Forest Ecology and Management 364 (2016) 90–100

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Factors influencing organic-horizon carbon pools in mixed-species stands of central Maine, USA

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ARTICLE INFO

Article history:
Received 4 August 2015
Received in revised form 7 January 2016
Accepted 11 January 2016

Keywords:
Silviculture
Forest soil
Forest floor
Carbon storage
Bryophytes
Pedotransfer functions

ABSTRACT

The overall goal of this study was to evaluate the correlation of multiple abiotic and biotic factors with organic-horizon (O-horizon) carbon (C) content on the Penobscot Experimental Forest in central Maine, USA. O-horizon samples were collected and their associated depths were recorded from stands managed with a range of silvicultural and harvesting treatments (i.e., selection, shelterwood, and commercial clearcut) and an unmanaged control. The overall mean for O-horizon C content from all samples was 25.6 ± 16.1 Mg ha^{-1} (mean ± SD). The samples were used to develop a pedotransfer function for predicting O-horizon C content from O-horizon depth (R^2 = 0.47, RMSE = 1.6 Mg ha^{-1}) so that an average of O-horizon C content could be calculated for permanent sample plots on which abiotic and biotic factors were quantified. O-horizon depth measurements recorded along transects on permanent sample plots were used to calculate plot average O-horizon C content. There were no significant differences in average predicted O-horizon C content among selection, shelterwood, and commercial clearcut treatments. However, variation in predicted O-horizon C content between stands where the same treatment was applied was statistically significant and was likely due to the timing of harvests and abundance of dead wood buried within O horizons. Depth to redoximorphic features, cartographic depth to water table or saturated zone, drainage class, fine woody debris mass, downed woody debris volume, tree basal area, and the relative basal area of conifer species were not significant predictors of predicted O-horizon C content at the plot level. When the individual predicted values of O-horizon C content were modeled, within-plot variation accounted for 83.8% of the variance. Bryophyte mass, which was predicted from bryophyte cover, only explained 1.2% of the variation in O-horizon C content at the microsite level. These results highlight the sizeable variability in O-horizon C content within and among these mixed-species stands with various forest management and natural disturbance histories.

1. Introduction

Forests play an essential role in the global carbon (C) cycle because of their ability to sequester large amounts of C from the atmosphere. Pan et al. (2011) estimated that the world's forests accumulated 1.1 ± 0.8 Pg C year^{-1} for 1990–2007 and C storage in forests was 861 ± 66 Pg C in 2007. One sizeable forest C pool is that of the soil organic (O) horizon. Also referred to as the forest floor in some studies, O horizons are dominated by organic material in various stages of decomposition and often overlie mineral soil horizons. In forests and woodlands of the Northern Hemisphere, Goodale et al. (2002) estimated that 28 Pg C was contained in the forest floor compared to 83 Pg C in live vegetation. Carbon balance in USA forests indicates a net C sink and is primarily driven by tree biomass and wood products (i.e., forest management) and woody encroachment of former non-forested lands (Pacala et al., 2001).

In the USA, Heath et al. (2011) used a modeling approach (Smith and Heath, 2002) to estimate that forestlands contained 4.9 Pg C in the forest floor in 2008. Woodall et al. (2012) used data from soil samples across USA forests to estimate that median forest floor C was 25.6 Mg ha^{-1}. However, there was high spatial variability in these estimates. Hence, an improved understanding of the

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http://dx.doi.org/10.1016/j.foreco.2016.01.009
0378-1127/

numerous factors that control the magnitude of this pool would inform strategies for maintaining or enhancing C storage in forest soils. Also, collecting and processing O-horizon samples to determine C content can be time consuming and expensive, so alternative methods for quantifying O-horizon C content are needed.

In soil science, pedotransfer functions are used to predict hard-to-measure soil properties from properties that are less difficult to measure or more often available (Wosten et al., 1999; Cornelis et al., 2001; Schwarzel et al., 2009). Tremblay et al. (2002) developed pedotransfer functions for predicting forest floor C content in upland forests of Quebec, Canada. Predictor variables included O-horizon depth, latitude, longitude, and mean growing season precipitation. In plant ecology, similar functions have been developed to predict bryophyte and lichen mass in Finland (Muukkonen et al., 2006). In that study, the percentage of bryophyte and lichen cover was found to be a significant predictor of bryophyte and lichen mass. Estimates of O-horizon C content and bryophyte mass that are made at the same locations could be used to examine the correlation between these variables. While the influence of bryophytes on O-horizon C content in boreal ecosystems has been well documented (Harden et al., 1997; Turetsky, 2003; Turetsky et al., 2010), less is known about the correlation between these variables in temperate broadleaf and mixed-species forests that are in transitional zones between deciduous forests to the south and boreal forests to the north.

In addition to bryophytes, a number of other factors are known to control the magnitude of O-horizon C content. For example, Nave et al. (2010) found that timber harvesting caused forest floor C content to decline by an average of 30% across a range of soil types. Such declines have been attributed to enhanced mixing of O-horizon materials into the mineral soil horizons (Yanai et al., 2003), losses due to erosion (Elliot, 2003), leaching of dissolved organic C (Kalbitz et al., 2000), and accelerated decomposition (Covington, 1981). After harvesting, decomposition of forest floor C can be temporarily stimulated by warmer and possibly wetter soil conditions due to reduced evapotranspiration (Jandl et al., 2007). Other studies have found that forest floor C content increases after harvesting due to a reduction in soil biotic activity and moisture content, which reduce decomposition rates of surface litter (Lal, 2005). Aside from changes in the microclimate, litterfall is reduced in heavily thinned stands, which reduces the accumulation of organic materials in the forest floor (Jandl et al., 2007). Harvesting that minimizes forest floor disturbance can maintain pre-harvest C pools, and harvest residues left on site may compensate for any post-harvest reductions in litter input (Yanai et al., 2003; Lal, 2005; Jandl et al., 2007).

Timber harvesting can also influence O-horizon C content through alterations in tree species composition, bryophyte species composition and abundance, and dead wood C pools. Tree species composition can affect O-horizon C content through its influence on litter quality (Rustad and Cronan, 1988; Delaney et al., 1996; Finzi and Canham, 1998; Vesterdal et al., 2013). O-horizon mass, and hence its C content, is influenced by the balance between litter inputs and litter decomposition. Litter decomposition is known to vary according to environmental factors (e.g., climate and soil properties), litter quality, and the decomposer community (e.g., activity and composition) (Berg et al., 1993). The litter of several hardwood species can decrease bryophyte mass through chemical interactions or through smothering (Saetre et al., 1997; Fenton et al., 2005; Légaré et al., 2005), which, in turn, can affect O-horizon C content. Generally, bryophytes buffer the O horizon from atmospheric climate extremes due to their low thermal conductivity, high porosity, and significant water holding capacity (Turetsky, 2003; Startsev et al., 2007). This buffer creates a cool, moist environment that slows decomposition of dead wood and other organic material (Hagemann et al., 2010). Dead wood is a potential source of high C concentration material that can be incorporated into the O horizon as it decomposes, and when buried within the O horizon it can persist there for decades (McFee and Stone, 1966; Hagemann et al., 2009).

