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

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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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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