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Article

Soil Organic Carbon Storage and Stability in the Aspen-Conifer Ecotone in Montane Forests in Utah, USA

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Abstract: To assess the potential impact of conifer encroachment on soil organic carbon (SOC) dynamics and storage in montane aspen-conifer forests from the interior western US, we sampled mineral soils (0–15 cm) across the aspen-conifer ecotones in southern and northern Utah and quantified total SOC stocks, stable SOC (*i.e.*, mineral-associated SOC (MoM)), labile SOC (*i.e.*, light fraction (LF), decomposable (CO_2 release during long-term aerobic incubations) and soluble SOC (hot water extractable organic carbon (HWEOC)). Total SOC storage (47.0 ± 16.5 Mg C ha^{-1}) and labile SOC as LF (14.0 ± 7.10 Mg C ha^{-1}), SOC decomposability (cumulative released CO_2-C of 5.6 ± 3.8 g C g^{-1} soil) or HWEOC (0.6 ± 0.6 mg C g^{-1} soil) did not differ substantially with vegetation type, although a slight increase in HWEOC was observed with increasing conifer in the overstory. There were statistically significant differences (p = 0.035) in stable MoM storage, which was higher under aspen (31.2 ± 15.1 Mg C ha^{-1}) than under conifer (22.8 ± 9.0 Mg C ha^{-1}), with intermediate values under mixed (25.7 ± 8.8 Mg C ha^{-1}). Texture had the greatest impact on SOC distribution among labile and stable fractions, with increasing stabilization in MoM and decreasing bio-availability of SOC with increasing silt + clay content. Only at lower silt + clay contents (40%–70%) could we discern the influence of vegetation on MoM content. This highlights the importance of chemical protection mechanisms for long-term C sequestration.

Keywords: *Populus tremuloides*; conifer encroachment; soil organic carbon; SOC stabilization; mineral-associated SOC; SOC decomposability; mixed aspen-conifer forests

Abbreviations

CM; Cedar Mountain; DBH; diameter at breast height; FB; Franklin Basin; HWEOC; hot water extractable organic carbon; IC; inorganic carbon; LBA; live basal area; LME; linear mixed effects; LF; light fraction; MA > 53 µm; mineral-associated soil organic carbon in the sand fraction; MoM; mineral-associated soil organic carbon in the silt and clay fraction; SD; standard deviation; SOC; soil organic carbon; SUVA; specific ultra violet absorbance at 254 nm; TOC; total organic carbon; TC; total carbon.

1. Introduction

Efforts to optimize C sequestration in forest ecosystems have mainly focused on enhancing stand biomass productivity and density by adapting rotation length, thinning intensity and tree species composition. Less attention is often paid to the effect of forest management and changes in species composition on soil organic carbon (SOC) storage and dynamics. Soils store two thirds of total C in terrestrial ecosystems [1], which is equivalent to 1400–1500 Pg C in the first meter [2,3]. Even small changes in SOC storage or dynamics, whether induced by anthropogenic or natural factors, can alter the ecosystem C balance [4], with significant impact on atmospheric CO_2 levels at the regional scale.

SOC storage at the landscape scale is determined by the interaction of climate, soil properties, vegetation, relief, land use history, disturbance regime and the chemical composition of soil organic matter [5]. The balance between C input, primarily as litter or rhizodeposition, and C output via soil respiration determines whether forest soils are C sources or sinks [6,7]. For particular site conditions (e.g., soil properties, aspect, climate, *etc.*), forest species composition and stand development determine the amount, allocation (aboveground and belowground) and chemistry of organic matter inputs [6,8–10]. Soil environmental conditions (e.g., temperature, water and O_2 availability, pH), the abundance and type of microbes and the chemical composition of organic matter, in turn, regulate SOC decomposition rates [11]. Biochemical recalcitrance (*i.e.*, resistance to microbial decomposition due to intrinsic molecular make-up) has greater control over decomposition rates in the litter layer. In the mineral soil, the persistence of SOC is further enhanced by the mineral matrix through additional protection mechanisms, such as the isolation of organic matter inside aggregates (*i.e.*, physical protection) and surface interactions between organic compounds and mineral particles, mainly from the silt and clay fraction (*i.e.*, chemical protection) [12]. The interaction of these protection mechanisms and soil microclimate creates a continuum of SOC pools with different chemical composition and residence time [13,14] that differs among forest species [7,15].

Quaking aspen (*Populus tremuloides* Michx.) is an iconic species of the Intermountain West, USA. Aspen is typically a seral species, eventually replaced by more shade-tolerant species, like Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) at lower elevations or subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) at higher elevations [16]. As a pioneer species, aspen regeneration frequently depends on small or coarse-scale disturbances, like fires or landslides [17]. However, aspen is ecologically versatile and has multiple modes of regeneration and stand development [17,18]. Aspen can form stable, uneven aged stands that regenerate continuously or through gap-phase regeneration [17] and is also found in coexistence with conifers in mixed stands for several decades or centuries [17,18]. Decline in aspen extent in the Intermountain West (so-called sudden aspen decline or SAD) has been attributed to natural succession coupled with fire suppression, ungulate grazing and climate change [19–23].

Aspen and conifer stands from semi-arid montane and subalpine forests differ considerably in soil microclimate [24–27], hydrology [24], litter quality [27,28], soil chemistry [27,29], soil microbial community structure [27] and SOC content and dynamics [25–27]. Woldeselassie *et al.* [26] found that montane aspen stands in northern Utah had higher SOC stock (96.2 ± 26.7 Mg C ha^{-1}) than adjacent conifer stands (66.9 ± 18.6 Mg C ha^{-1}) in the top 60 cm of mineral soil. SOC under aspen was also more persistent than SOC from conifer soils and had a higher proportion of mineral-associated SOC (55% ± 13% in aspen *vs.* 41% ± 13% in conifers) [25,26]. A shift towards mixed and conifer-dominated stands could thus modify SOC dynamics and potentially reduce long-term SOC storage (*i.e.*, SOC sequestration potential).

Several studies have addressed the properties of SOC under mixed aspen-conifer stands in the boreal climate [15,30], but studies of SOC storage and stability in mixed stands in semi-arid climates are largely missing. In particular, we do not know whether changes in SOC properties occur gradually or abruptly at critical composition thresholds. It is also possible that mixed aspen-conifer stands have distinct SOC dynamics and, thus, represent an alternate state. The objective of this study was to assess the influence of forest composition on SOC storage and SOC stabilization in the mineral soil at the aspen-conifer ecotone in montane forests of Utah. The underlying hypotheses were: (1) SOC storage will decrease from aspen to conifer dominated stands; (2) with increasing conifer encroachment, a greater proportion will be stored as labile SOC; and (3) the proportion and quantity of protected SOC will conversely decrease with conifer encroachment. Understanding the processes controlling SOC storage and stabilization along the aspen-conifer gradient will provide insight to forecast the fate of SOC with conifer encroachment or climate change-induced vegetation shifts and may also inform management decisions when focusing on C sequestration as an ecosystem service.