Despite information relating abiotic and biotic factors to O-horizon C, much remains unknown about the influence of factors that control the magnitude of this pool in mixed-species forests with complex age structures, which result from repeated partial harvesting or low- to moderate-severity natural disturbances. Most research on quantifying O-horizon C content has taken place during or following the use of even-aged silvicultural systems (Johnson et al., 1991; Pregitzer and Euskirchen, 2004) and/or in nearly pure softwood- and hardwood-dominated forests (Parker et al., 2001; Hobbie et al., 2007; Diochon et al., 2009; Raymond et al., 2013). Of the studies that have investigated O-horizon C content in mixed-species forests, Berger et al. (2002) found that pure stands of Norway spruce (*Picea abies* (L.) Karst.) stored more C in the forest floor compared to mixed-species stands, which were mainly composed of Norway spruce and European beech (*Fagus sylvatica* L.).

Our overall goal was to evaluate the correlation of the above-mentioned factors with O-horizon C content in a mixed-species forest with several long-term silvicultural and harvesting experiments, maintained since the 1950s. Our objectives were to: (1) develop pedotransfer functions to predict O-horizon C content and bryophyte mass from field measurements of O-horizon depth and bryophyte cover; (2) compare the predicted O-horizon C content among selection, shelterwood, and commercial clearcut treatments; (3) determine the correlation between predicted O-horizon C content and factors other than silvicultural and harvesting treatment; (4) assess the variation in predicted O-horizon C content attributable to within-plot differences. We hypothesized that: (1) average predicted O-horizon C content would be lowest in stands that had been treated with commercial clearcutting due to a shift in species composition toward more early successional species (mainly hardwoods); (2) predicted O-horizon C contents would be highest for locations with poor drainage within stands due to slower decomposition rates of organic material associated with anaerobic conditions; (3) predicted O-horizon C contents would be highest for stands with high amounts of bryophytes and woody debris, and high proportions of conifer basal area; (4) within-plot variation in predicted O-horizon C content would be high due to factors such as pit-and-mound microtopography and buried wood abundance.

2. Methods

2.1. 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). Tree species composition is diverse and includes balsam fir (*Abies balsamea* (L.) Mill), red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* (L.) Carriere), 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 U.S. Department of Agriculture, 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 forest management treatment was assigned to two experimental units (referred to as stands in this study) ranging from 7 to 18 ha in size. In each stand, 8–21 permanent sample

Table 1
Mean (and standard deviation) and range of forest attributes on permanent plots by treatment. Data are from measurements of trees ⩾1.3 cm diameter at breast height.

Attribute	Treatment			
	Reference	5-year selection	3-stage shelterwood	Commercial clearcut
Number of plots	10	32	16	27
Tree density	833 (287)	3538 (2125)	8162 (3219)	7583 (4208)
(trees ha^{-1})	432–1359	507–8093	3897–15,333	3286–24,871
QMD	29.3 (5.7)	12.5 (4.7)	9.0 (1.6)	7.6 (1.3)
(cm)	20.6–40.6	7.6–27.5	5.9–11.7	4.6–9.9
Total basal area	51.9 (6.1)	32.0 (5.4)	47.6 (8)	31.1 (6)
(m^2 ha^{-1})	45.3–60.5	20.6–42.1	33.7–65.3	21–40.5
Conifer basal area	89.3 (7.8)	89.2 (8)	87.8 (11.4)	58.3 (21.3)
(% of total basal area)	73.4–98.4	65–100	51.6–97.9	18.3–87.5

QMD, quadratic mean diameter.

plots (PSPs) were systematically located and established for measuring trees and other forest attributes. The PSPs consist 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) are measured on the entire 0.08-ha plot, trees ⩾6.4 cm are measured on the 0.02-ha plot, and trees ⩾1.3 cm are measured on the 0.008-ha plot.

For the present study, the O-horizon C pool was 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; all merchantable trees were removed without stand tending or attention to regeneration. This study made use of one reference area (stand 32B) as a control. 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 may contribute to between-stand variation of forest attributes at any given point in time.

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 Forest Service's silvicultural experiment began in the 1950s, tree species composition in the stands used for the present study was largely eastern hemlock, balsam fir, red spruce, hardwoods (mostly red maple (*Acer rubrum* L.)), and other softwoods (mostly northern white-cedar) (Sendak et al., 2003). Eastern white pine was a minor component of the stands (<10% of BA), except in the reference (20%). The stands were irregularly uneven-aged, with relatively low stem density in the larger size classes (Sendak et al., 2003; Kenefic and Brissette, 2014). Since the 1950s, stem-only harvesting (tree tops and branches cut from the tree bole and left on site) has been primarily conducted and is usually confined to the winter months. Logging equipment varied since 1950 as technology changed, starting with horse logging and progressing to cut-to-length harvesters with forwarders. Most stands were harvested using chainsaws and rubber-tired skidders. Current stand attributes for areas associated with this study are shown in Table 1.

This study was conducted on soils derived from glacial till parent material. Soils that occupy upland positions include 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) (Natural Resources Conservation Service, 2012). Soils derived from glacial till that occupy lower positions include loamy, mixed, active, acid, frigid, shallow Aeric Endoaquepts (Monarda series) and loamy, mixed, superactive, nonacid, frigid, shallow Histic Humaquepts (Burnham series). According to the Natural Resources Conservation Service (2012) second-order soil maps, all of these soil series occur in each of the treatments that were evaluated in this study, except for the reference stand, which only includes the Plaisted series. Pit-and-mound microtopography, which is predominately formed by tree uprooting and results in variation in hydrologic conditions and litter accumulation at the scale of a few meters or less (Hazlett et al., 2011), is common across the PEF.

