. Carbon pools of managed and unmanaged stands of ponderosa and lodgepole pine forests in Wyoming. Can. J. For. Res. **39**(10): 1893–1900. doi:10.1139/X09-112.

Childs, S.W., and Flint, A.L. 1990. Physical properties of forest soils containing rock fragments. *In* Sustained productivity of forest soils. Proceedings of the 7th North American Forest Soils Conference. *Edited by* S.P. Gessel, D.S. Lacate, G.F. Weetman, and R.F. Powers. University of British Columbia, Faculty of Forestry Publication, Vancouver, B.C. pp. 95–121.

D'Amato, A.W., Bradford, J.B., Fraver, S., and Palik, B.J. 2011. Forest management for mitigation and adaptation to climate change: insights from long-term silviculture experiments. For. Ecol. Manage. **262**(5): 803–816. doi:10.1016/j.foreco.2011.05.014.

Fahey, T.J., Siccama, T.G., Driscoll, C.T., Likens, G.E., Campbell, J., Johnson, C.E., Battles, J.J., Aber, J.D., Cole, J.J., Fisk, M.C., Groffman, P.M., Hamburg, S.P., Holmes, R.T., Schwarz, P.A., and Yanai, R.D. 2005. The biogeochemistry of carbon at Hubbard Brook. Biogeochemistry, **75**(1): 109–176. doi:10.1007/s10533-004-6321-y.

Fraver, S., Ringvall, A., and Jonsson, B.G. 2007. Refining volume estimates of down woody debris. Can. J. For. Res. **37**(3): 627–633. doi:10.1139/X06-269.

Graves, S., Piepho, H.P., Selzer, L., and Dorai-Raj, S. 2012. multcompView: visualizations of paired comparisons. R package version 0.1-5 [online]. Available from http://CRAN.R-project.org/package=multcompView.

Guldin, J.M. 1991. Uneven-aged BDq regulation of Sierra Nevada mixed conifers. J. For. **89**(9): 29–36.

Halliday, W.E.D. 1937. A forest classification for Canada. Department of Mines and Resources, Lands, Parks and Forests Branch, Dominion Forest Service, Ottawa, Ontario, Bulletin No. 89.

Harmon, M.E., and Marks, B. 2002. Effects of silvicultural practices on carbon stores in Douglas-fir western hemlock forests in the Pacific Northwest, USA: results from a simulation model. Can. J. For. Res. **32**(5): 863–877. doi:10.1139/x01-216.

Harmon, M.E., Woodall, C.W., Fasth, B., and Sexton, J. 2008. Woody detritus density and density reduction factors for tree species in the United States: a synthesis. USDA Forest Service Gen. Tech. Rep. NRS-29.

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., and Yatkov, M. 2011. Differences between standing and downed dead tree wood density reduction factors: a comparison across decay classes and tree species. USDA Forest Service Res. Pap. NRS-15.

Husch, B., Beers, T., and Kershaw, J.A., Jr. 2003. Forest mensuration. John Wiley & Sons, Inc., Hoboken, N.J., USA.

Kenefic, L.S., and Brissette, J.C. 2014. History of the Penobscot Experimental Forest, 1950–2010. *In* Penobscot Experimental Forest: 60 years of research and demonstration in Maine, 1950–2010. *Edited by* L.S. Kenefic and J.C. Brissette. USDA Forest Service Gen. Tech. Rep. NRS-P-123.

Kenefic, L.S., and Nyland, R.D. 2005. Diameter-limit cutting and silviculture in northeastern forests: a primer for landowners, practitioners, and policy makers. USDA Forest Service, Northeastern Area State and Private Forestry Publication NA-TP-02-05.

Keyser, T.L. 2010. Thinning and site quality influence aboveground tree carbon stocks in yellow-poplar forests of the southern Appalachians. Can. J. For. Res. **40**(4): 659–667. doi:10.1139/X10-013.

Lamlom, S.H., and Savidge, R.A. 2003. A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass Bioenergy, **25**(4): 381–388. doi:10.1016/S0961-9534(03)00033-3.

Lenth, R.V. 2014. lsmeans: least-squares means. R package version 2.13 [online]. Available from http://CRAN.R-project.org/package=lsmeans.

Li, R., Weiskittel, A., Dick, A.R., Kershaw, J.A., and Seymour, R.S. 2012. Regional stem taper equations for eleven conifer species in the Acadian Region of North America: development and assessment. North. J. App. For. **29**(1): 5–14. doi:10.5849/njaf.10-037.

Maine Association of Professional Soil Scientists. 2002. Key for the identification of soil drainage class. Maine Association of Professional Soil Scientists (MAPSS). Available from http://www.mapss.org/catena&drain.htm.

McKinley, D.C., Ryan, M.G., Birdsey, R.A., Giardina, C.P., Harmon, M.E., Heath, L.S., Houghton, R.A., Jackson, R.B., Morrison, J.F., Murray, B.C., Pataki, D.E., and Skog, K.E. 2011. A synthesis of current knowledge on forests and carbon storage in the United States. Ecol. Appl. **21**(6): 1902–1924. doi:10.1890/10-0697.1. PMID:21939033.

Melin, Y., Petersson, H., and Nordfjell, T. 2009. Decomposition of stump and root systems of Norway spruce in Sweden — a modelling approach. For. Ecol. Manage. **257**(5): 1445–1451. doi:10.1016/j.foreco.2008.12.020.

Miles, P.D., and Smith, W.B. 2009. Specific gravity and other properties of wood and bark for 156 tree species found in North America. USDA Forest Service Res. Note NRS-38.

