Storage and Stability of Soil Organic Carbon in Aspen and Conifer Forest Soils of Northern Utah

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This study compares the amount, distribution, and stability of soil organic carbon (SOC) in six paired quaking aspen *(Populus tremuloides* Michx) and conifer plots at three locations in northern Utah, to assess the influence of vegetation cover and other biotic and abiotic drivers on SOC storage capacity in seasonally dry environments. Aspen soils accumulated significantly more SOC in the mineral soil (0–60 cm) (92.2 ± 26.7 Mg C ha^{-1} vs. 66.9 ± 18.6 Mg C ha^{-1} under conifers), and despite thicker O horizons under conifers that contained higher amounts of SOC (11.6 ± 8.8 Mg C ha^{-1} under conifers vs. 1.65 ± 0.38 Mg C ha^{-1} in aspen), across all sites SOC storage was 25% higher under aspen. Shallow soil cores (0–15 cm) did not indicate significant differences in SOC with vegetation type. The SOC under aspen was also more stable, indicated by well-developed mollic epipedon (A horizon 38–53-cm thick vs. 5.5–34 cm under conifers), slower turnover of surficial SOC deduced from long-term laboratory incubations (67.7 ± 15.7 g CO_2–C per kg C for aspen vs. 130.9 ± 41.3 g CO_2–C per kg C for conifer soils), and a greater preponderance of mineral-associated SOC (55±13% in aspen vs. 41±13% in conifer). Aspen soils were generally wetter and we hypothesize that rapid litter turnover coupled with greater water supply may have caused greater downward redistribution and adsorption of dissolved organic carbon (DOC) in aspen soils.

Abbreviations: CMI, cumulative soil moisture index; DBH, diameter at breast height; DLL, Deseret Land and Livestock; DOC, dissolved organic carbon; LBA, live basal area; LF, light fraction; MOC, mineral-associated organic carbon; POC, particulate organic carbon; SOC, soil organic carbon; TWDEF, T.W. Daniel Experimental Forest.

Quaking aspen is a widely distributed tree species in North America, and besides Canada's Central Provinces, it is most abundant in the western United States, where 75% of the aspen occurs in Colorado and Utah (Jones, 1985; Bartos, 2001). In the west, aspen provides numerous ecological and economical services such as forage for livestock, habitat for wildlife, landscape diversity, esthetics, and water yield (DeByle and Winokur, 1985; Bartos, 2001). Aspen is a very iconic component in the western landscape; thus, there is great concern about its recent decline (Rogers, 2002; Kulakowski et al., 2004; Rehfeldt et al., 2009; Rogers et al., 2010), thought to be the result of a combination of successional processes, fire suppression, and long-term use by ungulates (Bartos and Campbell, 1998; Bartos, 2001).

The successional replacement of western aspen by more shade-tolerant conifers is associated with changes in soil properties (Bartos and Amacher, 1998; Bartos and Campbell, 1998), site hydrology (Harper et al., 1981; Gifford et al., 1984; LaMalfa and Ryel, 2008), a decline in forage production (Mueggler, 1985), loss of biodiversity, and change in ecosystem function. For example, surface soils under aspen are characterized by higher pH and higher base saturation (Hoff 1957; Tew, 1968; Morgan, 1969; Alban, 1982; Paré and Bergeron, 1996), attributed

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to deep cation pumping and accumulation in the humus layer (Alban, 1982). Encroachment of aspen by other vegetation types has been associated with a decrease of soil pH below 6.0 and a lowering in soil nutrient levels; changes believed to suppress aspen regeneration (Cryer and Murray, 1992).

The potentially detrimental effect of conifer encroachment has gained renewed interest within the context of C sequestration and global climate change. Aspen forests differ from associated vegetation types in amount, distribution, and character of organic matter and nutrients (Jones and DeByle, 1985; Van Miegroet et al., 2005). Aspen is believed to be a strong C sink (Chen et al., 1999), and a number of earlier studies in the West have shown higher soil organic matter content in aspen compared to other adjacent vegetation types (Hoff, 1957; Tew, 1968; Jones and DeByle, 1985). LaMalfa and Ryel (2008) further showed higher soil moisture in the upper soil in aspen relative to adjacent conifer plots, in part a result of differential snow accumulation. Some have also postulated that conifer encroachment in aspen stands lowers soil temperature due to increased canopy shading (Cryer and Murray, 1992; Amacher et al., 2001). Such changes in soil microclimate may affect SOC storage by influencing microbial activity and decomposition (Olsen and Van Miegroet, 2010). Thus, increased dominance of conifers in the landscape can affect important site characteristics that control C storage.

While it has been hypothesized that increased presence of conifer has detrimental effects on aspen in the West, our understanding of these vegetation impacts on soils, including SOC storage, soil morphology, and soil chemical properties; and the implications of conifer encroachment on soil function are hampered by a lack of specific studies conducted in the western United States, where seasonal drought may cause fundamental differences in forest and soil function compared to the more humid regions in central North America. To begin to fill some of these knowledge gaps relative to the potential impacts of conifer encroachment, we contrasted aspen and conifer soils as representatives of end-point communities in northern Utah using a paired plot design. Specifically, our study objectives were: (i) to quantify the amount and variability of SOC under aspen and conifer; (ii) characterize various SOC-related soil properties such as soil morphology, SOC turnover and stability, and soil microclimate; and (iii) assess the role of biotic and abiotic drivers of SOC variability under the two vegetation types.

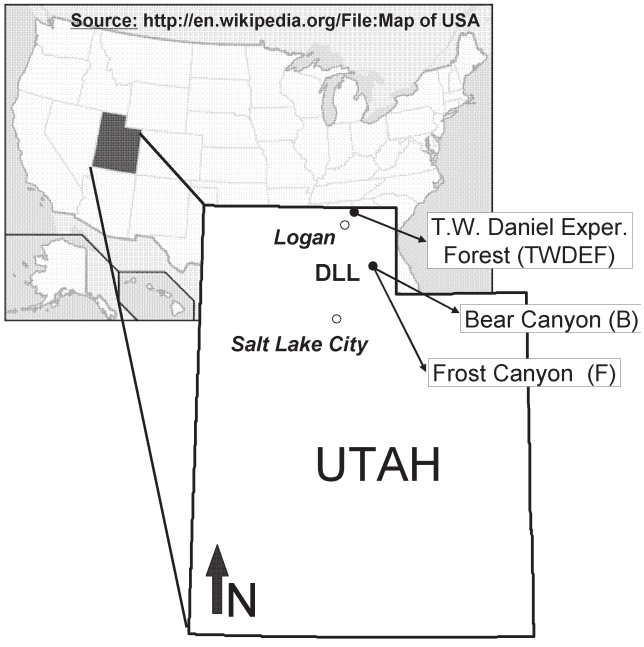

Fig. 1. Locations of study sites at Deseret Land and Livestock and T.W. Daniel Experimental forest in northern Utah.

MATERIALS AND METHODS

Study Sites

The study was conducted in three locations in northern Utah: Upper parts of Frost Canyon (890 ha) and Bear Canyon (1100 ha) Watersheds in Deseret Land and Livestock (DLL) and at Sunset Ridge, a 10-ha research site in the T.W. Daniel Experimental Forest (TWDEF, 1000 ha) (Fig. 1). These study sites were chosen because of their suitability for a paired plot design as both aspen and conifer vegetation are present in close proximity to each other and geology is similar among all sites (i.e., Wasatch conglomerate).