2.2. Data collection

2.2.1. Collection of O-horizon and bryophyte samples

In mid-July through August 2012, one O-horizon sample was collected 3 m outside of 74 PSPs on glacial till parent material. Two additional samples were collected from outside of 9 of these PSPs, before it was determined that only one sample from each PSP could be collected during the field season with the available resources. O-horizon samples were collected using a circular, 30-cm diameter sampling frame after understory plants were clipped from above the forest floor. All woody debris at the surface of the forest floor was also removed from the sampling frame. O-horizon depth was measured at four equally spaced locations along the edge of the sampling frame, and an average depth was used in the analysis (see Section 2.3.1. Pedotransfer functions). The portion of the O horizon that could be easily removed using a brush with fine bristles was collected as the O_i horizon, and the remaining O horizon was collected as the O_e and O_a horizon. The boundary between the O_a horizon and the mineral soil was relatively easy to distinguish because an E horizon, which was light-gray in color compared to the dark-brown O_a horizon with distinct and abrupt boundaries, was usually present below the O horizon of these soils. Furthermore, the chemical properties of the $O_e + O_a$ fine fractions (Tables 2 and 3) were similar to those reported in other studies (e.g., Fernandez, 2008), suggesting that incorporation of mineral soil in the O-horizon samples was likely nominal.

Samples were brought to the laboratory and stored in a temperature controlled room at 65 °C until they could be oven-dried. O_i samples were dried to constant mass at 65 °C in a convection oven and weighed. Subsamples of the O_i materials were then ground to 0.85 mm using a Thomas-Wiley laboratory mill and analyzed for percent total C (TC) and percent total N (TN) concentrations by combustion analysis at 1350 °C using a LECO CN-2000 analyzer

Table 2
Mean (and standard deviation) of attributes associated with components from 32 O horizons (4, 9, 10, and 9 from the reference, selection, shelterwood, and commercial clearcut, respectively) that were processed after being air-dried in 2013. $O_e + O_a$ charcoal (⩾6.4 mm) was sorted from samples, but not analyzed for total C (TC). The number of samples is in italics.

O-horizon component	Treatment			
	Reference	5-year selection	3-stage shelterwood	Commercial clearcut
O_i non-woody materials	*4*	*9*	*10*	*9*
TC (%)	50.0 (2.9)	50.2 (2.4)	51.6 (0.5)	50.3 (1.0)
C:N ratio	38.8 (0.9)	38.8 (3.1)	37.9 (3.3)	32.4 (3.5)
Relative contribution (%)[a]	36.7 (22.3)	20.3 (10.5)	22.4 (12.3)	21.7 (8.7)
O_i buried wood	*4*	*7*	*10*	*9*
TC (%)	51.7 (1.3)	49.4 (1.9)	51.4 (0.6)	50.2 (1.3)
C:N ratio	74.9 (6.8)	87.7 (31.3)	61.5 (8.6)	57.0 (12.3)
Relative contribution (%)	2.3 (1.4)	0.3 (0.3)	1.1 (0.8)	1.5 (1.0)
$O_e + O_a$ fines	*4*	*9*	*10*	*9*
TC (%)	45.4 (2.5)	41.9 (5.3)	43.3 (5.6)	39.0 (7.8)
C:N ratio	31.8 (2.6)	33.3 (5.9)	35.4 (6.3)	29.3 (3.1)
Relative contribution (%)	52.1 (28.3)	58.5 (10.7)	55.7 (8.6)	58.2 (7.5)
$O_e + O_a$ PDL	*2*	*7*	*9*	*3*
TC (%)	52.8 (1.3)	51.5 (2.1)	51.5 (1.4)	50.5 (1.7)
C:N ratio	36.8 (2.2)	41.7 (10.7)	34.2 (5.8)	32.0 (4.3)
Relative contribution (%)	0.8 (1.0)	3.5 (3.9)	1.8 (2.5)	0.2 (0.2)
$O_e + O_a$ roots	*4*	*9*	*10*	*9*
TC (%)	51.6 (0.6)	50.3 (0.6)	50.4 (0.7)	49.6 (0.5)
C:N ratio	84.6 (33.4)	112.2 (40.1)	96.0 (27.4)	91.3 (22.1)
Relative contribution (%)	1.0 (0.5)	9.0 (9.2)	8.8 (7.9)	10.2 (7.5)
$O_e + O_a$ buried wood	*4*	*9*	*10*	*9*
TC (%)	54.6 (1.6)	52.4 (2.2)	52.7 (2.2)	51.9 (2.4)
C:N ratio	82.8 (30.3)	90.9 (27.4)	67.1 (19.1)	61.0 (17.6)
Relative contribution (%)	7.1 (5.2)	8.3 (6.1)	9.5 (6.8)	6.3 (7.9)

[a] Relative contribution of the component to the total O-horizon C content; PDL, partially decomposed litter.

Table 3
Mean (and standard deviation) of attributes associated with components from 92 O horizons (10, 43, 17, and 22 from the reference, selection, shelterwood, and commercial clearcut, respectively) that were processed after being oven-dried in 2012. $O_e + O_a$ charcoal (⩾6.4 mm) was sorted from samples, but not analyzed for total C (TC). The number of samples is in italics.

O-horizon component	Treatment			
	Reference	5-year selection	3-stage shelterwood	Commercial clearcut
O_i materials	*10*	*43*	*17*	*22*
TC (%)	49.0 (4.9)	50.4 (1.3)	51.7 (0.7)	50.8 (1.1)
C:N ratio	39.4 (3.8)	40.7 (6.5)	37.9 (3.0)	35.3 (4.5)
Relative contribution (%)[a]	49.3 (31.9)	18.5 (9.9)	21.7 (11.0)	16.3 (10.9)
$O_e + O_a$ fines	*10*	*43*	*17*	*22*
TC (%)	45.6 (5.3)	44.7 (4.9)	45.2 (6.0)	45.0 (6.4)
C:N ratio	32.6 (2.9)	33.7 (5.0)	34.4 (6.3)	35.9 (9.3)
Relative contribution (%)	47.1 (29.6)	72.0 (9.7)	70.5 (9.0)	74.5 (9.3)
$O_e + O_a$ roots	*6*	*40*	*16*	*18*
TC (%)	48.5 (0.7)	49.6 (1.2)	50.3 (0.6)	48.1 (0.8)
C:N ratio	70.0 (9.3)	112.2 (30.0)	95.5 (16.3)	123.0 (29.7)
Relative contribution (%)	0.9 (1.6)	4.3 (4.1)	3.4 (3.2)	5.0 (4.6)
$O_e + O_a$ buried wood	*8*	*40*	*17*	*21*
TC (%)	52.7 (2.3)	50.6 (2.3)	52.4 (2.1)	52.5 (2.4)
C:N ratio	85.6 (28.0)	72.4 (26.9)	80.2 (24.5)	83.0 (33.7)
Relative contribution (%)	2.6 (2.8)	4.7 (6.4)	3.6 (2.7)	4.0 (4.3)

[a] Relative contribution of the component to the total O-horizon C content.