2. Materials and Methods

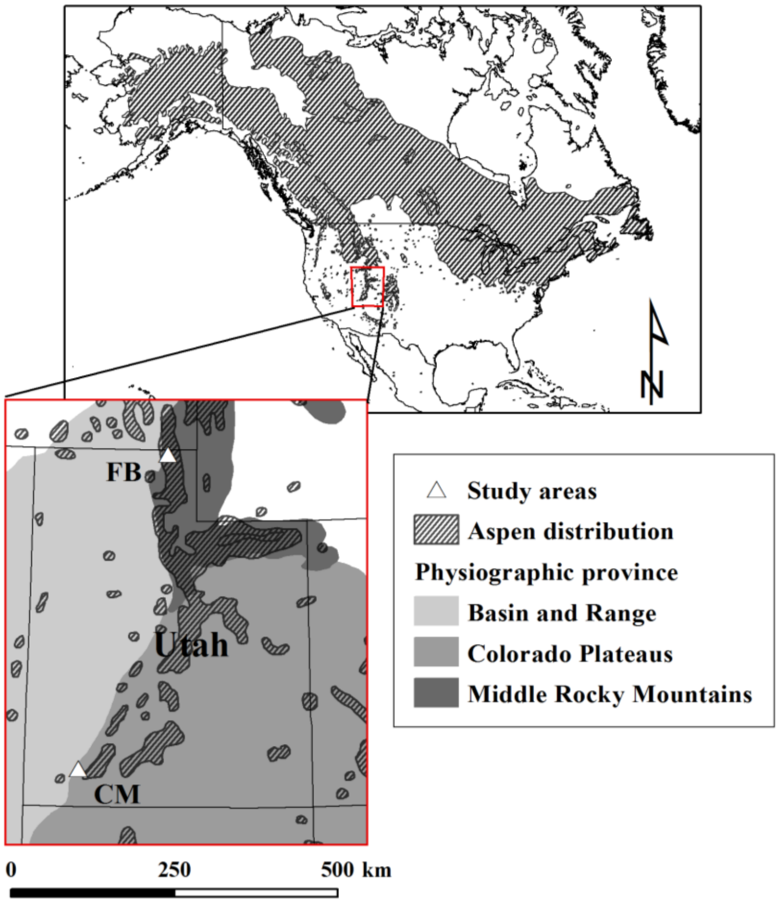
2.1. Study Sites

To test our hypotheses, we chose study sites from southern Utah (Cedar Mountain) and northern Utah (Franklin Basin), expanding the geographical scope of previous studies.

Cedar Mountain (CM) is a high elevation plateau (1800–3200 m) located within the Colorado Plateau region in southwestern Utah [31] (Figure 1). Mean annual precipitation is 812 mm [32], most of it as snow from October through April. Monsoonal storms are common in late summer [33]. The average monthly air temperature ranges from −3.8 °C in December to 15.5 °C in July [32]. Mountain grasslands consisting of Letterman needlegrass (*Stipa lettermani* Vasey) and Kentucky bluegrass (*Poa pratensis* L.) alternate with woodlands of quaking aspen as the predominant communities [34]. Subalpine fir, Douglas fir and white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.) appear scarcely in the landscape, mixed with aspen or forming small stands at the edges of the plateau. Patches of Gamble oak (*Quercus gambelii* Nutt.) occur in lower elevation areas [33].

Soil types are commonly Alfisols or Mollisols [31,35] developed mainly on sedimentary rock and igneous rock [36].

Figure 1. Aspen distribution in North America and the location of study areas.



Franklin Basin (FB) is a montane-subalpine area (1770–3030 m) located between the Bear River Range and the Wasatch Range in the central Rocky Mountains, distributed between northeastern Utah and southeastern Idaho [37] (Figure 1). The precipitation regime is snow dominated, with a mean annual precipitation of 1197 mm [32]. The monthly average temperature ranges from −6.9 °C in December to 16.4 °C in July [32]. Forest ecosystems are represented by quaking aspen and mixed conifer stands of Douglas fir, subalpine fir and limber pine (*Pinus flexilis* E. James). Non-forested areas are occupied by curl leaf mountain mahogany (*Cercocarpus ledifolius* Nutt. ex Torr. & A. Gray) or mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) [36]. Soils are commonly Alfisols and Mollisols, developed on limestone or quartzite sandstone.

2.2. Study Design and Field Sampling

This study used two sampling designs to characterize the influence of the overstory on SOC properties at different spatial scales. In the first design, the influence of a single tree or a small tree cluster on soil properties was evaluated [38,39]. The second design used plots of a 10-m radius as sampling units to characterize stand composition along the gradient from pure aspen stands to pure conifer stands.

In October of 2011, four sites at CM and two sites at FB were sampled following the first design, hereafter referred to as "transects", with three transects per site (Table 1). Within each transect, two soil cores (5-cm diameter; 0–15-cm depth) were taken in the mineral soil beneath aspen, mixed and conifer cover. The cores were divided by 5-cm intervals at the field and stored separately. Slope, elevation and aspect were similar within each transect. Pure conifer clusters were absent in one site at CM (CM1), while samples from one transect at another site (CM57) were excluded from the inventory, due to discrepancies in sampling and storage protocol. We did not describe soil pedons in our sites, but the characteristics of the topsoil were in agreement with those described in previous studies [26,37]. We generally observed a thin O horizon (*i.e.*, superficial horizon dominated by organic matter, > 20% by weight of SOC) and a relatively deep A horizon (*i.e.*, mineral topsoil with accumulation of organic matter, < 20% by weight of SOC) under aspen, whereas conifer soils had a thicker O horizon and a shallower and lighter A horizon.

Table 1. Topographic characteristics (mean ± SD) and parent material of transects at Cedar Mountain (CM) and Franklin Basin (FB). Parent material not available (n.a.).

Site	Elevation (m)	Slope (degrees)	Aspect	Parent Material
CM 1	2552 ± 8	14 ± 9	N	Basalt
CM 2	2756 ± 12	24 ± 12	N	Basic and intermediate igneous rock
CM 57	2773 ± 11	24 ± 11	W	n.a.
CM 111	2685 ± 9	46 ± 2	N	Limestone, sandstone and shale
FB 1	2098 ± 9	10 ± 4	NE	Quartzite, sandstone and limestone
FB 2	2196 ± 18	15 ± 5	E	Limestone

The second design, hereafter named "plots", was applied in CM the summers of 2011 and 2012. Potential sampling areas were identified *a priori* with the National Agricultural Imagery Program (NAIP) 1-m orthophoto (2009) and topographic maps using ArcGIS 9.3 (Esri, Redlands, CA., USA). Sampling areas were selected based on the existence of conifer, mixed and aspen patches of at least a 40-m diameter under similar slope, elevation and aspect conditions. Four to five plots of a 10-m radius were located at five different locations, for a total of 24 plots (Table 2). The minimum distance between adjacent plots was 30 m, and the conditions of overstory composition and structure in the surrounding 10-m buffer were homogenous to those within the plot to avoid edge effects. Five soil cores (5-cm diameter; 0–15-cm depth) were randomly sampled within each plot and combined into one composite sample per plot. Two additional cores were collected and the 5–10 cm excised to calculate bulk density. Tree species, status (dead or alive) and diameter at breast height (DBH) (*i.e.*, stem diameter at a 1.30-m height) of all trees >3 cm in diameter were recorded and used to calculate live basal area (LBA) by species (m^2 ha^{-1}) and live stem density (n ha^{-1}). Overstory composition was classified by the percentage of live basal area occupied by aspen in three categories: aspen dominated (>75% LBA aspen), mixed (25%–75% LBA aspen) and conifer dominated (<25% LBA aspen).

Table 2. Topographic and overstory characteristics of plots at Cedar Mountain. LBA, live basal area.