Deseret Land and Livestock is a privately owned ranch in Rich County, Utah, located at 41.10° N, 111.25° W. Vegetation on the eastern half of the ranch, at an elevation of 1920 m, is dominated by sagebrush (*Artemisia tridentata* Nutt.) steppe; the western, at an elevation of 2652 m, is dominated by mountainous, semi-open brush and grasslands with scattered stands of aspen and conifer, mainly Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco]. Mean annual precipitation is 890 mm with 74% as snow accumulation; the wettest months are April, May, June, and September. Mean annual air temperature is about 4.5°C, mean winter temperature is about −4.9°C and mean summer temperature is about 15.1°C, based on 10 yr of data measured at the nearby USGS SNOTEL site (Horseridge) (http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=533&state=ut). Frost Canyon and Bear Canyon do not have uniform geologies (Shakespeare, 2006), but the study plots were established on the same geological substrate, namely the Wasatch conglomerate. The most common soil orders present at DLL are Mollisols, Entisols, Aridisols, and Inceptisols (Washington-Allen et al., 2004).

The TWDEF is located at an elevation of 2600 m about 30 km Northeast from Logan, UT (41.86° N and 111.50° W). The annual precipitation is 950 mm with an 80% snow accumulation (Van Miegroet et al., 2000). Average low temperature is -10°C in January and the highest monthly temperature is 14°C in July (Schimpf et al., 1980; Skujins and Klubek, 1982). Vegetation in the study area ranges from forb meadows and sagebrush to conifer forest, predominantly Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir [*Abies lasiocarpa* (Hook.) Nutt], and lodgepole pine (*Pinus contorta* ex Louden), and aspen forest. The soil orders present at TWDEF are Mollisols and Alfisols (Van Miegroet et al., 2005; Olsen and Van Miegroet, 2010), formed in eolian deposits overlying residuum and colluvium from the Wasatch formation.

Experimental Design and Sampling

A total of six aspen–conifer plot pairs were established, two each in Upper Frost Canyon (F1, F2), Bear Canyon (B1 and B2) at DLL; and at TWDEF (T1, T2). Paired plots (20 by 20 m) were generally located within 25 m of each other in Bear and Frost and between 10 m (T1) and about 100 m (T2) at TWDEF, and were selected for proximity of aspen and conifer stands and similarity in elevation and slope.

A representative pedon (1 m wide and ≤1-m depth) was manually excavated in each plot in summer 2006, described in the field following standard methods (Soil Survey Division Staff, 1993) and classified. Soil samples were taken from each genetic horizon using cores (5 cm diam., 3 cm length), dried at 105°C, sieved (2-mm mesh), weighed, and the fine fraction ground with mortar and pestle before C and N analysis using a CN analyzer (Leco CHN 1000, Leco Corp., St Joseph, MI). Bulk density and percent gravel were determined using the core method (Blake and Hartge, 1986). Total C content was calculated for each horizon from C concentration (<2 mm), bulk density, gravel content, and horizon depth, and was then summed across all depths. Total C content was normalized to the shallowest depth of 60 cm to bedrock to allow comparison of soil content across all plots.

Forest floor C content in the aspen and conifer plots was determined by excavating O horizon samples within frames: in fall 2007 one sample per plot was collected at all sites using a 12.7 by 12.7 cm frame; in fall 2008 (TWDEF) and fall 2009 (DLL) three samples per plot were taken using a larger frame 16 by 16 cm and 25 by 25 cm frame, respectively. Samples were dried at 65°C, weighed, ground, and analyzed for C concentration using a Leco C analyzer.

Qualitative differences in SOC were expressed by biological and physical parameters. The accessibility of SOC to microbial breakdown, hereafter in the text referred to as "SOC decomposability", was assessed from long-term aerobic laboratory incubation (Paul et al., 2001) of fresh upper mineral soil samples taken in July 2007. Five soil cores (0–15 cm) were taken in each plot, and composited into two replicates per plot. Approximately 50 g of field-moist soil was placed in a 120-mL cup, brought to 30% gravimetric soil moisture content (~60% of water holding capacity; Olsen and Van Miegroet, 2010) by adding distilled water, and incubated in glass jars for 10 mo at 25°C (n = 24 total). Three blanks (incubation jars without soil) were included in the design. Incubation jars were aerated weekly and soils were periodically weighed and water added to maintain initial soil moisture contents. Carbon dioxide evolution was measured periodically (biweekly for the first 8 wk, monthly thereafter) using 20 mL 2 M NaOH as a trapping agent, followed by back titration with 2 M HCl. Pre-incubation subsamples were analyzed for C concentration using a LECO analyzer. All CO_2 release values were expressed on a soil dry weight basis, and were normalized for soil C content.

Relative stability/protection of SOC (physical fractionation) was determined on ancillary soil samples that were collected at the three sites in 2004 (TWDEF) and 2009 (DLL) as part of other studies at locations close to the paired plots. At TWDEF, soil samples were derived from the upper horizons of pedon pits in three conifer and aspen plots (see Olsen and Van Miegroet, 2010); at DLL, the soil cores (0–15 cm) were obtained at points along three transects that were clearly under aspen, conifer, or aspen and conifer influence based on crown cover. All soil samples were air dried, and subjected to size-density fractionation as per Six et al. (2002a), followed by C analysis of the different size-density fractions using a LECO analyzer.

Soil moisture was measured in the field using ECH_2O moisture probes (Decagon, Pullman, WA) installed between 0- and 20-cm soil depth in the center of each plot. Field moisture readings (millivolt) were taken using a hand-held device (ECH_2O5 Check, Decagon Devices, Inc., Pullman, WA) in early June, mid-July, August, and October of 2007. These readings were converted into gravimetric (Θm) and volumetric soil moisture (Θv) content based on lab calibrations using reconstructed soil cores from each plot that were subjected to drying and wetting cycles while core weights and ECH_2O readings were recorded. The R^2 for aspen and conifer in Upper Frost Canyon was 0.95 and 0.93, respectively; while the R^2 for aspen and conifer in Bear Canyon was 0.98 and 0.99, respectively. For TWDEF, prior calibration curves for aspen and conifer soils were used (Olsen and Van Miegroet, 2010). To obtain a measure of available water content for each soil type, the volumetric moisture above a threshold 0.10 m^3 m^{-3} was calculated and plotted for each measurement date. The chosen threshold roughly corresponded to wilting point based on soil texture and tension-moisture relationships described in Saxton et al. (1986). Then a cumulative soil moisture index (CMI) for the entire summer and early fall of 2007 (June- October) was calculated as the area under the curve using the trapezoidal rule. This enabled integration and meaningful comparison across sites of soil moisture data that were temporally variable (Woldeselassie, 2009).

The soil temperature of the sites was measured at 2-h intervals using Stowaway Tidbits dataloggers (Onset Computer Corp., Bourne, MA) installed in the center of the plot at 10- to 15-cm soil depth. Due to the malfunction of several tidbits, we were able to record temperature data only in FA1, BA1, BA2, TA2, and TC2 for the period 8 Aug. 2006 through 13 June 2007, limiting our ability to compare soil temperature regime between forest types (except for one plot pair at TWDEF). In our analysis, temperature data were divided and averaged into four periods: late summer (8 Aug.–21 Sept. 2006), fall (22 Sept.–16 Oct. 2006), winter (17 Oct. 2006–3 May 2007) and spring-early summer (14 May–13 June 2007).