(LECO Corp.). The $O_e + O_a$ samples were oven-dried to constant mass at 65 °C and sieved through a 6.4 mm screen to separate fine from coarse fractions. Coarse organic fractions were further sorted into roots, buried wood, coarse charcoal, and residual organic material. All of the $O_e + O_a$ components were weighed, and subsamples were ground and analyzed for percent total C and total N using the same methods as the Oi, with the exception of coarse charcoal. For coarse charcoal, we used an estimate of 80% C concentration based on research of charcoal derived from live trees and downed woody debris after wildfire (Tinker and Knight, 2000; Forbes et al., 2006). For each $O_e + O_a$ component, C content was calculated by multiplying the component's oven-dry mass by its total C concentration. For each sample location, the O_i and $O_e + O_a$ component C contents were summed to derive total O-horizon C content.

In mid-July through August 2013, we also collected one O-horizon sample from outside 4–5 PSPs in each stand for total C, total N, and pH analysis on the $O_e + O_a$ fine fractions. The pH analysis required different methods for processing O-horizon samples than those used in 2012, but the differences in methodologies did not affect estimates of total O-horizon C content between years. Hence, O-horizon samples from both years ($n = 124$) were used in subsequent analyses. The subset of plots from which samples were collected in 2013 was selected in a random, stratified process, with stratification according to the proportion of major soil types on glacial till within each stand. For the O_i materials, fine woody debris (FWD) buried in the O_i horizon was separated from other materials. Both O_i components were dried to constant mass at 65 °C in a convection oven and weighed. Subsamples of the O_i components were then ground and analyzed for total C and total N as in 2012. For the $O_e + O_a$ materials, samples were air-dried in a greenhouse before components were separated. Subsamples of the air-dried fine fractions were taken to determine moisture content, which was used to express fine fraction mass on an oven-dry basis. Subsamples were also used to determine pH, which was measured with an electrode using a 1:5 ratio of deionized water to O-horizon fine fractions. Coarse organic fraction components were separated by roots, buried wood, partially decomposed litter (cone scales and relatively undecomposed hardwood leaves), and coarse charcoal. Coarse roots, buried wood, and partially decomposed litter were oven-dried and weighed, and subsamples were ground for total C and total N analysis.

In mid-July through August 2013, bryophytes were clipped and collected from 0.25-m^2 quadrats before the O horizon was sampled. Additional bryophyte samples were collected from some PSPs to increase the total sample size to 44 samples. Bryophyte aerial percent cover was estimated with transparent grid sheets before clipping. In the laboratory, samples were oven-dried at 65 °C to a constant mass, weighed, and ground for total C and total N analysis.

2.2.2. Transect measurements of bryophyte cover and O-horizon depth

Bryophyte aerial percent cover and O-horizon depth were measured on transects within PSPs for the purpose of better capturing the observed patchiness in these variables. From these variables, O-horizon C content and bryophyte mass would be predicted using pedotransfer functions to gain a more robust estimate of O-horizon C content and bryophyte mass than could be made with the limited number of destructive samples (1 or 3 depending on the PSP) associated with each PSP. Transects were established on 5 PSPs in each stand, except for the reference stand and one of the commercial clearcut stands where transects were established on 4 PSPs. These were the same PSPs from which O-horizon samples were collected in 2013. Transects were established from plot center to the plot boundaries at 0, 60, 120, 180, 240, and 300° true north. Along each transect, measurements were taken at 4, 7, 10, 13, and 16 m for a total of 30 observations of each variable for each PSP. However, observations within portions of transects that intersected access roads were removed from the data set, which resulted in a total of 944 locations. Bryophytes were not identified to species, but field notes indicate that *Bazzania trilobata* (L.) S. Gray var. *trilobata*, *Hylocomium splendens* (Hedwig) W.P. Schimper in B.S.G., *Pleurozium schreberi* (Willdenow ex Bridel) Mitten, and *Polytrichum* spp. were common.

2.2.3. Measurement of stand and site variables

Trees were measured on PSPs in accordance with the nested plot design to assess tree species composition and density. Species and dbh were recorded for each tree, and total basal area and the relative basal area of conifers, eastern white pine, red spruce, eastern hemlock, and balsam fir were calculated for trees ⩾1.3 cm dbh. FWD was measured along line transects within PSPs and FWD oven-dry mass was calculated using formulas developed by Brown (1974). Each downed woody debris piece (DWD; large end diameter ⩾7.6 cm) was measured (large and small end diameters and length) on the 0.02-ha plots; DWD volume of each piece was calculated using the conic-paraboloid formula (Fraver et al., 2007), and these volumes were summed to produce a plot-level DWD volume. For PSPs where transects were established for direct bryophyte and O-horizon measurements, an open-face soil pit was excavated to estimate 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 an estimate of depth from the ground surface to the water table or saturated zone.

2.3. Data analyses

2.3.1. Pedotransfer functions for predicting O-horizon C content and bryophyte mass

We developed pedotransfer functions for predicting O-horizon C content from O-horizon depth using the 124 O-horizon samples collected in 2012 and 2013, and bryophyte mass from bryophyte cover using the 44 bryophyte samples collected in 2013. Linear models and non-linear models that included power and exponential functions of the predictor variables were evaluated. For bryophyte mass, a model with a sigmoidal function of cover used by Muukkonen et al. (2006) was also evaluated. For both response variables, non-linear models with a power function of the predictor provided the best fit to the data in terms of root mean square error and biological interpretation. Variance weighting functions in the nlme package (Pinheiro et al., 2014) within R (R Development Core Team, 2014) were also used to account for heterogeneity in the standardized residuals of the pedotransfer functions. The final pedotransfer functions were used to predict O-horizon C content and bryophyte mass at 944 locations where O-horizon depth and bryophyte cover were measured along transects within PSPs. These values were then used to calculate an average of O-horizon C content and bryophyte mass for each PSP to be used in subsequent analyses.

2.3.2. Testing for a treatment effect on predicted O-horizon C content

The influence of treatment on predicted O-horizon C content was tested using mixed effects modeling. The plot average predicted O-horizon values were used as the response variable and only data from the replicated treatments (selection, shelterwood, and commercial clearcut) were evaluated due to lack of replication of the reference area. Treatment was used as a fixed effect because we were specifically interested in estimating potential differences in predicted O-horizon C content among treatments. Depth to redoximorphic features, cartographic depth-to-water, and drainage class were also considered for inclusion in the model 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. The lme function in the nlme package (Pinheiro et al., 2014) in R (R Development Core Team, 2014) was used to fit the linear mixed-effects models.