Site	Plot	Elevation (m)	Slope (degrees)	Aspect	Live Basal Area (m^2 ha^{-1})		Contribution of Aspen to LBA (%)	Live Stem Density (n ha^{-1})	
					Aspen	Conifer		Aspen	Conifer
CM 5	CM 5-1	2764	4	NE	28.9	6.1	82.5	1,055.6	223.9
CM 5	CM 5-2	2766	8	NE	0.0	67.0	0.0	0.0	2,499.4
CM 5	CM 5-3	2746	8	NE	35.5	17.5	66.9	649.2	519.4
CM 5	CM 5-4	2759	9	NE	21.4	0.3	98.4	710.0	41.8
CM 8	CM 8-1	2651	19	NW	43.0	0.0	100.0	1,353.0	0.0
CM 8	CM 8-2	2656	16	N	8.8	50.1	15.0	241.1	551.2
CM 8	CM 8-3	2704	23	NW	56.9	37.3	60.4	563.5	1,390.0
CM 8	CM 8-4	2700	26	NW	27.6	9.7	73.9	827.5	157.6
CM 8	CM 8-5	2685	26	NW	11.3	100.6	10.1	118.2	630.4
CM 15	CM 15-1	2636	28	W	57.0	36.6	60.9	641.1	1,518.5
CM 15	CM 15-2	2638	22	W	0.0	47.4	0.0	0.0	914.2
CM 15	CM 15-3	2688	20	NW	38.6	12.6	75.4	468.7	692.9
CM 15	CM 15-4	2654	24	W	28.0	4.1	87.1	634.7	1,025.2
CM 15	CM 15-5	2636	26	W	27.0	6.7	80.0	305.9	183.5
CM 17	CM 17-1	2725	4	W	1.4	36.7	3.6	32.0	1,439.4
CM 17	CM 17-2	2738	4	NW	35.3	7.9	81.8	4,286.2	287.9
CM 17	CM 17-3	2725	7	W	21.8	1.2	94.6	1,615.5	64.6
CM 17	CM 17-4	2714	3	W	13.1	6.7	66.3	1,340.6	127.7
CM 17	CM 17-5	2710	3	W	0.9	16.6	5.3	223.4	861.8
CM 20	CM 20-1	2883	4	N	49.9	0.0	100.0	3,262.6	0.0
CM 20	CM 20-2	2901	3	N	26.7	15.3	63.5	408.6	367.7
CM 20	CM 20-3	2907	4	N	27.5	46.0	37.4	383.8	639.7
CM 20	CM 20-4	2903	4	NW	12.4	34.1	26.6	127.9	671.7
CM 20	CM 20-5	2895	5	N	33.4	25.6	56.6	481.1	609.4

2.3. Laboratory Analyses

Transects (0–5 cm) and plot composite samples (0–15 cm) were sieved (2-mm mesh) and stored at 4 °C to minimize microbial decomposition. Middle core sections (5–10 cm) from transects and plots were oven dried at 105 °C for 24 h, sieved (2-mm mesh), weighed to determine bulk density and the percent of fine earth mass. Fine fraction samples were ground with a mortar and pestle and analyzed for total carbon (TC), inorganic carbon (IC) and total organic carbon (TOC) with a Skalar Primacs^{SLC} Analyzer (Skalar, Inc., Breda, The Netherlands). Average TOC concentration from the 5–10 cm, depth, bulk density and fine earth percentage were used to calculate SOC stocks (Mg C ha^{-1}) for the first 15 cm of mineral soil. As bulk density increases with depth, while SOC concentration decreases, we considered the 5–10 cm section to represent the average properties of the entire 0–15 cm core. Soil texture analysis was performed with the pipette method [40] in transect (0–5 cm) and composite plot (0–15 cm) samples.

A multitude of fractionation methods have been developed with the purpose of dividing SOC into fractions with presumably different turnover rates [41,42]. In this study, we used a simplified size fractionation method: 20 g of air dried soil (0–15-cm depth for plot samples, 0–5-cm depth for transect samples) were processed under the premise that free, large particulate organic matter and SOC associated with mineral particles of different sizes and mineralogy differ in the degree of stabilization and turnover time. The mineral-associated SOC in the clay and silt fraction (MoM) was separated by wet sieving through a 53-µm sieve, with the >53 µm fraction further divided into a light fraction (LF) and mineral-associated SOC in the sand fraction (MA > 53) using electrostatic attraction, following a modification from Kaiser *et al.* [43]. The LF is generally composed of free and intra-aggregate particulate organic matter (*i.e.*, relatively fresh organic matter, mainly of plant origin). MoM is considered to be more protected and to have a long residence, whereas SOC in the sand fraction is weakly bonded and has lower residence, but may also be partly composed of relatively recalcitrant charred material [41,44]. All fractions were ground with a mortar and pestle and analyzed for TC content with Skalar Primacs^{SLC} Analyzer (Skalar, Inc., Breda, The Netherlands), which constituted TOC, given that IC content was negligible in the bulk samples. The C recovery and relative contribution of each fraction to bulk SOC was calculated from the fractions' relative weights, TC concentrations and bulk soil TOC concentration. C recovery was on average 98.0% ± 11.3%, with five samples somewhat outside this range.

SOC decomposability (*i.e.*, biologically available SOC) was determined with long-term (10 months) aerobic laboratory incubations of fresh soil samples (0–5 cm transect, 0–15 cm plot) following the protocol of Paul [45], as modified by Woldeselassie *et al* [26]. Cumulative CO_2-C respired was expressed on a dry soil weight basis (mg CO_2-C g $soil^{-1}$) and normalized to C content (mg CO_2-C g C^{-1}) as an indicator of qualitative differences in SOC. Only plot samples collected in 2011 (n = 16) were incubated.

Hot water extractable organic carbon (HWEOC), considered by some authors as a good indicator of biologically available SOC [46,47], was determined by mixing field-moist soils with distilled water in falcon tubes (1:10 soil-water (w/v)) and heating the slurry in a hot bath at 85 °C for one hour. The solution was filtered through Whatman GF/F filters (pore size ~0.7 µm) and the extractant analyzed for dissolved organic carbon (DOC) with a Phoenix 8000 Carbon Analyzer (Tekmar-Dohrmann, Mason, OH., USA). Specific ultraviolet absorbance at 254 nm (SUVA) of HWEOC, an estimate of DOC aromaticity which is used as an indicator of chemical recalcitrance [48], was measured with a Genesys 10 spectrophotometer (Thermo Scientific, Madison, WI., USA).

2.4. Statistical Analyses

Relationships between SOC properties were explored with Spearman's rank correlation coefficient using the R package, Hmisc, version 3.10–1.10 (R Foundation for Statistical Computing, Vienna, Austria) [49].

Linear mixed effects (LME) models were applied to test the effect of vegetation and soil texture on the SOC properties in both datasets. In the transect dataset, vegetation class (aspen, mixed and conifer) was treated as a categorical fixed effect and silt + clay content (%) as a continuous fixed effect variable. The site and transect were considered random effect variables, with transect nested within site to account for the dependency among samples from the same transect and site. LME models applied to the plot dataset included overstory composition (aspen percent of LBA) and soil texture (silt + clay (%)) as continuous fixed effect variables and site as a random effect variable.

LME models with vegetation class or overstory composition as explanatory variables were applied to sand (%), silt (%) and clay (%) as response variables to ensure that potential differences in SOC properties across the vegetation gradient were not merely due to the occurrence of aspen and conifers in different soil conditions.

Data were transformed with the logarithm in base 10, the square root, the reciprocal transformation or the reciprocal square root when the assumptions of normality and homogeneity of variance were not met. Linear mixed models were applied with the R package, lmer, Test 2.0–3.0 [50]. Fixed effects were tested with Type III ANOVA, using Satterthwaite approximation for the degrees of freedom of the denominator for the F statistics. Bonferroni pairwise comparisons were used to test differences among estimated means when the main effect of vegetation class was statistically significant ($p < 0.05$). The estimated slope for silt + clay content in transect LME models was reported when the ANOVA test found it statistically significant, to inform on the magnitude and direction of the effect. Estimates for the intercept and slopes for overstory composition and silt + clay content were reported for all the plots LME models.