Overstory vegetation cover of the two vegetation types was measured using a fixed area plot, where the diameter at breast height (DBH) of each individual tree >5 cm was measured within the circular plot of a radius of 10 m. This information was used to calculate live basal area (LBA) and tree density. The LBA was divided by the number of trees in the fixed plot to derive average tree diameter, an indicator of stand structure that was

found to have greater predictive power of SOC patterns in pure aspen as discussed in Woldeselassie (2009).

Statistical Analysis

All field data were analyzed using a one way ANOVA with a randomized complete block design using PROC MIXED, followed by pair-wise comparisons using Tukey–Kramer adjustment; and paired *t* tests using PROC TTEST in SAS Release 9.1 (SAS Institute, 2003). Before the ANOVA, normality tests were done and where needed, data were log and square root transformed to meet the normality criteria. Differences were considered significant at $p \leq 0.10$. Since both the ANOVA and paired *t* tests yielded similar *p* values, only one *p* value is reported here. In addition, regression analysis was used to evaluate the role of biotic and abiotic site characteristics as explanatory variables of SOC (0–60 cm) content under the two vegetation types. Differences in SOC characteristics between aspen and conifer soils, that is, decomposability determined from cumulative CO_2 release at the end of the incubation (~350 d), and relative C distribution among the light and the mineral-associated were tested using a simple or paired *t* tests, as appropriate for the sampling design.

RESULTS AND DISCUSSION

Soil Morphology

Soils under aspen were classified as Mollisols, except for one soil at TWDEF (TA1) that was classified as an Alfisols and exhibited characteristics of a mollic epipedon; soils under the conifers were classified as Alfisols (BC1, TC1, TC2), Entisols (BC2), or Inceptisols (FC1, FC3) (Table 1). These soil classifications were consistent with the previously published results for the DLL and TWDEF sites (Skujins and Klubek, 1982; Washington-Allen et al., 2004; Van Miegroet et al., 2005). Aspen soils typically had a more pronounced and deeper A horizon (range 38–53 cm) compared to the adjacent conifer soils (range 5.5–34 cm), and the difference in thickness of the A horizon between aspen (43.3±6.6 cm) and conifer soils (16.2±12.4 cm) was statistically significant across all sites ($p = 0.01$). In contrast, very little O horizon was present in the aspen plots while conifer sites had distinct O horizons, ranging in depth from 0.5 to 10 cm, likely reflecting more rapid decomposition of aspen litter compared to conifer litter (Alban and Pastor, 1993; Bartos and DeByle, 1981; Prescott et al., 2000). O horizons were generally thinner in DLL than in the TWDEF conifer sites, which could be attributed to a difference in soil temperature (DLL was slightly warmer) resulting in differential decomposition rates (Trofymow et al., 2002).

Conifer soils at TWDEF were further characterized by an accumulation of clay in subsoil with a characteristic Bt horizon, consistent with the observations of Van Miegroet et al. (2005). Soils in both sites were generally characterized by high base saturation (Table 1), an indication of limited moisture and restricted cation leaching (Van Miegroet et al., 2005).

Soil Organic Carbon Distribution and Pools

In all aspen and conifer plots, the SOC concentration typically declined with depth (Table 1). The SOC concentrations in the upper pedon horizon samples (0–20 cm) were not significantly different from those obtained from multiple cores (0–15 cm) in aspen ($p = 0.93$) or conifer ($p = 0.55$) soils; thus the C data obtained from the upper horizon in the pedons were representative for plot values with an overall average of 28.9 ± 8.2 mg C g^{-1} in aspen and 29.6 ± 11.3 mg C g^{-1} in conifer soils. These aspen SOC concentrations were within the range of values reported earlier for the site [34.6 mg C g^{-1} (1–4 cm) and 13.8 mg C g^{-1} (4–6 cm)], while conifer values were somewhat higher (Van Miegroet et al., 2005).

Using data from the 0- to 15-cm soil cores, SOC content in the upper mineral soil did not differ significantly among vegetation types ($p = 0.55$) with an average of around 50 Mg C ha^{-1} in both forest types (Table 2). These values were within the range of published values for the upper 20 cm of many forest soils in the United States (Franzmeier et al., 1985; Grigal and Ohmann, 1992). When the comparison was extended to the 60-cm soil depth using the pedon data, however, aspen mineral soils contained significantly more SOC ($p = 0.009$), with an average of 96 Mg C ha^{-1} vs. 67 Mg C ha^{-1} for conifers. Differences in SOC content between aspen and conifer soils varied considerably with location, ranging from a high of 54.4 Mg ha^{-1} in B1 to a low of 7.5 Mg ha^{-1} in T2 (Table 2). Consistent with the O-horizon depth results, conifers accumulated more than five times more SOC in the forest floor ($p = 0.0035$), again with considerable variability among sites (Table 2). In only one site (T2) did the higher SOC in the O horizon in conifers compensate for lower SOC accumulation in the mineral soil. Across the entire dataset, inclusion of the forest floor did not fundamentally change the outcome, as the amount of SOC accumulated in the O horizon plus the upper 60 cm of the mineral soil was 25% higher under aspen (98 Mg C $ha^{-1)}$ than under conifer (78.5 Mg C ha^{-1}, $p = 0.02$).

Our total SOC in aspen mineral soils (0–60 cm) was lower than the SOC estimates (0–40 cm) derived from 33 sampling pits in stable aspen stands at Upper Frost in DLL (111.9 ± 29.1 Mg C ha^{-1}) (Woldeselassie, 2009). As with our data, that study revealed tremendous spatial variability in SOC content within aspen, with a nearly threefold difference between highest and lowest estimates, attributed to differences in aspect, soil microclimate and stand characteristics. The lower aspen SOC contents reported in our study may reflect the incipient effect of conifer encroachment, resulting in a slight decrease in SOC, as many aspen stands were not pure and contained some conifer saplings. Lower SOC contents previously measured at the TWDEF site for aspen (53 Mg C ha^{-1} at 0–130 cm) and conifer (90 Mg C ha^{-1} at 0–150 cm) may reflect the influence of stand structure, as these sites had lower aspen and conifer tree density (Van Miegroet et al., 2005) compared to our study plots (Table 2). Finally, our SOC content estimates for both aspen and conifers are lower than the values reported by Grigal and Ohmann (1992) in the Lake States (123 Mg C ha^{-1} for aspen; 181 Mg C ha^{-1} for balsam fir) and by O'Neill et al. (2002) in

Table 1. Soil morphology, classification, and chemical and physical soil properties of aspen and conifer pedons at Deseret Land and Livestock (DLL) and T.W. Daniel Experimental Forest (TWDEF).