2.3.3. Modeling predicted O-horizon C content with variables other than treatment

A separate mixed-effects model of predicted O-horizon C content was developed with explanatory variables from all stands that were not correlated with treatment, depth to redoximorphic features, cartographic depth-to-water, and drainage class. The explanatory variables that were evaluated for inclusion in the model as fixed effects were plot average predicted bryophyte mass, FWD mass, DWD volume, tree basal area, and the relative basal area of conifers, eastern white pine, red spruce, eastern hemlock, and balsam fir. Plots from the reference stand and managed stands were included in this analysis because of the emphasis on stand dynamics and species composition as opposed to specific treatment effects. The focus on stand dynamics is also advantageous because of differences in the timing of harvests between stands where the same treatment was applied.

2.3.4. Accounting for within-plot variation in predicted O-horizon C content

While plot average predicted O-horizon C content values were developed to evaluate the influence of plot-level factors on O-horizon C content, we were also interested in evaluating within-plot variation. To address this objective, two mixed-effects models were developed using the individual predicted O-horizon C content values. The first model was fit with data from the managed stands and treatment was used as a fixed effect. The second model was fit with data from all stands and predicted bryophyte mass was used as a fixed effect. "Stand" and "plot" within stand were used as random effects. In both models, spatial dependence was detected in variograms of the residuals and was modeled using the corLin function in the nlme package (Pinheiro et al., 2014) in R (R Development Core Team, 2014).

3. Results

3.1. Pedotransfer functions for predicting O-horizon C content and bryophyte mass

For the O-horizon samples ($n = 124$) from all stands (across silvicultural and harvesting treatments), C content was 25.6 ± 16.1 Mg ha^{-1} (mean ± SD) and O-horizon depth was 6.9 ± 3.8 cm. Coarse charcoal was present in 23% of the samples and was detected in all stands except for one (a 5-year selection stand). For samples that were air-dried before being processed, buried wood in the $O_e + O_a$ horizon accounted for 8.0 ± 6.6% of the total O-horizon C content (Table 2). For these same samples, pH, total C, and C:N ratio of the $O_e + O_a$ fine materials were 3.9 ± 0.4, 42.0 ± 6.1%, and 32.6 ± 5.5. For samples that were oven-dried before being processed, buried wood in the $O_e + O_a$ horizon accounted for 4.1 ± 5.1% of the total O-horizon C content (Table 3). For these same samples, total C and C:N ratio of the $O_e + O_a$ fine materials were 44.9 ± 5.2% and 34.4 ± 6.6, respectively.

Table 4
Power-function parameter estimates (standard errors in parentheses) for predicting O-horizon C content (Mg ha^{-1}) and bryophyte mass (Mg ha^{-1}). Also shown are the R^2 and root mean square error (RMSE) for the respective models.

Model	Parameter		Fit statistics	
	a	*b*	R^2	RMSE
O-horizon C content	5.288 (0.654)	0.826 (0.069)	0.47	1.646
Bryophyte mass	0.012 (0.003)	1.045 (0.084)	0.77	0.022

O-horizon C content = $a * \text{depth}^b$; depth, O-horizon depth (cm).
Bryophyte mass = $a * \text{cover}^b$; cover, bryophyte aerial cover (%, 0–100).

The pedotransfer function of O-horizon C content from all stands indicated that O-horizon depth explained 47% of the variation in O-horizon C content (Fig. 1, Table 4). The function was then used to predict O-horizon C content at locations where only O-horizon depth was measured on transects within PSPs. The predicted C content at these 944 locations was 22.6 ± 13.3 Mg ha^{-1} (mean ± SD; the SD reported here and in other instances involving predicted values is the SD of the individual predicted values and does not represent an estimate of model uncertainty). For the selection, shelterwood, commercial clearcut, and reference, predicted O-horizon C content was 27.3 ± 15.6, 22.6 ± 12.1, 21.7 ± 10.5, and 14.3 ± 11.7 Mg ha^{-1}, respectively. O-horizon depth was 7.6 ± 5.3 in the selection, 6.0 ± 3.9 in the shelterwood, 5.7 ± 3.3 in the commercial clearcut, and 3.6 ± 3.6 cm in the reference.

For the bryophyte samples, oven-dry mass was 0.39 ± 0.54 Mg ha^{-1} and bryophyte cover was 26.7 ± 31.9%. For 20 of the 44 bryophyte samples from which sufficient material could be obtained for chemical analysis, total C, total N, and C:N ratio were 44.5 ± 0.6%, 1.19 ± 0.20%, and 38.3 ± 6.3, respectively. Using the mean oven-dry mass and total C values, bryophyte C content was 0.17 Mg ha^{-1} compared to 25.6 Mg ha^{-1} for the O-horizon samples from all stands.

The pedotransfer function of bryophyte mass indicated that bryophyte cover explained 77% of the variation in bryophyte mass (Fig. 1, Table 4). This function was used to predict bryophyte mass at locations where only bryophyte cover was measured on transects within PSPs. The predicted bryophyte mass at these 944 locations was 0.28 ± 0.39 Mg ha^{-1}. For the selection, shelterwood, commercial clearcut, and reference, predicted bryophyte mass was 0.49 ± 0.52, 0.25 ± 0.35, 0.17 ± 0.21, and 0.16 ± 0.24 Mg ha^{-1},