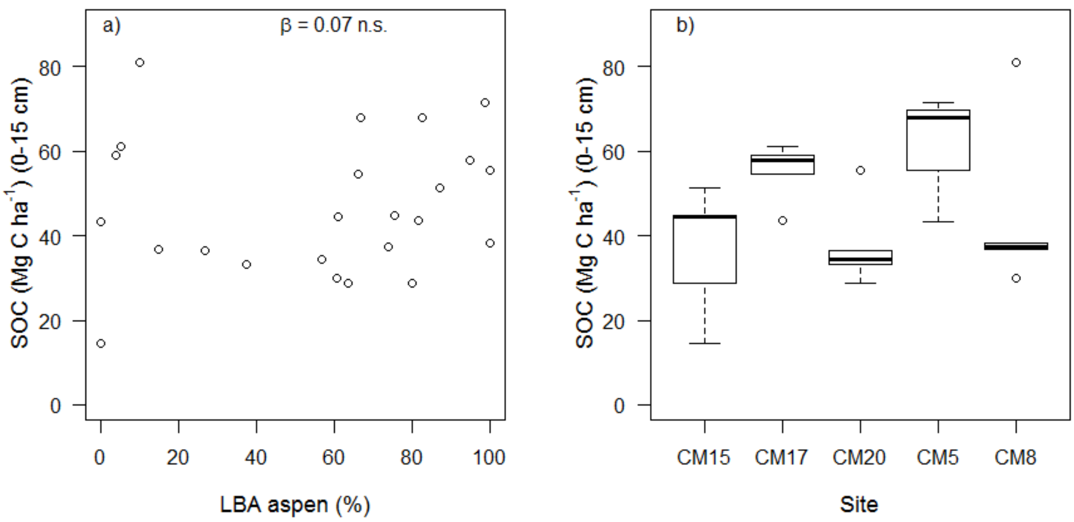
3. Results and Discussion

The plots at Cedar Mountain represented a broad gradient from pure aspen stands to conifer stands, with varying degrees of conifer encroachment and stand structure (Table 2). Across all plots, mean aspen LBA was 25.3 ± 17.0 m^2 ha^{-1}, a similar value to the 20.7 ± 13.8 m^2 ha^{-1} reported by Rogers *et al.* [31] for stable aspen stands in Cedar Mountain. The mean conifer LBA (min-max) was 24.4 (0–100.6) m^2 ha^{-1}. The average tree density (min-max) was 642 (0−2499) live conifer ha^{-1} and 822 (0−4286) live aspen ha^{-1}, higher than the 315 ± 201 aspen stems ha^{-1} reported previously for this area [31]. The relative dead basal area was higher for aspen (33.5% ± 32.5%) than conifer (5.5% ± 10.6%) across all sampling sites. Nine plots had aspen dominated overstory (LBA aspen 21–50 m^2 ha^{-1}), four of them showing signs of conifer encroachment; six plots had conifer dominated overstory (LBA conifer 17–101 m^2 ha^{-1}); nine plots had mixed overstory (total

LBA 20–94 m^2 ha^{-1}). The distribution by diameter classes suggested that seven mixed plots may continue the succession towards conifer stands.

The SOC concentration in surface soils did not differ by vegetation class in the transect samples (Table 3), with an overall mean (± SD) of 48.1 ± 18.1 mg C g $soil^{-1}$. In the plots, SOC concentration ranged between 10.0 and 150 mg C g $soil^{-1}$, with a mean (± SD) of 46.8 ± 27.1 mg C g $soil^{-1}$. The SOC content (Mg C ha^{-1}) in the transects was not statistically different among vegetation classes, with an overall mean (± SD) of 47.2 ± 16.8 Mg C ha^{-1}, but followed the trend: aspen > mixed > conifer. The SOC content in the plots ranged between 14.4 and 80.9 Mg C ha^{-1}, with a mean (± SD) of 46.8 ± 16.2 Mg C ha^{-1}. SOC content did not follow any pattern nor did it change abruptly at a critical LBA threshold across the aspen-conifer gradient, but it varied across sampling sites (Figure 2 and Table 3). Our values for SOC content are comparable to those found by Woldeselassie *et al.* [26], who similarly did not find significant differences in SOC content in the top 15 cm of mineral soil between aspen (49.5 ± 7.9 Mg C ha^{-1}) and conifer stands (54.9 ± 20.3 Mg C ha^{-1}) in montane forests from northern Utah.

Figure 2. SOC content (mg C ha^{-1}) (0–15 cm) for the plots at Cedar Mountain (**a**) *vs.* aspen contribution to LBA (%) and (**b**) by site. β represents the slope for aspen LBA (%).Statistically non-significant, n.s. The boxes represent the 25 and 75 percentiles. The median is represented by the horizontal bold line. The whiskers represent the 10th and 90th percentiles, and the circles correspond to outliers.



Although we did not find differences in SOC storage along the vegetation gradient, differences in distribution among labile and stable SOC fractions may be more relevant for C sequestration. Across all samples, over half of the SOC was stored in the more persistent MoM fraction (mean ± SD: 56.1% ± 12.7% for transects; 60.5% ± 13.4% for plots), with around one-third stored as LF (mean ± SD: 37.0% ± 11.9% for transects; 30.4% ± 10.3% for plots). Mineral-associated SOC in the sand fraction was a minor contributor, accounting for <10% of total SOC (mean ± SD: 6.9% ± 3.3% for transects; 9.1% ± 5.5% for plots) and, therefore, was not further considered in the statistical analyses. MoM content in the transect soils was statistically significantly higher under aspen (31.18 Mg C ha^{-1}) than under conifer (22.84 Mg C ha^{-1}), with mixed stands having intermediate values (25.67 Mg C ha^{-1}) (Table 3). This pattern was not visible along the aspen-conifer gradient in the plots (Figure 3b and Table 4), nor was there an obvious LBA threshold. However, there was a positive correlation between MoM C concentration (mg C g^{-1} soil) and aspen contribution to LBA (%) (Figure 3a). The relative distribution of SOC among the different fractions (expressed by the percent of SOC) was similar across the vegetation types in plots and transects, probably due to the high variability in LF content in our sites. These results somewhat contradict previous observations from montane semi-arid [26] and boreal aspen-conifer forests [30], where aspen stands had a significantly higher proportion of SOC in the MoM fraction than mixed and conifer stands.

Figure 3. (**a**) MoM C concentration (mg C g^{-1} soil) *vs.* aspen contribution to LBA (%). (**b**) MoM content (Mg C ha^{-1}) *vs.* aspen contribution to LBA (%). β represents the slope for aspen LBA (%) (**c**) MoM content *vs.* silt + clay content by dominant overstory in Cedar Mountain plots.