Horizon	Depth	Color (Dry)	Field texture	Clay	Bulk density	Coarse fraction	Field pH	C	C/N	CEC†	BS	Horizon	Depth	Color (Dry)	Field texture	Clay	Bulk density	Coarse fraction	Field pH	C	C/N	CEC	BS
	cm			%	g cm^{-3}	g kg^{-1}		g kg^{-1}		cmolc kg^{-1}	%		cm			%	g cm^{-3}	g kg^{-1}		g kg^{-1}		cmol$_c$ kg^{-1}	%
Upper Frost Canyon Watershed																							
FA1 (Aspen) Typic Haploxeroll												**FC1 (Conifer) Humic Haploxerepts**										
A1	0–14	10YR 5/4	L	12	1.14	4	6.0	20.3	14	6.8	92	A	1–12.5	7.5YR 2/2	SIL	12	0.80	20	5.9	28.1	9	14.8	100
A2	14–38.5	10YR 5/4	L	13	1.23	28	5.8	8.1	12	4.8	100	Bw1	12.5–46.5	10YR 6/4	SIL	9	1.32	17	5.8	8.1	12	5.7	83
Bw1	38.5–58.5	10YR 5/4	SIL	15	1.47	11	5.8	10.9	13	3.6	98	Bw2	46.5–67	10YR 6/4	SIL	13	1.16	6	5.6	3.2	10	1.6	100
Bw2	58.5–83	10YR 6/4	SIL	16	1.26	9	5.6	5.2	7	2.2	96	Bw3	67–95	10YR 6/4	SIL	14	1.23	4	5.3	2.8	9	1.2	63
BC	83–100	10YR 6/4	SIL	11	na	20	5.5	na	na	na	na												
FA2 (Aspen) Pachic Haploxerolls												**FC2 (Conifer) Humic Haploxerepts**										
A1	0–16.5	10YR 2/2	LS	5	0.84	37	5.3	30.9	16	15.9	92	A	2–7.5	7.5YR 5/4	L	14	1.26	154	5.8	20.7	17	6.8	100
A2	16.5–38	10YR 5/3	SL	7	1.16	29	4.9	14.6	13	10.1	100	Bw1	7.5–36	7.5YR 5/6	GRL	15	1.1	43	5.5	14.3	15	4.5	98
A3	38–60	10YR 5/3	GRSL	8	1.1	55	4.6	11.4	11	6.2	100	Bw2	36–66	7.5YR 5/4	SIL	10	1.28	79	5.6	7.2	15	2.8	100
C	60–90	7.5YR 6/4	GRSL	7	1.47	189	5.7	2.9	8	1.8	100	C	66–100	5YR 6/6	L	12	nd	nd	5.8	nd	nd	1.6	100
Bear Canyon Watershed																							
BA1 (Aspen) Pachic Haploxerolls												**BC1 (Conifer) Typic Haploxeralfs**										
A1	0–25.5	10YR 5/4	L	8	0.91	8	6.2	39.8	17	12.4	100	A	0.5–7.5	10YR 4/3	L	12	0.84	6	6.3	43.8	18	18.2	100
A2	25.5–50.5	10YR 5/4	L	10	1.00	7	6.1	17.1	13	6.2	100	AB	7.5–32	7.5YR 4/4	L	14	1.08	3	5.9	16.5	15	7.2	100
Bw1	50.5–70	7.5YR 4/6	L	16	1.13	6	5.7	10.5	12	4.4	100	Bw1	35–52	7.5YR 5/6	SL	19	1.16	19	6.2	7.5	11	3.2	100
BC	70–100	7.5YR 4/6	L	14	1.30	3	5.8	6.8	10	3.1	100	Bt	52–81	5YR 6/6	SCL	25	1.33	13	6	3.7	8	3.2	100
BA2 (Aspen) Typic Haploxerolls												**BC2 (Conifers) Typic Xerorthents**										
A	0–40	10YR 5/3	SL	10	1.05	10	5.2	17.2	13	6.5	100	A1	1–7.5	10YR 6/4	SIL	10	1.16	33	5.5	19.7	14	7.7	94
Bw1	40–50	10YR 7/3	SL	8	1.40	1	5.5	4.3	9	1.7	100	A2	7.5–35	7.5YR 6/4	SIL	8	1.18	3	5.4	8.2	10	4.4	76
Bw2	50–80	10YR 7/3	LS	13	1.46	42	5.8	2.7	12	1.5	100	C1	35–42.5	7.5YR 6/4	SIL	13	0.87	2	5.3	6.6	10	1.8	82
C	80–100	10YR 6/3	GRLS	14	1.42	3	5.4	3.8	9	1.7	94	C2	42.5–60	2.5YR 7/8	GRSIL	14	1.73	258	5.4	3.1	10	4.8	41
T.W. Daniel Experimental Forest																							
TA1 (Aspen) Mollic Haplocryalf												**TC1 (Conifer) Typic Haplocryalfs**										
A	0–40	10YR 4/4	GRSCL	21	1.05	226	4.9	18.5	8	11.3	100	A	10–40	10YR 5/4	GRSL	17	0.86	195	5.2	12.75	16	8.7	84
Bt1	40–68	7.5YR 4/6	GRSICL	30	1.11	66	4.9	7	9	19	39	Bt1	40–73	10YR 4/4	GRSCL	25	1.01	144	5.6	3.5	7	8.3	82
Bt2	68–80	5YR 4/6	GRVSICL	27	1.19	42	4.7	4.2	8	18.4	40	Bt2	73–100	5YR 5/6	GRSCL	21	1.21	442	5.4	4.2	9	9.3	83
TA2 (Aspen) Pachic Haplocryolls												**TC2 (Conifer) Typic Haplocryalfs**										
A1	0–8	10YR 5/3	GRSL	10	0.76	348	5.3	42.2	19	13.8	88	A	4–13.5	10YR 5/4	GRSIL	18	0.86	195	5.4	26.3	18	21.4	73
A2	8–53	10YR 5/3	GRSL	9	1.14	122	5.4	9.4	10	6.8	70	Bt1	13.5–35	10YR 6/3	GRSIL	22	1.01	144	6.0	16.0	15	19.2	77
C	53–95	7.5 YR 6/4	CBXLS	7	1.17	290	5.5	6	9	4.2	67	Bt2	35–90	7.5YR 4/6	VGRCL	57	1.21	442	5.5	4.8	9	5.23	52

† Abbreviations: CEC = cation exchange capacity, BS = base saturation, na = not applicable, L = loam, SIL = silt loam, SL = sandy loam, LS = loamy sandy, SCL = sandy clay loam, SICL = silty clay loam, C = Clay, GR = gravelly, GRV = very gravelly, CB = cobbly, CBX = extremely cobbly.

Table 2. Site characteristics and soil organic carbon (SOC) contents in aspen and conifer plots at Deseret Land and Livestock (DLL) and T.W. Daniel Experimental Forest (TWDEF).

Site ID	Vegetation type	LBA†	Tree density	Average tree diameter	Cumulative moisture index‡	SOC content			
						TOTAL (O horizon + 0–60 cm mineral soil)	O horizon	Mineral soil (0–15 cm)	Mineral soil (0–60 cm)
		m^2 ha^{-1}	no. of trees ha^{-1}	cm	m^3 m^{-3}	Mg C ha^{-1}			
Frost (F1)	Aspen	21.9	478	24.2	13.13	88.9	1.04	45.3	87.9
	Conifer	46.1	573	32.0	11.71	70.4	2.32	63.0	68.1
Frost (F2)	Aspen	18.3	892	16.7	7.79	105.3	1.84	56.7	103.5
	Conifer	36.4	350	36.4	5.41	85.4	3.5	90.6	81.9
Bear (B1)	Aspen	41.5	1561	18.4	21.2	147.8	1.44	57.4	146.4
	Conifer	37.3	1274	19.3	10.42	104.8	12.75	47.9	92.0
Bear (B2)	Aspen	25.8	1242	16.3	11.97	83.1	1.58	56.0	81.5
	Conifer	34.2	860	22.5	8.51	61.6	8.13	36.7	53.5
TWDEF (T1)	Aspen	53.0	2197	17.5	19.33	87.3	1.97	38.8	85.3
	Conifer	34.8	637	26.4	12.55	65.9	25.21	36.5	40.7
TWDEF (T2)	Aspen	25.4	1227	17.5	6.4	74.7	2.05	44.5	72.6
	Conifer	25.2	541	24.3	8.38	82.6	17.46	54.6	65.1
Mean across all sites	Aspen	31.0±13.4§	1266±586	18.4±3.0	13.30±5.98	97.9±26.5	1.65±0.38	49.5±7.9	96.2±26.7
	Conifer	35.7±6.7	706±323	26.8±6.3	9.49±2.61	78.5±15.9	11.6±8.8	54.9±20.3	66.9±18.6
Vegetation effect		$p = 0.48$	**$p = 0.05$**	**$p = 0.02$**	**$p = 0.04$**	**$p = 0.02$**	**$p = 0.0035$**	$p = 0.55$	**$p = 0.009$**

† Abbreviations: LBA, live basal.