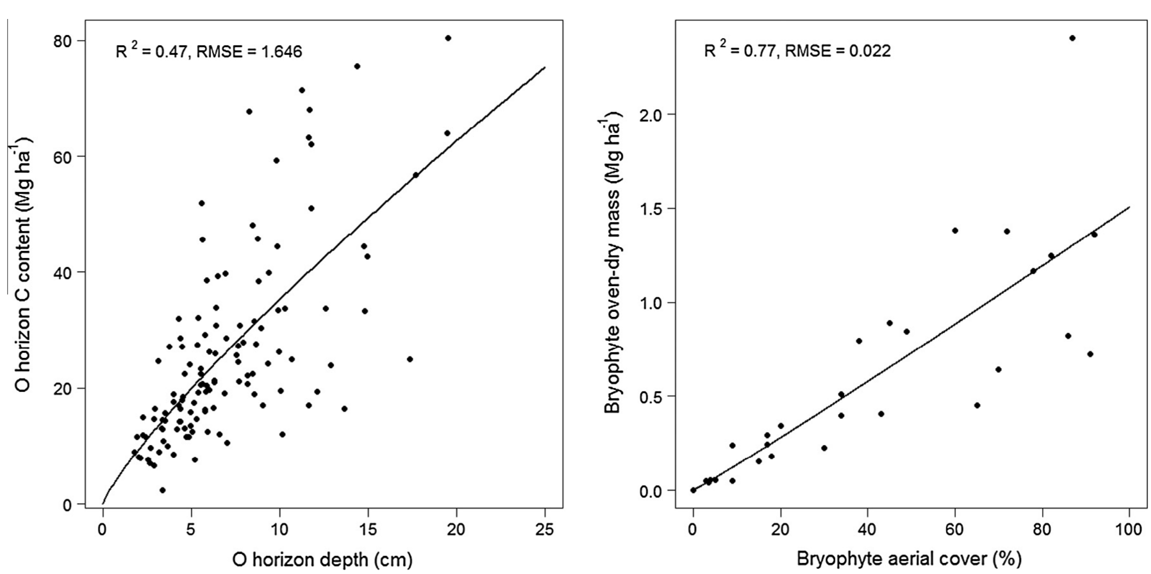

Fig. 1. Generalized, non-linear models of O-horizon C content and bryophyte mass fit to data from 124 O-horizon samples and 44 bryophyte samples across all stands. RMSE = root mean square error.

Table 5
Mean (and standard deviation) and range of continuous variables that were evaluated as being potentially correlated with plot average predicted O-horizon C content. Data are from permanent plots where transect measurements of O-horizon depth and bryophyte cover were recorded. The bryophyte mass statistics are from plot average predicted bryophyte mass values.

	Treatment			
Attribute Number of plots	Reference 4	5-year selection 10	3-stage shelterwood 10	Commercial clearcut 9
O-horizon C content	14.3 (2.8)	27.1 (4.9)	22.6 (2.8)	21.7 (2.9)
(Mg ha^{-1})	11.5–17.1	19.3–34.8	17.9–26.1	17.7–25.5
Depth to water table	44 (15)	34 (17)	38 (11)	30 (9)
(cm)	30–64	0–51	15–53	15–43
Cartographic DTW	90 (47)	128 (106)	117 (66)	138 (93)
(cm)	28–132	27–318	50–268	16–266
Bryophyte mass	0.16 (0.09)	0.50 (0.23)	0.25 (0.17)	0.17 (0.06)
(Mg ha^{-1})	0.03–0.24	0.26–0.94	0.03–0.58	0.08–0.25
FWD mass	5.4 (2.7)	4.5 (2.5)	4.5 (2.2)	3.3 (1.8)
(Mg ha^{-1})	2.0–8.5	1.3–9.3	0.9–8.0	1.1–7.3
DWD volume	51.8 (16.4)	14.9 (13.4)	3.6 (2.9)	9.7 (11.9)
(m^3 ha^{-1})	40.9–76.1	0–43.8	0.4–9.4	1.1–34.8
Total basal area	54.0 (7.0)	30.4 (6.3)	47.3 (8.8)	28.3 (6.6)
(m^2 ha^{-1})	47.7–60.5	20.6–42.1	33.7–65.3	21.2–38.9
Conifer basal area	91.1 (4.0)	89.7 (8.4)	89.6 (7.6)	45.7 (22.9)
(% of total basal area)	86.7–96.4	72.1–100	77.2–97.9	18.4–79.1
Pine basal area	34.4 (14.2)	4.1 (6.9)	22.4 (18.9)	3.6 (3.4)
(% of total basal area)	13.6–45.4	0–18.9	0–60.5	0–9.9
Spruce basal area	2.2 (2.4)	18.3 (10.9)	20.2 (16.4)	2.9 (2.1)
(% of total basal area)	0–5.5	5.3–42.3	5.4–44.2	0–6.7
Hemlock basal area	50.5 (22.2)	47.8 (21.1)	4.7 (3.8)	3.3 (3.6)
(% of total basal area)	32.9–82.8	18.3–81.4	0.9–11.3	0–9.8
Balsam fir basal area	0.5 (0.5)	15.7 (13.0)	41.8 (18.0)	33.9 (20.6)
(% of total basal area)	0–1.1	0.8–36.2	18.5–71.3	10.9–70.4

Depth to redoximorphic features was used as an indicator of depth to water table; DTW, depth-to-water; FWD, fine woody debris; DWD, downed woody debris.

respectively. Bryophyte cover was 33.1 ± 34.7 in the selection, 17.5 ± 23.4 in the shelterwood, 12.0 ± 14.3 in the commercial clearcut, and 11.2 ± 16.2% in the reference.

3.2. Testing for a treatment effect on predicted O-horizon C content

For PSPs from the managed stands, plot average predicted O-horizon C content was 23.9 ± 4.3 Mg ha^{-1} and showed a relatively normal distribution. For each treatment, mean plot average predicted O-horizon C contents are shown in Table 5. Treatment, depth to redoximorphic features, and their interaction were included in the initial mixed-effects model. However, likelihood ratio tests using maximum likelihood estimation suggested that these terms were not significant. The interaction term and depth to redoximorphic features were eliminated from the model, but treatment was retained in the final model to account for the nested structure of the data. In the final model, the *P*-value associated with the *F*-ratio for treatment was not significant (0.258). A likelihood ratio test indicated that there was significant variation in predicted O-horizon C content between stands where the same treatment was applied ($df = 1$, $L = 6.628$, $P = 0.005$). Stand-level variation in predicted O-horizon C content accounted for 34% of the components of variance of the mixed-effects model. Because depth to redoximorphic features was correlated with cartographic depth-to-water ($r = 0.42$), cartographic depth-to-water and drainage class were used in place of depth to redoximorphic features. However, using these variables resulted in the same final model (i.e., a model with forest management treatment as the only fixed effect).

3.3. Modeling predicted O-horizon C content with variables other than treatment

For PSPs from all stands, plot average predicted O-horizon C content was 22.7 ± 5.2 Mg ha^{-1} and showed a relatively normal distribution. For each stand, mean predicted O-horizon C content