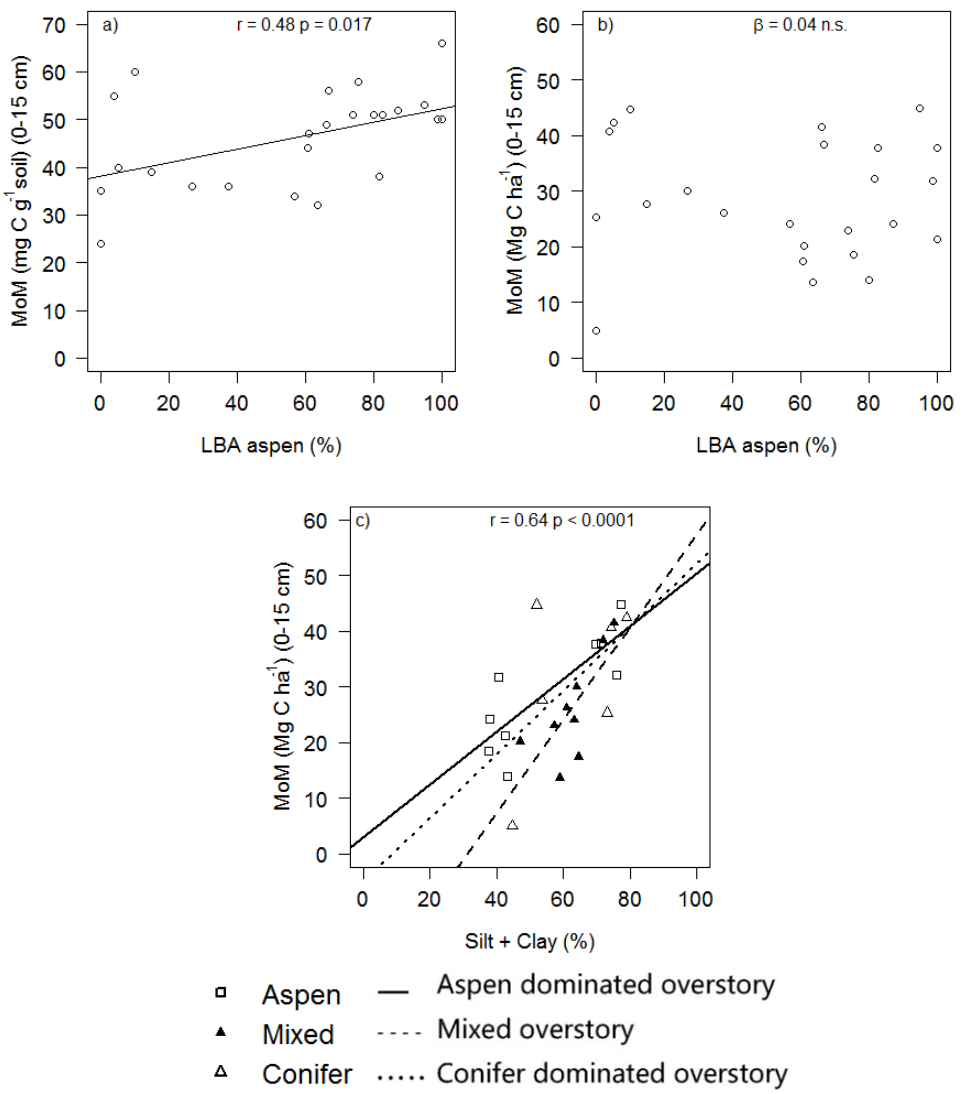


Table 3. Mean values and standard deviation of the soil properties of transect samples by vegetation class, and the *p*-values from the Type III ANOVA testing the main effects of vegetation and silt + clay content (%). Different letters indicate statistically significant differences among the means at a 5% probability level. TOC, total organic carbon; SOC, soil organic carbon; MoM, mineral-associated SOC in the clay and silt fraction; MA > 53 μm, mineral-associated SOC in the sand fraction; LF, light fraction; Cum. CO_2-C, cumulative released CO_2-C in long term incubations; HWEOC, hot water extractable organic carbon; DOC, dissolved organic carbon; SUVA, specific ultra violet absorbance at 254 nm; P, P value.

	Bulk Density (g cm^{-3})	TOC (mg C g^{-1}) (0–5 cm)	TOC (mg C g^{-1}) (5–10 cm)	SOC (Mg C ha^{-1}) (0–15 cm)	MoM (Mg C ha^{-1}) (0–15 cm)	MA > 53 μm (Mg C ha^{-1}) (0–15 cm)	LF (Mg C ha^{-1}) (0–15 cm)	MoM (% SOC)	MA > 53 μm (% SOC)
Aspen	0.85 ± 0.15	67.1 ± 23.4	49.9 ± 22.0	51.8 ± 22.6	31.2 ± 15.1 a	3.2 ± 1.9	17.5 ± 11.5	59.0 ± 14.7	6.8 ± 3.6
Mixed	0.83 ± 0.15	69.7 ± 18.0	49.1 ± 16.2	47.4 ± 10.0	25.7 ± 8.8 ab	3.2 ± 1.6	18.5 ± 5.9	53.5 ± 11.0	7.5 ± 3.7
Conifer	0.82 ± 0.13	78.3 ± 21.8	44.4 ± 18.1	40.9 ± 13.3	22.8 ± 9.0 b	3.0 ± 1.8	15.1 ± 6.9	55.6 ± 12.0	6.7 ± 2.9
P Vegetation	0.842	0.264	0.674	0.274	0.035		0.544	0.200	
P Silt + Clay		0.009	0.102	0.583	0.255		0.718	0.050	

	LF (% SOC)	Cum. CO_2-C (mg C g soil^{-1})	Cum. CO_2-C (mg C g C^{-1})	HWEOC (mg DOC g soil^{-1})	HWEOC (mg DOC g C^{-1})	SUVA (abs × 100 mg C^{-1})	Clay (%)	Silt (%)	Sand (%)
Aspen	34.2 ± 13.3	5.1 ± 3.0	86.2 ± 61.8	0.6 ± 0.4	9.4 ± 6.3	2.7 ± 0.4	23.2 ± 7.7	35.9 ± 13.6	40.9 ± 19.3
Mixed	39.9 ± 11.4	7.4 ± 5.8	109.3 ± 87.4	0.6 ± 0.4	8.9 ± 4.6	2.7 ± 0.3	22.6 ± 10.0	40.0 ± 14.3	37.6 ± 20.1
Conifer	36.9 ± 10.5	6.2 ± 2.0	81.5 ± 27.3	0.9 ± 1.1	11.3 ± 10.6	2.8 ± 0.8	25.0 ± 8.7	42.8 ± 13.5	32.2 ± 19.7
P Vegetation	0.160	0.228	0.530	0.398	0.640	0.625	0.162	0.691	0.376
P Silt + Clay	0.190	0.209	0.045	0.364	0.120	0.488			

Table 4. Linear mixed effects model estimates for the intercept, the slope for the contribution of aspen to LBA (%), the slope for silt + clay (%) and the variance explained by the site and residuals for different SOC properties from the plot samples.

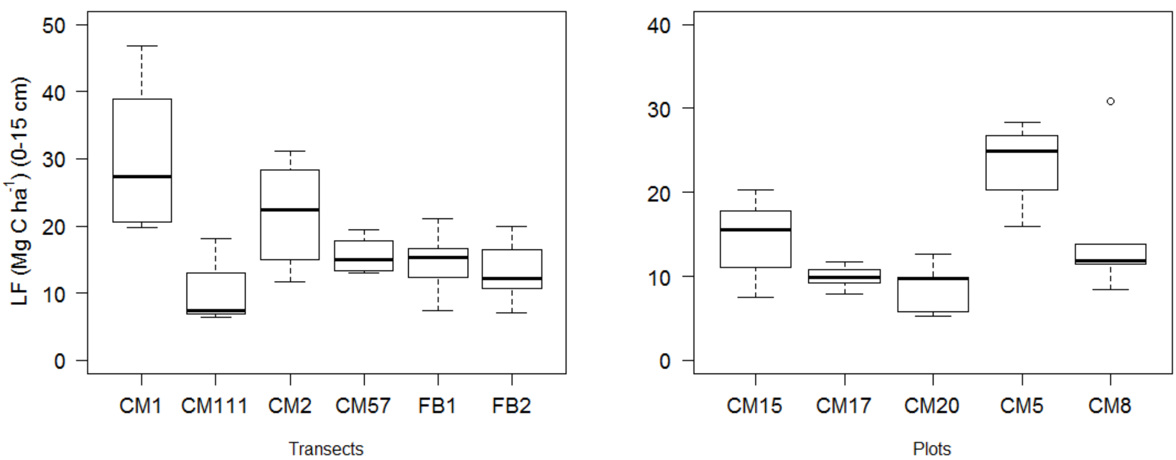
Response Variable	Intercept	*t*-Value	*p*	Aspen LBA (%)	*t*-Value	*p*	Silt + Clay (%)	*t*-Value	*p*
SOC (Mg C ha^{-1})	33.06 ± 20.55	1.61	0.143	0.07 ± 0.09	0.79	0.438	0.17 ± 0.31	0.55	0.598
MoM (Mg C ha^{-1})	−4.45 ± 9.36	−0.48	0.639	0.04 ± 0.05	0.71	0.489	0.51 ± 0.14	3.81	0.001
LF (Mg C ha^{-1}) [1]	−0.28 ± 0.08	−3.25	0.005	$4.43 \times 10^{-4} \pm 3.18 \times 10^{-4}$	1.39	0.181	$-6.18 \times 10^{-4} \pm 1.25 \times 10^{-3}$	−0.49	0.628
MoM (%)	28.79 ± 13.23	2.18	0.048	$3.59 \times 10^{-3} \pm 0.05$	0.07	0.946	0.52 ± 0.20	2.66	0.019
LF (%)	43.09 ± 10.96	3.93	0.001	−0.01 ± 0.04	−0.31	0.757	−0.20 ± 0.16	−1.23	0.235
Cum. CO_2-C (mg C g soil^{-1}) [2]	1.24 ± 0.86	1.44	0.177	$3.32 \times 10^{-3} \pm 2.96 \times 10^{-3}$	1.12	0.287	$-3.96 \times 10^{-3} \pm 0.01$	−0.33	0.744
Cum. CO_2-C (mg C g C^{-1}) [2]	4.84 ± 0.78	6.20	<0.0001	$1.38 \times 10^{-3} \pm 2.53 \times 10^{-3}$	0.55	0.598	−0.01 ± 0.01	−1.08	0.301
HWEOC (mg DOC g soil^{-1})	0.52 ± 0.25	2.14	0.048	$-1.98 \times 10^{-3} \pm 9.14 \times 10^{-4}$	−2.17	0.044	$1.04 \times 10^{-3} \pm 3.62 \times 10^{-3}$	0.29	0.778
HWEOC (mg DOC g C^{-1})	16.66 ± 5.09	3.28	0.006	−0.06 ± 0.02	−3.13	0.006	−0.05 ± 0.08	−0.60	0.560
SUVA (abs × 100 mg C^{-1}) [2]	0.78 ± 0.52	1.50	0.161	$2.48 \times 10^{-4} \pm 2.05 \times 10^{-3}$	−0.12	0.906	0.03 ± 0.01	4.01	0.002
Clay (%)	22.68 ± 3.52	6.45	<0.001	−0.01 ± 0.03	−0.42	0.681			
Silt (%)	40.57 ± 4.31	9.41	<0.0001	−0.05 ± 0.03	−1.48	0.157			
Sand (%)	36.74 ± 6.25	5.88	0.001	0.06 ± 0.05	1.27	0.220			