‡ For explanation of term and numeric calculation, see Methods section.

§ Vegetation average ± standard deviation about the mean.

Interior Alaska (163 Mg C ha^{-1} for aspen; 129 Mg C ha^{-1} for white spruce), which might be attributed to the very cold temperatures at those sites slowing down decomposition and causing greater SOC accumulation.

Site Characteristics and Soil Organic Carbon

As microclimate and stand characteristics proved important in determining SOC content in pure aspen stands (Woldeselassie, 2009), these biotic and abiotic site factors were also compared as potential drivers for differences in SOC accumulation among vegetation types. The stand and soil characteristics of all plots are summarized in Table 2. Overstory cover, as expressed by LBA, was not significantly different between aspen and conifer plots ($p = 0.48$) and total SOC (0–60 cm) was uncorrelated to this stand parameter at the plot level. In contrast, tree density (trees per ha) was significantly higher ($p = 0.05$) and the average tree diameter significantly lower ($p = 0.02$) in the aspen plots. These findings indicated a difference in forest structure between aspen and conifer, with the latter composed of fewer larger trees, whereas the aspen stands were densely vegetated with smaller trees. Across all plots, SOC content increased with tree density ($R^2 = 0.18$, $p = 0.16$) and decreased with average tree diameter ($R^2 = 0.14$, $p = 0.23$), but these correlations were not statistically significant (data not shown). From this we conclude that the variability in overstory characteristics among the experimental plots and between aspen and conifer were not the main driver in the observed differences in SOC storage.

Statistical analysis of the CMI showed that aspen soils had greater moisture content than adjacent conifer soils in summer 2007 ($p = 0.04$). In another study at DLL, LaMalfa and Ryel (2008) similarly observed that average shallow soil moisture content was higher in the aspen plots relative to the adjacent conifer plots, which was attributed to higher porosity and higher water holding capacity in aspen soils relative to conifers. A hydrologic study in Montana (Moore and McCaughey, 1997) also showed lower soil moisture status of the conifers relative to the aspen stands especially in late spring due to lower snow accumulation under conifers. In contrast, Olsen and Van Miegroet (2010) observed that conifer soils at the TWDEF site were less dry in summer 2005 compared to other vegetation types including aspen. This indicates that moisture regime can be site-specific and vary temporally as well. We found that across sites and vegetation types, SOC storage was positively correlated with CMI (Fig. 2), with differences in soil moisture explaining 25% of the variability in SOC content ($p = 0.09$). While this correlation was largely driven by a single aspen site (BA1), it is interesting to note that at all locations (except T2), conifer plots consistently showed a concurrent decline in CMI and SOC content relative to corresponding aspen soils (Fig. 2, Table 2).

Our intent had been to also evaluate the influence of differences in soil temperature regime on SOC, but due to equipment failure a complete temperature data set for all the plots could not be obtained. Salvaged data from four aspen and one conifer stands showed that the average daily soil temperature under aspen was 11.8°C in late summer, 3.9°C in fall, −0.5°C in winter, and 8.1°C in spring–early summer while corresponding average soil temperatures in the conifer stand were 9.7°C, 3.7°C, 0.1°C and 5.7°C in late summer, fall, winter and spring–early summer, respectively. This limited soil temperature data suggests that aspen soils might be slightly warmer, especially in spring and

summer. Results are consistent with the Olsen and Van Miegroet (2010), where conifers had lower and less variable temperature. Because of the incomplete data, relationships between SOC and temperature could not be analyzed further.

Soil Organic Carbon Characteristics

Differences in SOC storage between aspen and conifer soils were consistent with qualitative differences in SOC among these soils as expressed by the biological and physical parameters used in this study. Cumulative CO_2 release during aerobic incubation of soil cores taken between 0- and 15-cm depth showed that SOC in conifer soils was more accessible for microbial breakdown (i.e., more decomposable) (Fig. 3, $p = 0.01$) than SOC in aspen mineral soils (conifer mean of 130.9 ± 41.3 g CO_2–C per kg C for vs. 67.7 ± 15.7 g CO_2–C per kg C for aspen soils), with vegetation differences in SOC decomposability varying substantially among locations (ranging from 10% to threefold difference), mostly due to large fluctuations in conifer values (Fig. 3). The plots with the highest SOC decomposability (BC2 and TC1) also had the lowest SOC pools in the mineral soil (Table 2) and across the entire dataset there is general inverse relationship between SOC decomposability and SOC stored in the top 60 cm of the mineral soil ($r = -0.58$, $p = 0.04$) (Fig. 4), mostly driven by the conifer forest soils. Our multi-site comparison strongly supports the patterns suggested in an earlier study at TWDEF (Olsen and Van Miegroet, 2010) and agrees with Giardina et al. (2001), who similarly found during long-term incubations that upper soils under aspen contained SOC that was less mineralizable than the SOC found in pine stands in northern Colorado. It is also consistent with a short-term incubation study of temperate forest soils by Moukoumi et al. (2006), which showed that SOC in the topsoil under spruce was more biodegradable than SOC in soils under broadleaf cover (primarily consisting of beech). They also noted, however, that SOC decomposability was lowest in soils under Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco).

This lower microbial SOC turnover in aspen soils could be the result of many factors: intrinsic differences in chemical composition of SOC and C inputs, differences in microbial abundance and composition, and/or protection of SOC making it less accessible to microbes (Six et al., 2002b; Rovira and Vallejo, 2003; Davidson and Janssens, 2006). Since we did not conduct a full chemical characterization of the SOC in each system beyond what was reported for TWDEF in Van Miegroet et al. (2005), we cannot conclusively preclude differences in SOC chemistry and recalcitrance. Nor can we preclude differences in microbial communities often found between coniferous and broadleaved forest soils.

The rapid turnover of aspen litter, indicated by the limited O-horizon accumulation, and the greater SOC stability in the mineral soil, expressed by a well-developed mollic horizon in the aspen sites, represents somewhat of a contradiction. This disconnect between litter and belowground SOC dynamics is not a new observation, but has previously been reported in a

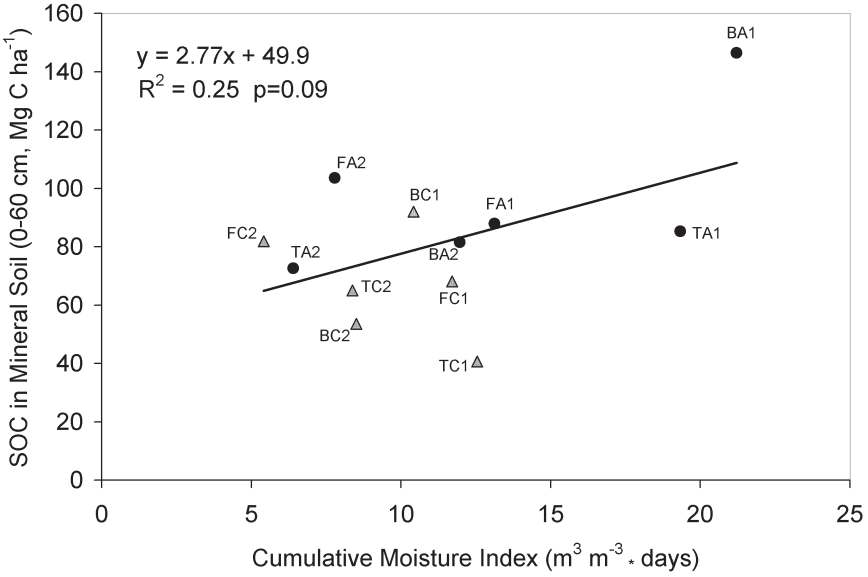

Fig. 2. Regression of soil organic carbon (SOC) storage in the mineral soil (0–60 cm) against cumulative soil moisture index for the sites (circle indicates aspen, triangle indicates conifer soils, Plot ID labels as per Table 1).