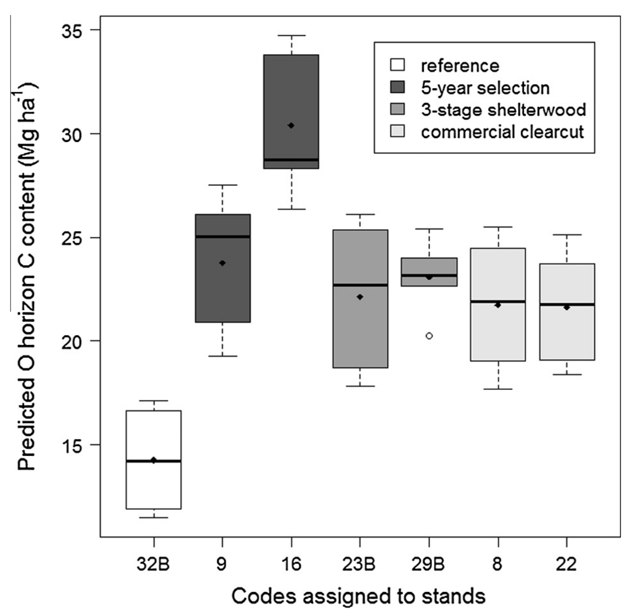

Fig. 2. Plot average predicted O-horizon C content by stand. Data are from 5 permanent plots per stand, except for stands 32B and 8 in which 4 plots were sampled. The horizontal line and black dot in each box are the median and mean, respectively. The boxes define the hinge (25–75% quartile, and the line is 1.5 times the hinge), and points outside the hinge are represented as dots.

and range of predicted O-horizon C content values within stands are shown in Fig. 2. FWD mass, DWD volume, tree basal area, and the relative basal area of conifers, red spruce, eastern hemlock, and balsam fir had no statistically significant relationships with predicted O-horizon C content. The relative basal area of eastern white pine and bryophyte mass had significant linear correlations with predicted O-horizon C content ($r = -0.40$ and 0.38, respectively). However, when included in the mixed-effects model and thereby accounting for the correlation structure of the data, likelihood ratio tests using maximum likelihood estimation suggested that the relative basal area of eastern white pine, bryophyte mass, and their interaction were not significant. Hence, the final model only included the stand random effect. The variation in predicted O-horizon C content among stands accounted for 66% of the observed variance.

3.4. Accounting for within-plot variation in predicted O-horizon C content

In two separate models, the individual predicted O-horizon C content values were used to evaluate variation in predicted O-horizon C content among and within stands, as well as, within-plot variation in predicted O-horizon C content. In the first model, values from the managed stands were used with treatment as a fixed effect. Stand and plot within stand were used as random effects. Treatment was not significant (*F*-ratio = 2.906, $P = 0.199$), but was retained in the model to account for the nested structure of the data. The correlation between plots in the same stand was low ($r = 0.02$–0.03), as well as between observations from the same plot ($r = 0.03$–0.07). These correlations were lowest in selection stands and highest in commercial clearcut stands. Between-stand variation and variation among plots within the same stand accounted for 1.6 and 1.7% of the components of variance, respectively. The residual variance, which represents within-plot variation, accounted for 96.7% of the components of variance.

For the second model, values from all stands were used, and predicted bryophyte mass was used as a fixed effect and stand was used as a random effect; predicted bryophyte mass was not used in the first model because it can be influenced by silvicultural or harvesting treatment. A likelihood ratio test and *F*-test indicated that predicted bryophyte mass was significant ($P = 0.045$ and 0.037, respectively). However, predicted bryophyte mass only explained 1.2% of the variation in predicted O-horizon C content and had a negative correlation with predicted O-horizon C content. The correlation between plots in the same stand was low ($r = 0.07$–0.20), as well as between observations from the same plot ($r = 0.09$–0.23). Variation among stands, variation among plots within the same stand, and residual variance accounted for 14.0, 2.2, and 83.8% of the components of variance, respectively. There was also spatial correlation among O-horizon measurements taken within 3.5 m of one another, which was accounted for in both models (see Section 2.3.4. Accounting for within-plot variation in predicted O-horizon C content).

4. Discussion

In this study, mean plot average predicted O-horizon C content for managed stands (23.9 Mg ha^{-1}) was comparable to estimates within this region made 17 years after harvesting at Weymouth Point, Maine (24 Mg ha^{-1}) and 50 years after wildfire at Acadia National Park, Maine (27 Mg ha^{-1}) (Parker et al., 2001). The average O-horizon C content observed in this study falls between those for hardwood (17.5 Mg ha^{-1}) and softwood forests (42.3 Mg ha^{-1}) reported by Fernandez (2008) in this region. It is also close to the nationwide (USA) estimate of median forest floor C content (25.6 Mg ha^{-1}) (Woodall et al., 2012). Our values were also similar to those found in 60-year-old broadleaf and conifer stands in the Netherlands (12.3–30.9 Mg ha^{-1}) (Schulp et al., 2008) and mixed Norway spruce and broadleaf stands on acidic soils in Austria (~15 Mg ha^{-1}) (Berger et al., 2002). They are also similar to the estimate for European forests (22.1 Mg ha^{-1}) made by De Vos et al. (2015). As expected, the average O-horizon C content for the managed stands was lower than estimates from other studies without recent harvesting (Parker et al., 2001; Diochon et al., 2009; Raymond et al., 2013). In contrast, the mean plot average predicted O-horizon C content of the unmanaged reference stand in this study (14.3 Mg ha^{-1}) was lower than those of other studies without recent harvesting.

The low number of replicates of the selection, shelterwood, and commercial clearcut treatments ($n = 2$), combined with the high between- and within-stand variability in predicted O-horizon C content, are important considerations in evaluating the ability to detect a significant treatment effect. Stand-level variability is likely due in part to differences in the timing of harvests between stands where the same treatment was applied. For instance, in stand 16, selection cutting had occurred the winter before our measurements of O-horizon depth along transects; in stand 9, selection cutting had occurred three years prior to our measurements (Fig. 2). Hence, the recent harvest may be partially responsible for the higher O-horizon C content in stand 16 due to the relatively recent incorporation of logging residues into the O horizon. For O-horizon samples collected in 2013, the relative contribution of O_i non-woody materials and O_i buried wood to the total O-horizon C content were 16.0 ± 5.5 and 0.2 ± 0.2% in stand 9 compared to 25.8 ± 13.6 and 0.4 ± 0.3% in stand 16. Furthermore, surface FWD in stands 9 and 16 were 2.9 ± 1.4 and 6.0 ± 2.5 Mg ha^{-1}, respectively. For stand 16, field notes also indicate that many of the locations where O-horizon depth measurements were made included buried wood in the form of highly decomposed logs. These locations tended to have the thickest O horizons. It is likely that the high abundance of buried logs in this stand originated from a disturbance event, such as a major windstorm, prior to the 1950s.