Mund, M., and Schulze, E.-D. 2006. Impacts of forest management on the carbon budget of European beech (*Fagus sylvatica*) forests. Allg. Forst- Jagdztg. **177**(3–4): 47–63.

Murphy, P.N.C., Ogilvie, J., Meng, F.-R., White, B., Bhatti, J.S., and Arp, P.A. 2011. Modelling and mapping topographic variations in forest soils at high resolution: a case study. Ecol. Model. **222**(14): 2314–2332. doi:10.1016/j.ecolmodel.2011.01.003.

Nunery, J.S., and Keeton, W.S. 2010. Forest carbon storage in the northeastern United States: net effects of harvesting frequency, post-harvest retention, and wood products. For. Ecol. Manage. **259**(8): 1363–1375. doi:10.1016/j.foreco.2009.12.029.

Olson, M.G., and Wagner, R.G. 2010. Long-term compositional dynamics of Acadian mixedwood stands under different silvicultural regimes. Can. J. For. Res. **40**(10): 1993–2002. doi:10.1139/X10-145.

Perez-Garcia, J., Lippke, B., Comnick, J., and Manriquez, C. 2005. An assessment of carbon pools, storage, and wood products market substitution using life-cycle analysis results. Wood Fiber Sci. **37**: 140–148.

Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., and R Core Team. 2014. nlme: Linear and nonlinear mixed effects models. R package version 3.1-117 [online]. Available from http://CRAN.R-project.org/package=nlme.

Poesen, J., and Lavee, H. 1994. Rock fragments in top soils: significance and processes. Catena, **23**(1–2): 1–28. doi:10.1016/0341-8162(94)90050-7.

Powers, M., Kolka, R., Palik, B., McDonald, R., and Jurgensen, M. 2011. Long-term management impacts on carbon storage in Lake States forests. For. Ecol. Manage. **262**(3): 424–431. doi:10.1016/j.foreco.2011.04.008.

Profft, I., Mund, M., Weber, G.-E., Weller, E., and Schulze, E.-D. 2009. Forest management and carbon sequestration in wood products. Eur. J. For. Res. **128**(4): 399–413. doi:10.1007/s10342-009-0283-5.

Puhlick, J.J. 2015. How silvicultural treatments and site quality affect carbon storage on the Penobscot Experimental Forest: a 60-year perspective. Ph.D. dissertation, School of Forest Resources, University of Maine, Orono, Maine.

Puhlick, J.J., Fernandez, I.J., and Weiskittel, A.R. 2016*a*. Evaluation of forest management effects on the mineral soil carbon pool of a lowland, mixed-species forest in Maine, USA. Can. J. Soil Sci. **96**(2): 207–218. doi:10.1139/cjss-2015-0136.

Puhlick, J.J., Fraver, S., Fernandez, I.J., Weiskittel, A.R., Kenefic, L.S., Kolka, R.K., and Gruselle, M.-C. 2016*b*. Factors influencing organic-horizon carbon pools in mixed-species stands of central Maine, USA. For. Ecol. Manage. **364**: 90–100. doi:10.1016/j.foreco.2016.01.009.

Puhlick, J.J., Weiskittel, A.R., Fraver, S., Russell, M.B., and Kenefic, L.S. 2016*c*. 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. **46**(9): 1092–1102. doi:10.1139/cjfr-2016-0177.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org.

Russell, M.B., and Weiskittel, A.R. 2012. Assessing and modeling snag survival and decay dynamics for the primary species in the Acadian forest of Maine, USA. For. Ecol. Manage. **284**: 230–240. doi:10.1016/j.foreco.2012.08.004.

Schaetzl, R.J. 1991. Factors affecting the formation of dark, thick epipedons beneath forest vegetation, Michigan, USA. J. Soil Sci. **42**(3): 501–512. doi:10.1111/j.1365-2389.1991.tb00426.x.

Schaetzl, R.J., and Anderson, S. 2005. Soils genesis and geomorphology. Cambridge University Press, Cambridge, UK.

Sendak, P.E., Brissette, J.C., and Frank, R.M. 2003. Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest. Can. J. For. Res. **33**(11): 2116–2128. doi:10.1139/x03-140.

Skog, K.E. 2008. Sequestration of carbon in harvested wood products for the United States. For. Prod. J. **58**(6): 56–72.

Skovsgaard, J.P., and Vanclay, J.K. 2013. Forest site productivity: a review of spatial and temporal variability in natural site conditions. Forestry, **86**(3): 305–315. doi:10.1093/forestry/cpt010.

Smith, J.E., Heath, L.S., Skog, K.E., and Birdsey, R.A. 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. USDA Forest Service Gen. Tech. Rep. NE-343.

UNB Forest Watershed Research Center. 2014. Cartographic depth-to-water mapping using latest DEM coverage for CFRU priority areas. University of New Brunswick, Fredericton, New Brunswick.

White, B., Ogilvie, J., Campbell, D.M.H., Hiltz, D., Gauthier, B., Chisholm, H.K., Wen, H.K., Murphy, P.N.C., and Arp, P.A. 2012. Using the cartographic depth-to-water index to locate small streams and associated wet areas across landscapes. Can. Water Resour. J. **37**(4): 333–347. doi:10.4296/cwrj2011-909.

Young, H.E., and Carpenter, P.M. 1967. Weight, nutrient element and productivity of seedlings and saplings of eight tree species in natural ecosystems. Maine Agriculture Experiment Station Tech. Bull. 28.

Young, H.E., Ribe, J.H., and Wainwright, K. 1980. Weight tables for tree and shrub species in Maine. University of Maine, Life Sciences and Agriculture Experiment Station Misc. Rep. 230.