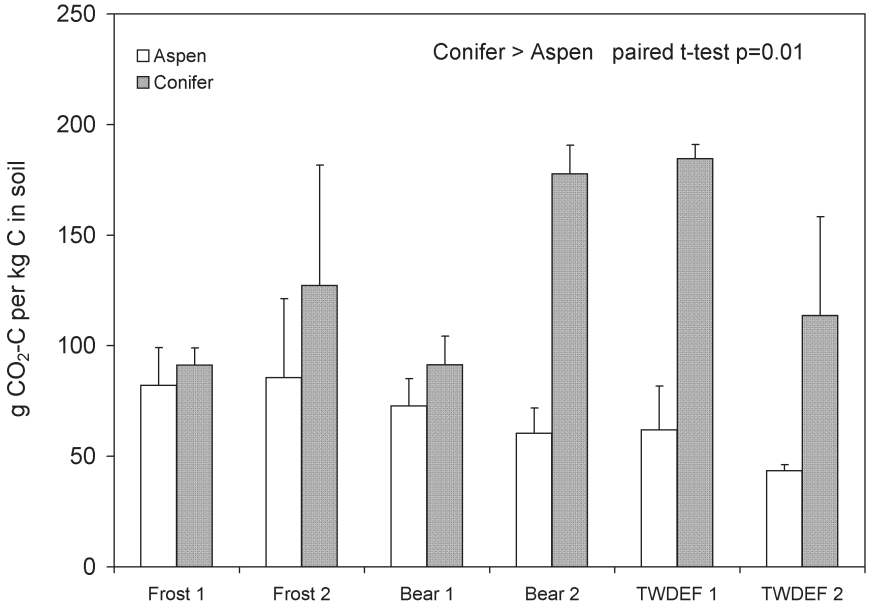

Fig. 3. Cumulative CO_2–C release per unit C in after 350 d of incubation of mineral soils (0–15 cm) taken in paired aspen and conifer plots at different locations. Error bars represent standard deviations about the mean ($n = 2$).

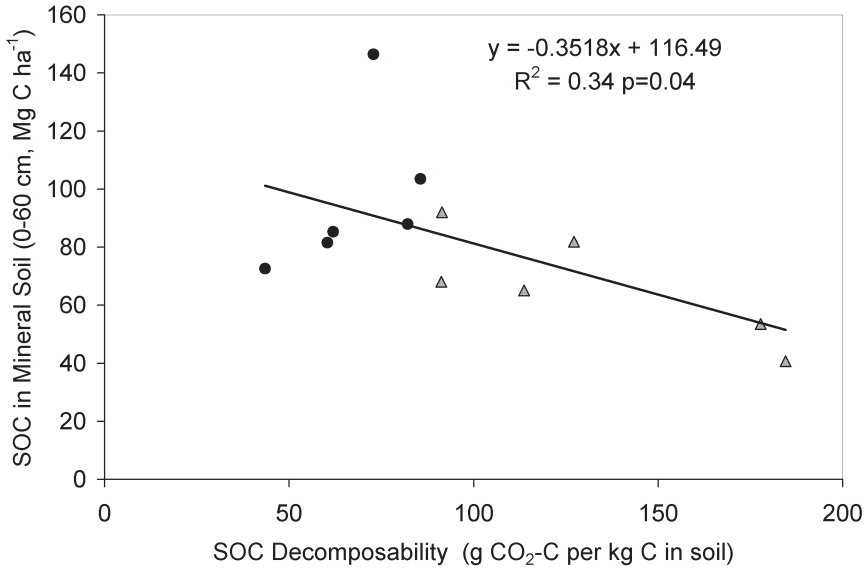

Fig. 4. Relationship between soil organic carbon (SOC) storage in the mineral soil (0–60 cm) and SOC decomposability during incubation of mineral soil (0–15cm) (circle indicates aspen soils, triangle indicates conifer soils).

variety of forest soils in the United States (Garten, 2009) and Europe (Rovira and Vallejo, 2003; Hagedorn and Machwitz, 2007).

Physical fractionation of the SOC into free, occluded, and adsorbed SOC, points at some interesting differences in relative SOC distribution in the upper aspen and conifer soils that may explain the greater stability of SOC in aspen soils. Contrary to observations by Six et al. (2002a), particulate organic matter C occluded within the aggregates represented only a small fraction of total SOC (<10%) that did not differ with vegetation type (Table 3). Most SOC in both soil types was accounted for by light fraction (LF) C and mineral-associated carbon (MOC), similar to observations by Rovira and Vallejo (2003). There were significant differences in the relative distribution among these fractions between aspen and conifer soils. A greater proportion of total SOC was mineral associated (i.e., adsorbed to the clay and silt surfaces) in surficial aspen soils (mean 55±13%) compared to conifer soils (mean 41±13%)(t test p = 0.01), whereas LF-SOC was slightly more important in conifer soils (mean 52±23%) than aspen soils (39.5±11%) (t test p = 0.01).

Table 3. Relative proportion of on soil organic carbon (SOC) (%) in heavy and light fraction.

Vegetation type	Light Fraction OC	Mineral-associated OC	Particulate OC
Bear (2009 Transect Cores)			
Aspen	33±7%	63.5±5%	3.3±2.3%
Conifer	47±16%	50±15%	3.0±1.7%
Frost (2009 Transect Cores)			
Aspen	43±6%	50.5±9%	6.1±3.9%
Conifer	59±10%	30±13%	11.0±9.9%
TWDEF† (2004 Pedons-first Horizon)			
Aspen	42±10%	51±12%	7.3±6.3%
Conifer	49±6%	43±7%	7.5±2.8%
TWDEF (2004 Pedons-second Horizon)			
Aspen	20±6%	75±5%	5.3±1.5%
Conifer	37±12%	57±10%	6.4±4.1%

† Abbreviations: TWDEF, T.W. Daniel Experimental Forest.

The difference in SOC fractionation between aspen and conifer was even more pronounced in the second horizon of the TWDEF soils (Table 3, p = 0.04 for MOC and p = 0.06 for LF), even though the majority of SOC was mineral associated in both systems. This depth profile in SOC speciation agrees with Rovira and Vallejo (2003), who found strongest linear increases for the LF with increasing SOC content across sites, but a decline in the importance of the LF with increasing soil depth. Our findings are also consistent with a recent study by Díaz-Pinés et al. (2011), comparing SOC storage and stability under Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.) ecosystems in central Spain and found that the higher SOC stocks measured under conifers were mainly due to preferential accumulation of nonmineral-associated SOC (POM-C in their case) in the mineral soil, which is considered more labile (von Lützow et al., 2007). Laganiere et al. (2011) similarly found that under spruce more SOC was stored in less protected fractions compared to trembling aspen.