Variation in O-horizon C content among PSPs within the same stand is likely due to gap dynamics and differences in harvesting intensities within stands. In the selection stands, variation in O-horizon C content may be partially due to the varying spatial arrangement of trees (Saunders and Wagner, 2008). In canopy gaps, lower O-horizon C content might be expected due to increased temperature of the forest floor, which hastens litter decomposition (Hobbie, 1996; Wickland et al., 2010). However, more illumination in gaps may favor some bryophyte species, which buffer the soil climate from extreme temperatures and provide recalcitrant litter inputs to the O horizon (Turetsky, 2003; Startsev et al., 2007). The practice of felling of trees into gaps so that damage to residual trees is avoided may also concentrate logging residues in gaps making it available for incorporation into the O horizon. Even within stands where commercial clearcutting occurred, harvest intensity was not uniform and created irregular patches of conifers (Kenefic, 2014), which likely influenced within-stand variation in O-horizon C content. Past fires could have also contributed to within-stand variability in O-horizon C content depending on the areas burned within stands. While the frequency and severity of forest fires on the forest is not known, coarse charcoal was detected in O-horizon samples in all but one stand (stand 9 in Fig. 2). Fire can consume surface fuels and O-horizon materials, and increase hardwood composition, which can result in lower O-horizon C content (Parker et al., 2001).

In models that were fit to plot-averaged data from all stands, there was high variation in predicted O-horizon C content among and within stands. Although our metrics related to species composition (i.e., the relative basal area of conifer species) were not significant in the final model of predicted O-horizon C content, differences between species in regard to their litter quality and input rates and crown architecture likely influenced O-horizon C content. For example, conifer litter generally has higher C:N ratios and lignin content than hardwood litter (Rustad and Cronan, 1988; Delaney et al., 1996), which can result in slower decomposition rates. While litter recalcitrance can influence conifer litter decomposition, Albers et al. (2004) found that conifer litter decomposition was more sensitive to the decomposition environment (such as forest floor and stand conditions) than broadleaf litter. When conifer species are compared, eastern white pine litter can have C:N ratios that are initially higher than those of spruce (Rustad and Cronan, 1988). However, the observed loose habit of pine litter can provide more aeration, which may accelerate decomposition. Kulmatiski et al. (2004) found that forest floor C content was significantly lower in stands that were primarily composed of pine rather than eastern hemlock. This can partially explain the lower O-horizon C content in the reference stand, which had a much higher pine component (Table 5) and lower contributions of buried wood, roots, and fines in the $O_e + O_a$ horizon (Table 3) than other stands.

Our results also indicated that there is extremely high variability in O-horizon C content within PSPs on the PEF. This variation may be due to localized bryophyte and buried-wood abundance, as well as pit-and-mound microtopography. However, bryophyte mass only had a small influence (1.2% of the variance attributable to fixed effects) on O-horizon C content at the microsite scale. The lower C:N ratios for bryophytes in this study when compared to those for other ecosystems (Lang et al., 2009; Fenton et al., 2010) might suggest more rapid decomposition of bryophyte litter in this system. The weak negative correlation between bryophyte mass and O-horizon C content may be partially due to interactions involving overstory trees. For example, thick O horizons can develop under dense tree canopies due to high litter inputs, but these same conditions could prevent bryophytes from becoming established due to low light levels. While the presence or absence of buried wood was not recorded for each O-horizon depth measurement on transects, field notes indicate that thick O horizons were usually the result of buried dead wood. Pit-and-mound microtopography is also common across the PEF and may result in differences between O-horizon properties, depths, and C content within and among plots as has been shown in other studies (Dwyer and Merriam, 1981; Beatty and Stone, 1986; Schaetzl, 1990; Lawrence et al., 2013). Also litter accumulation along the upslope portions of DWD has been shown to be greater than in other locations within stands (Martin and Timmer, 2006), which may have contributed to the observed within plot variation in O-horizon C content on the PEF.

Interestingly, the proportion of buried wood in the $O_e + O_a$ horizon of samples that were air-dried before being processed, which accounted for $8.0 \pm 6.6\%$ of the total O-horizon C content (or $7.1 \pm 6.0\%$ of the total O-horizon mass), was lower than the proportion of buried wood (17.5–26% of forest floor mass) reported by McFee and Stone (1966) for mixed-species stands in New York, USA. However, the mass of buried wood in the $O_e + O_a$ horizon (3.8 ± 4.8 Mg ha^{-1}) was similar to estimates (6.9–7.7 Mg ha^{-1}) reported by McFee and Stone (1966). For hardwood forests within the Acadian Forest, Moroni and Ryan (2010) found that average buried-wood mass was $\leqslant 0.8$ Mg ha^{-1} for three different forest management strategies. While our average O-horizon depths were similar to those found by Moroni and Ryan (2010), the higher proportion of softwoods at our study site may partially explain differences in average buried-wood mass between studies. Our estimate of average buried-wood mass was within the lower range of values reported for study sites in boreal and subalpine forests (Lang et al., 1981; Moroni, 2006; Moroni et al., 2015).

5. Conclusions

We found that the average O-horizon C content did not differ among selection cutting, shelterwood cutting, and commercial clearcutting treatments that had been maintained for nearly 60 years on the PEF. Because harvesting is usually confined to the winter months, physical disturbance of the forest floor is minimized, which may have ensured that pre-harvest O-horizon C reserves remained relatively unaltered. Also, stem-only harvesting has been traditionally practiced on the PEF (across all three treatments), which suggests that logging residues were continually available for incorporation into the O horizon. While we found no differences among treatments, we found significant variation in O-horizon C content between managed stands within treatments. This variation may be due to the observed abundance of dead wood buried within the O horizon, as well as the unsynchronized timing of harvests within treatments, given that stands more recently harvested tended to have higher O-horizon C contents. Hence, forest management activities that ensure that a proportion of logging residues and downed woody debris is left on site may temporarily enhance O-horizon C storage. Although species composition varied between treatments, the relative basal areas of several conifer species were not significant in our models of O-horizon C content. The high variation in O-horizon C content among stands may have confounded our ability to detect a tree species influence on O-horizon C content. We found that most of the variation in O-horizon C content was due to factors at the microsite level, that is, within the permanent sample plots. Across all stands, bryophyte mass explained only 1.2% of the variation in O-horizon C content at this scale. Further research is needed to determine the relative influence that specific microsite-level factors have on O-horizon C content.

Acknowledgements

We thank Valerie Kurth (Flathead Conservation District) who provided useful comments that helped us to improve this manuscript. We also thank Robert Seymour (University of Maine) and John Brissette (U.S. Forest Service) for their discussions about the project. We acknowledge Lindsey Rustad (U.S. Forest Service) and Bruce Hoskins, Sue Erich, and Cheryl Spencer (University of Maine) for their advice on soil sampling and laboratory procedures. Funding for this project was provided by the U.S. Forest Service, Northern Research Station and Northeastern States Research Cooperative; the Maine Agricultural and Forest Experiment Station; and the Penobscot Experimental Forest Research Fund.

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