[1] Transformed with the reciprocal root ($-1/x^{0.5}$); [2] transformed with the logarithm in base 10.

On the other hand, silt + clay (%) had a significant positive effect on MoM content in the plots (Figure 3c and Table 4) and on the relative proportion of SOC as MoM in both transects (Table 3) and plots (Table 4), indicative of the formation of organo-mineral associations on silt and clay particles. Individual LME models by dominant overstory in the plots (e.g., aspen (aspen LBA > 75%), mixed (aspen LBA 25%–75%) and conifer (conifer LBA > 75%)) suggest that at relatively low silt + clay (%), there is a vegetation effect, with aspen soils storing more MoM than soils in conifer and mixed forests. At higher silt + clay (%), the effect of vegetation is negligible or the potential for SOC stabilization is driven by soil texture rather than vegetation (Figure 3c). Collectively, these results suggest that SOC stabilization in the mineral-associated fraction is favored by the presence of aspen [26]. This greater accumulation of MoM under aspen may be driven either by a higher concentration of organic matter in the mineral-soil solution interface or a higher affinity between aspen-derived organic compounds and clay minerals or both. Our results indicate that whereas total SOC stocks in the upper mineral soil may not be affected by conifer encroachment, the amount of protected (*i.e.*, more persistent) SOC in soils with low and intermediate silt + clay contents may be below the full potential under conifer compared to similar soils under pure aspen.

The amount and relative contribution of LF was highly variable within and among sites in transects and plots (Figure 4) and was not significantly affected by either vegetation cover (LBA) or soil texture (Tables 3 and 4). The variability of LF among sites likely reflected differences in litter input, root growth and decomposition that were not captured by overstory characteristics in this study. This was somewhat unexpected, as LF is considered responsive to changes in overstory species and land use [7]. In their aspen-conifer comparison, Laganiere *et al* [30] and Woldeselassie *et al.* [26] had previously found a higher proportion of unprotected SOC under conifer stands than under aspen stands.

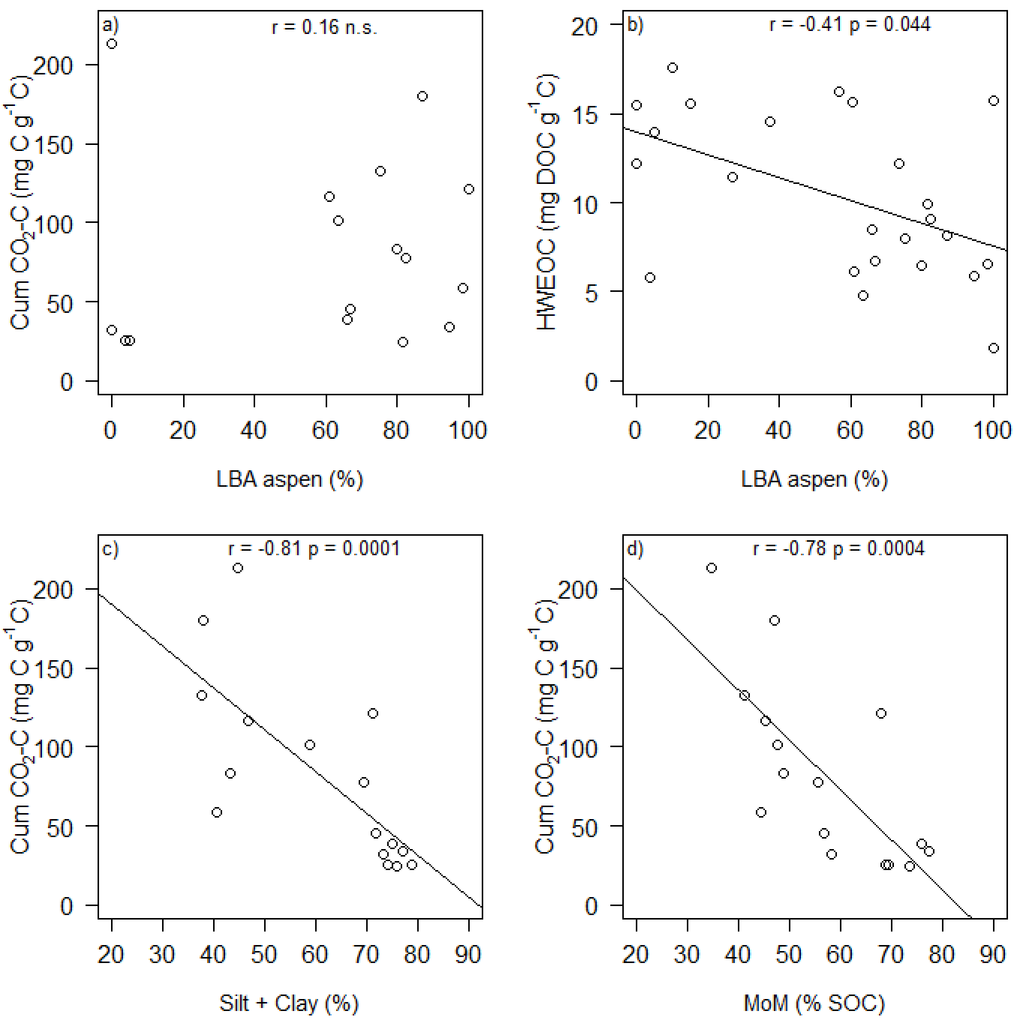
Figure 4. (**a**) Boxplots of LF stocks by sampled sites in Cedar Mountain and Franklin Basin transects; (**b**) Boxplots of LF stocks by sampled sites in the Cedar Mountain plots. The boxes represent the 25th and 75th percentiles. The median is represented by the horizontal black line. The whiskers represent the 10th and 90th percentiles, and the circles correspond to outliers.



The two methods used to characterize relatively labile SOC, *i.e.*, decomposability (long-term incubations) and solubility (hot water extractions) were positively, albeit weakly, correlated.

Correlation coefficients were $r = 0.34$ ($p = 0.024$) when data were expressed as concentrations on a soil dry weight basis and $r = 0.35$ ($p = 0.019$) when expressed per gram of SOC in the soil. This suggests that although the methods are not equivalent, HWEOC can be used as a fast and practical proxy of microbially available SOC when time and/or resources are limited. Our data showed no quantitative or qualitative differences in SOC decomposability with vegetation cover (Table 3) or the relative abundance of aspen in the overstory (Figure 5a and Table 4). Cumulative CO_2 release rates (5 to 7.5 g C g^{-1} soil) were in a similar range as those reported by Olsen and Van Miegroet [25] for the 0–10 cm of mineral soil under aspen (3.8 g C g^{-1} soil) and conifer stands (5.1 g C g^{-1} soil). Although in that study, no significant differences in SOC decomposability were found among vegetation classes in surface soils, vegetation had a significant effect at a 10–20-cm soil depth, with conifer soils containing more decomposable SOC than aspen. Similarly, Woldeselassie *et al.* [26] found that aspen-derived SOC was qualitatively less decomposable (67.7 mg C g C^{-1}) than conifer-derived SOC (130.9 mg C g C^{-1}).