Our data suggests that greater SOC storage and stabilization in the mineral soil under aspen is caused by adsorption to the fine fraction (i.e., silt+clay). This mechanism likely accounts for the importance of soil clay content as a predictor of SOC storage in regional assessments (Burke et al., 1989; Schimel et al., 1994; Homann et al., 1995; Amelung et al., 1998), even though this relationship did not hold in frigid or cryic soils of Montana (Sims and Nielsen, 1986). Greater OC adsorption rates can be due to a larger number of adsorption sites or by differences in the concentration and/or chemistry of the OC contacting these adsorption sites (e.g., Lilienfein et al., 2004). Since soils in the paired aspen–conifer plots had similar texture, and soils under aspen did not have higher clay contents (Table 1), it would appear that differences in texture or clay content per se (i.e., adsorption sites) were not the main cause for SOC storage differences between aspen and conifer soils. This would suggest differences in the OC supply as a more likely driver for differences in MOC. We propose a mechanism that can reconcile the rapid O turnover with greater SOC stability under aspen and is supported by previously collected data at one of the sites (TWDEF). The rapid decomposition of the aspen litter (mostly under the snowpack [H. Van Miegroet, unpublished data, 2007]) and hydrologic flow into the soil mostly during snowmelt and ceasing late spring (Scott Jones, personal communication, 2012; see also USGS SNOTEL-USU Doc Daniel: http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=1098&state=ut) could create a pulse in DOC that facilitates stabilization of SOC through adsorption on clay surfaces deeper in the mineral soil.

The higher water-extractable OC (used as an indicator of soluble or leachable SOC) levels throughout aspen pedons compared to nearby conifer soils observed in an earlier study at TWDEF lends support to this proposed scenario (Van Miegroet et al., 2005). In addition, Hongve et al.. (2000) observed that under similar climatic conditions, deciduous litter gives off proportionally more DOC than conifer litter. Alternatively, lower DOC flux from the conifer O horizon into the mineral soil could also be due to DOC retention within the thick conifer litter layer itself, as observed by Müller et al. (2009) in alpine soils. At this point, our study cannot ascertain whether differences in production and/or retention of DOC in the O horizon cause the previously observed differences in water-extractable OC. However, collectively, the available data from this and earlier studies, coupled with the evidence from the literature, point at the potential role of DOC production and transport in creating differences in the belowground SOC storage and stabilization among these two vegetation types. At this point, it remains a working hypothesis that, while reasonable, needs to be further verified with laboratory and field data.

SUMMARY AND CONCLUSIONS

While our understanding of SOC storage and stabilization is still incomplete, this study offers some interesting insights into the interaction between vegetation, climate, and SOC storage. First of all, the lack of significant differences in SOC content of the upper surface (0–15 cm) among the two vegetation types emphasizes the importance of soil sampling depth, and stresses the fact that surface sampling may not always yield very informative results. This is an important observation, as many ecological studies consider the A horizon and the forest floor "dynamic" constituents of the soil and routinely sample only at shallow depth, even though several researchers have found that most of the variability in SOC may occur at greater depths (e.g., Fernandez et al., 1993; Hammer et al., 1995; Harrison et al., 2003), and SOC in deeper soil horizons may be more responsive to management (Diochon and Kellman, 2009; Harrison et al., 2011). This is particularly relevant within the context of C sequestration and how it is influenced by land use changes or management that involves shifts in vegetation cover.

Second, the divergent SOC storage patterns above (O horizon) and below the surface (mineral soil) demonstrate the fallacy of using aboveground observations to infer belowground dynamics. The rapid turnover and low accumulation of aspen litter was actually associated with greater stability of SOC in the mineral soil, expressed by the development of a mollic epipedon, and resulting in a overall 25% higher SOC pool under aspen relative to conifer soils. The greater SOC storage in the aspen mineral soil was associated with lower decomposability of that SOC, which may in part be linked to greater SOC protection through adsorption to the clay surfaces. In environments such as these in western United Staates, where fire is an important disturbance agent, the ready redistribution of SOC from the O horizon into the mineral soil further contributes to the protection and longevity of SOC in aspen compared to conifer ecosystems.

The influence of vegetation on soil properties is not independent of climate. While considerable research has been conducted on nutrient cycling and soil properties of aspen forests in more mesic environments (e.g,. Alban, 1982; Paré and Bergeron, 1996; Laganiere et al., 2011), much less is known about aspen in semiarid or seasonally dry climates, and processes observed in mesic environments may have different outcomes in drier environments. Water limitation may play a significant role differentiating SOC dynamics within the mineral soil of conifer vs. aspen forests. Under aspen, soils were generally wetter, and this difference in water supply may have been sufficient to facilitate greater delivery and transport of DOC within the soil profile followed by adsorption to silt and clay surfaces, resulting in greater net accumulation and stabilization of SOC under aspen over time.

Finally, there is also still a large disconnect between the current state of the knowledge of what controls SOC stability and storage (sensu Six et al., 2002b; Jastrow et al., 2007) and how these concepts are portrayed in current SOC dynamics models [e.g., Century (Parton et al., 1987) or YASSO (Liski et al., 2005)]. In these models, vegetation impact on SOC storage is largely translated through the origin and biochemical composition of the litter input, using the content of lignin and lignin-like compounds as an indicator of recalcitrance and pathways of stabilization. They do not consider, however, that intrinsically labile and easily decomposable SOC or DOC can be stabilized through adsorption or occlusion. Our study suggests SOC stability and storage in the mineral soil may follow patterns that are quite different from litter dynamics.

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REFERENCES

Alban, D.H. 1982. Effects of nutrient accumulation by aspen, spruce and pine on soil properties. Soil Sci. Soc. Am. J. 46:853–861. doi:10.2136/sssaj1982.03615995004600040037x

Alban, D.H., and J. Pastor. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. 23:1744–1749. doi:10.1139/x93-220

Amacher, M.C., A.D. Johnson, D.E. Kutterer, and D.L. Bartos. 2001. First-year postfire and postharvest soil temperatures in aspen and conifers stands. Paper RMRS-RP-27. USDA Forest Serv. Res., Fort Collins, CO.

Amelung, W., W. Zech, X. Zang, R.F. Follett, H. Tiessen, E. Knox, and K.-W. Flach. 1998. Carbon, nitrogen and sulfur pools in particle-size fractions as influenced by climate. Soil Sci. Soc. Am. J. 62:172–181. doi:10.2136/sssaj1998.03615995006200010023x

Bartos, D.L. 2001. Landscape dynamics of aspen and conifer forests. In: W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew, editors, Sustaining aspen in western landscapes. Symposium Proceedings. USDA Forest Serv., Rocky Mountain Res. Stn., Fort Collins, CO. p. 5–14.

Bartos, D.L., and M.C. Amacher. 1998. Soil properties associated with aspen to conifer succession. Rangelands 20:25–28.

Bartos, D.L., and R.B. Campbell, Jr. 1998. Decline of quaking aspen in the interior west: Examples from Utah. Rangelands 20:17–24.

Bartos, D.L., and N.V. DeByle. 1981. Quantity, decomposition and nutrient dynamics of Aspen litterfall in Utah, USA. For. Sci. 27:381–390.