Figure 5. (**a**) SOC decomposability *vs.* contribution of aspen to LBA; (**b**) relative HWEOC concentration *vs.* the contribution of aspen to LBA; (**c**) SOC decomposability *vs.* silt + clay (%) or (**d**) MoM (% SOC).

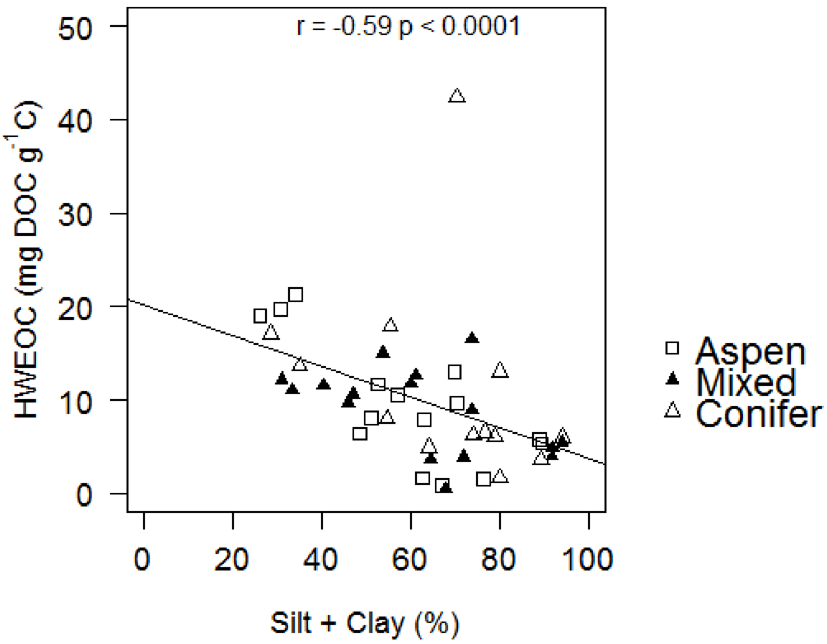


HWEOC concentration, expressed on a soil dry weight basis or per gram of SOC, did not differ among vegetation classes in the transect samples (Table 3). At the plot level, overstory composition had a significant effect on HWEOC concentration per gram of soil ($p = 0.044$) or as a fraction of SOC ($p = 0.006$). The small negative slopes (Table 4) suggest a slight, but statistically significant, decrease in SOC lability with the presence of aspen in the overstory (Figure 5b).

Variability in cumulative CO_2 release per gram of soil was not explained by texture in either transects or plot samples (Tables 3 and 4). Relative silt + clay content had a significant negative effect ($p = 0.045$) on the decomposability of SOC (CO_2 g^{-1} C) in the transects (Table 3), indicated by a negative slope for log-transformed CO_2-C release ($\beta = -0.016$). In the plot data, the effect of silt + clay (%) on decomposable SOC was non-significant when controlling for other factors (Table 4). However, the simple correlation between silt + clay (%) and SOC decomposability followed the same negative pattern (Figure 5c). The fraction of readily decomposable SOC (mg C g^{-1} C) was also negatively correlated with either silt (%) ($r = -0.47$, $p = 0.001$ transects; $r = -0.51$, $p = 0.044$ plots) or clay (%) separately ($r = -0.43$, $p = 0.004$ transects; $r = -0.79$, $p < 0.001$ plots). The percentage of SOC as MoM was further negatively correlated with decomposable SOC per gram of soil ($r = -0.30$, $p = 0.047$ transects; $r = -0.70$, $p = 0.002$ plots) or per gram of C (Figure 5d), suggesting that SOC was qualitatively less decomposable as a result of physical-chemical protection.

Silt + clay content (%) had no effect on HWEOC in transects or plot samples (Tables 3 and 4). However, in transect samples, absolute (mg DOC g^{-1} soil) and relative HWEOC concentration (mg DOC g^{-1} C) were negatively correlated with silt + clay content ($r = -0.40$, $p = 0.007$ and $r = -0.59$, $p < 0.0001$, respectively) (Figure 6) and MoM (% SOC) ($r = -0.81$, $p < 0.0001$ and $r = -0.77$, $p < 0.0001$, respectively). These relationships further support the hypothesis that organo-mineral associations reduce the biological availability of SOC and, therefore, overall SOC stability.

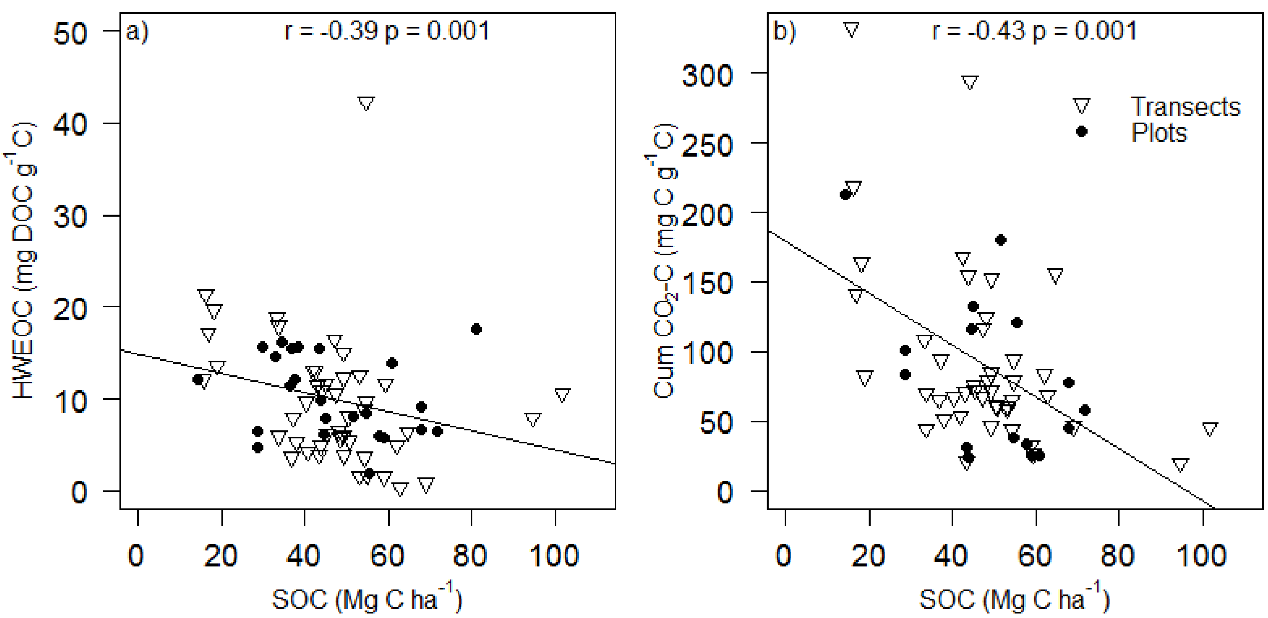
Figure 6. The inverse relationship between silt + clay content (%) and HWEOC expressed as the fraction of SOC in transect samples.



There were significant negative correlations between SUVA and HWEOC concentration (g DOC g^{-1} soil) ($r = -0.44$, $p = 0.020$) in the transects and between SUVA and SOC decomposability (CO_2 release g^{-1} soil or CO_2 g^{-1} C) (respectively: $r = -0.69$, $p = 0.005$ and $r = -0.68$, $p = 0.005$) in the plots. In other words, higher concentrations of recalcitrant DOC were associated with low bio-availability, as measured during incubation. We interpret these results as an indication that biochemically labile SOC is preferentially used by microbes and depleted from the SOC pool, leaving more recalcitrant SOC to accumulate [51]. Conversely, when labile compounds are more abundant in the soil, the overall concentration of aromatic SOC decreases through relative dilution.

Finally, the negative relationship between total SOC storage and SOC lability expressed as either HWEOC (Figure 7a) and cumulative respired CO_2-C (Figure 7b) is consistent with Woldeselassie *et al.* [26], suggesting that the presence of labile SOC in the soil is not conducive to long-term SOC storage. Rather, our results point to the importance of the mineral matrix and especially clay and silt in SOC stabilization and long-term C sequestration. Organic molecules change their spatial conformation when adsorbed to these mineral surfaces, effectively decreasing SOC decomposition (*i.e.*, C loss) by limiting the access of organic substrates to microbes or microbial enzymes [52]. Surface interactions between SOC and mineral particles thus results in the longer residence time of the MoM fraction and the accumulation of stable SOC. The relationship between clay content and total SOC storage has been used in regional and global SOC assessments [3,53–55]. In Mediterranean climates, clay content and soil properties contributing to stabilization mechanisms (e.g., polyvalent cations involved in organo-mineral associations) have also been found to favor SOC storage in evergreen oak forests [56].

Figure 7. (**a**) SOC storage (Mg C ha^{-1}) *vs.* relatively soluble SOC (**b**) *vs.* relative decomposable SOC in transects and plots.



The effect of forest species on total SOC stocks has been investigated in temperate and boreal forests, but without strong evidence or consistent differential SOC storage patterns between conifers and hardwoods [57,58]. Even fewer studies in the literature have focused on forest species effects on stable SOC pools. Unprotected SOC pools seem more responsive to changes in overstory composition, but there are not always significant effects of species composition on long-term C sequestration. Díaz-Pinés *et al.* [7] found that Scots pine (*Pinus sylvestris* L.) stored more SOC in unprotected fractions than Pyrenean oak (*Quercus pyrenaica* Willd.), while mineral-associated SOC content was similar across the pine-oak ecotone. Similarly, Laganière *et al.* [30] did not find differences in mineral-associated SOC between aspen and black spruce (*Picea mariana* (Mill.) Britton *et al.*), but reported more SOC in less protected fractions under black spruce. The content of recalcitrant SOC did not differ significantly between *Cunninghamia lanceolata* and *Michelia macclurei* in plantations in subtropical China [59]. In contrast, significantly higher mineral-associated SOC was found under *Acacia implexa* than under *Eucalyptus melliodora* [60] in native Australian forests.

While our study clearly supports the role of soil texture in site SOC sequestration potential, we further show that vegetation cover, in this case, the transition from aspen to conifer forests, leads to divergent SOC stabilization. However, the effect of overstory composition on SOC stabilization may be less pronounced in ecosystems where abiotic factors dominate belowground SOC dynamics, such as the presence/absence of mineral adsorption sites. Soils in our study sites were mostly loams, and within that textural class, differences in silt + clay content were a major factor controlling SOC stabilization. At higher clay + silt contents (*i.e.*, >70% silt + clay; silty clay to silt loam), the sheer abundance of sorption sites may have compensated for the potential differences in organic matter input and chemistry associated with differences in overstory cover, and vegetation management may prove less effective in creating large differences in belowground SOC storage and stabilization. However, our results suggest that below this range (*i.e.*, 40%–70% silt + clay), vegetation management towards preserving aspen in the landscape may lead to more long-term SOC storage.

Collectively, our results support the importance of MoM in long-term SOC storage, which is favored by the dominance of aspen in the overstory. Woldeselassie *et al.* [26] proposed that faster turnover of aspen litter, combined with rapid hydrological transport during snowmelt creates a pulse of DOC that enhances C adsorption to mineral surfaces. Slower decomposition of conifer needles, associated with O horizon accumulation, would conversely result in lower DOC concentrations and, thus, lower adsorption compared to aspen soils. Furthermore, rapid turnover of aspen litter may contribute to SOC stabilization through strong binding of microbial byproducts and dead microbial biomass to mineral surfaces [61]. Several studies have found that microbially-derived compounds are stabilized in the clay fraction [62,63], becoming part of an SOC pool with a long mean residence time. Thus, rapid turnover of litter and a lack of O horizon accumulation is indeed compatible with SOC stabilization in mineral soil. Conversely, thick O horizons (as typically observed under conifers) speak to litter recalcitrance, but not necessarily to SOC stability in the mineral soil. We observed some differences in SOC quality with vegetation type, but the few analyses performed in this study are insufficient to draw strong conclusions on the role in SOC stabilization of litter quality differences in aspen *vs.* conifers, an area that we are currently investigating. While SOC stability depends on the simultaneous action of biochemical recalcitrance and physico-chemical protection, biochemical recalcitrance may play a secondary role in SOC storage [64].

Belowground C allocation via rhizodeposition and fine root turnover may be another important contributor to the greater SOC stabilization under aspen [65]. Aspen develops a widespread shallow lateral root system, from which root suckers originate as a mechanism of asexual regeneration [66]. However, in the Canadian boreal forest, fine root net primary production and the relative contribution to total detritus input were lower for aspen than for jack pine (*Pinus banksiana* Lamb.) or black spruce (*Picea mariana* (Mill.) Britton *et al.*) [67]. Aspen root volume does not decline significantly in the initial stages of conifer encroachment and can contribute to 25%–50% of total fine root biomass in conifer dominated tree clusters [66,68]. Sheppard and Smith [66] reported changes in large root (>4 mm in diameter) volume and non-structural carbohydrate concentrations with stand age in the central Rocky Mountains of Colorado, and more recently, Hudler [69] showed an increase in soluble C compounds in the roots of aspen with increasing aspen LBA in Southern Utah. These root-derived non-structural compounds may constitute another pathway of C inputs to the soil. The lack of correlation between aboveground and belowground C allocation patterns may explain why using aspen LBA was not a strong predictor for many SOC properties. Changes in soil microbial community composition and abundance [27], microclimate [25] and hydrology [24] induced by conifer encroachment may further modify the species-specific mechanisms of SOC stabilization in aspen forests.

4. Conclusions

While differences in SOC storage across the aspen-conifer gradient were not always clearcut, potentially due to the high variability in abiotic factors (e.g., soil parent material, texture or landscape position), our results nevertheless suggest that aspen stores more SOC in association with silt and clay, increasing the pool of longer residence time SOC. In conifer-dominated stands, on the other hand, SOC is more susceptible to losses through microbial decomposition. This suggests that conifer encroachment may lead to an increase in less-protected SOC, which may turn over faster, depending on environmental conditions (e.g., soil temperature, soil moisture), accelerate decomposition of existing SOC (so-called priming effect) and result in a progressive decline in total SOC storage. Nevertheless, SOC in the mineral-associated fraction may be less affected by conifer encroachment in sites with high silt and clay content. Management strategies pursuing C sequestration in forest ecosystems should therefore not seek to simply increase SOC content, but rather enlarge SOC pools with a longer residence time, *i.e.*, stabilized through adsorption to the mineral surfaces, as they are less sensitive to disturbances or changes in environmental conditions [64].

The addition of large amounts of more labile SOC forms, at best, contributes to a temporary increase in SOC storage, as they are likely to turn over within a matter of years. Although the geographic scope of our study does not allow us to make broad generalizations for the entire distribution range of aspen in the western US, we observed 25%–30% more mineral-associated SOC in the top soil under aspen compared to adjacent conifer stands. Especially, for finer textured soils conducive to SOC stabilization, management efforts to increase stable SOC pools in the topsoil of montane and subalpine forests should concentrate on the conservation and regeneration of aspen.

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Author contributions

Initial concept (Helga Van Miegroet); sample collection, data processing, and statistical analysis (Mercedes Román Dobarco); experimental design, manuscript outline, interpretation of results and writing (Helga Van Miegroet & Mercedes Román Dobarco).

Conflicts of Interest

The authors declare no conflict of interest.

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