Blake, G.R., and K.H. Hartge. 1986. Bulk density. In: A. Klute, editor, Methods of soil analysis. Part 1. Physical and mineralogical methods. Agron. Monogr. 9. ASA, Madison, WI. p. 364–375.

Burke, I.C., C.M. Yonker, W.J. Parton, C.V. Cole, K. Flach, and D.S. Schimel. 1989. Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. Soil Sci. Soc. Am. J. 53:800–805. doi:10.2136/sssaj1989.03615995005300030029x

Chen, W.J., T.A. Black, P.C. Yang, A.G. Barr, H.H. Neumann, Z. Nesic et al. 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. Glob. Change Biol. 5:41–53. doi:10.1046/j.1365-2486.1998.00201.x

Cryer, D.H., and J.E. Murray. 1992. Aspen regeneration and soils. Rangelands 14:223–226.

Davidson, E.A., and I.A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature (London) 440:165–173. doi:10.1038/nature04514

DeByle, N.V., and R.P. Winokur, editors. 1985. Aspen: Ecology and management in the western United States. Gen. Tech. Rep. RM-119. USDA Forest Serv., Rocky Mountain Forest and Range Exp. Stn., Fort Collins, CO.

Díaz-Pinés, E., A. Rubio, H. Van Miegroet, F. Montes, and M. Benito. 2011. Does tree species composition control soil organic carbon pools in Mediterranean mountain forests? For. Ecol. Manage. 262:1895–1904. doi:10.1016/j.foreco.2011.02.004

Diochon, A.C., and L. Kellman. 2009. Physical fractionation of soil organic matter: Destabilization of deep soil carbon following harvesting of a temperate conifer forest. J. Geophys. Res. 114:G01016. doi:10:1029/2008JG000844.

Fernandez, I.J., L.E. Rustad, and G.B. Lawrence. 1993. Estimating total soil mass, nutrient content, and trace metals in soils under a low elevation spruce-fir forest. Can. J. Soil Sci. 73:317–328. doi:10.4141/cjss93-034

Franzmeier, D.P., G.D. Lemme, and R.J. Miles. 1985. Organic carbon in soils of North Central United States. Soil Sci. Soc. Am. J. 49:702–708. doi:10.2136/sssaj1985.03615995004900030035x

Garten, C.T., Jr. 2009. A disconnect between O horizon and mineral soil carbon– Implications for soil C sequestration. Acta Oecol. 35:218–226. doi:10.1016/j.actao.2008.10.004

Giardina, C.P., M.G. Ryan, R.M. Hubbard, and D. Binkley. 2001. Tree species and soil textural control on carbon and nitrogen mineralization rates. Soil Sci. Soc. Am. J. 65:1272–1279. doi:10.2136/sssaj2001.6541272x

Gifford, G.F., W. Humphries, and R.A. Jaynes. 1984. A preliminary quantification of the impacts of aspen to conifer succession on water yield—II. Modeling results. Water Resour. Bull. 20:181–186. doi:10.1111/j.1752-1688.1984.tb04669.x

Grigal, D.F., and L.F. Ohmann. 1992. Carbon storage in upland forests of the Lake States. Soil Sci. Soc. Am. J. 56:935–943. doi:10.2136/sssaj1992.03615995005600030042x

Hagedorn, F., and M. Machwitz. 2007. Controls on dissolved organic matter leaching from forest litter grown under elevated atmospheric CO_2. Soil Biol. Biochem. 39:1759–1769. doi:10.1016/j.soilbio.2007.01.038

Hammer, R.D., G.S. Henderson, R. Udawatta, and D.K. Brandth. 1995. Soil organic carbon in the Missouri forest-prairie ecotone. In: J.M. Kelly and W.W. McFee, editors, Carbon forms and functions in forest soils. SSSA, Madison, WI. p. 201–231.

Harper, K.T., R.A. Woodward, and K.B. Knight. 1981. Interrelationships among precipitation, vegetation and streamflow in the Uinta Mountains, Utah. In: K.T. Harper, editor, Potential ecological impacts of snowpack augmentation in the Uinta Mountains, Utah. Dep. of Botany and Range Sci., Brigham Young Univ., Provo, UT. p. 16–57.

Harrison, R.B., A.B. Adams, C. Licata, B. Flaming, G.L. Wagoner, P. Carpenter, and E.D. Vance. 2003. Quantifying deep-soil and coarse-soil fractions: Avoiding sampling bias. Soil Sci. Soc. Am. J. 67:1602–1606. doi:10.2136/sssaj2003.1602

Harrison, R.B., P.W. Footen, and B.D. Strahm. 2011. Deep soil horizons: Contribution and importance to soil carbon pools and in assessing whole-ecosystem response to management and global change. For. Sci. 57:67–76.

Hoff, C.C. 1957. A comparison of soil, climate, and biota of conifer and aspen communities in the Central Rocky Mountains. Am. Midl. Nat. 58:115–140. doi:10.2307/2422365

Homann, P.S., P. Sollins, H.N. Chappell, and A.G. Stangenberger. 1995. Soil organic carbon in a mountainous, forested region: Relation to site characteristics. Soil Sci. Soc. Am. J. 59:1468–1475. doi:10.2136/sssaj1995.03615995005900050037x

Hongve, D., P.A.W. VanHees, and U.S. Lindstron. 2000. Dissolved components in precipitation water percolated through forest litter. Eur. J. Soil Sci. 51:667–677.

Jastrow, J.D., J.E. Amonette, and V.L. Bailey. 2007. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. Glob. Change Biol. 80:5–23.

Jones, J.R. 1985. Distribution. In: N.V. DeByle and R.P. Winokur, editors, Aspen: Ecology and management in the Western United States. Gen. Tech. Rep. RM-119. USDA Forest Serv., Rocky Mountain Forest and Range Exp. Stn., Fort Collins, CO. p. 9–10.

Jones, J.R., and N.V. DeByle. 1985. Soils. In: N.V. DeByle and R.P. Winokur, editors, Aspen: Ecology and management in the Western United States. Gen. Tech. Rep. RM-119. USDA Forest Serv., Rocky Mountain Forest and Range Exp. Stn., Fort Collins, CO. p. 65–70.

Kulakowski, D., T.T. Veblen, and S. Drinkwater. 2004. The persistence of quaking of aspen (*Populus tremuloides*) in the Grand Mesa area, Colorado. Ecol. Appl. 14(5):1603–1614. doi:10.1890/03-5160

Laganiere, J., D.A. Angers, D. Paré, Y. Bergeron, and H.Y.H. Chen. 2011. Black spruce soils accumulate more uncomplexed organic matter than aspen soils. Soil Sci. Soc. Am. J. 75:1125–1132. doi:10.2136/sssaj2010.0275

LaMalfa, E.M., and R. Ryel. 2008. Differential snowpack accumulation and water dynamics in aspen and conifer communities: Implications for water yield and ecosystem function. Ecosystems 11:569–581. doi:10.1007/s10021-008-9143-2

Lilienfein, J., R.G. Qualls, S.M. Uselman, and S.D. Bridgham. 2004. Adsorption of dissolved organic carbon and nitrogen in soils of a weathering chronosequence. Soil Sci. Soc. Am. J. 68:292–305. doi:10.2136/sssaj2004.0620

Liski, J., T. Palosuo, M. Peltoniemi, and R. Sievänen. 2005. Carbon and decomposition model Yasso for forest soils. Ecol. Modell. 189:168–182. doi:10.1016/j.ecolmodel.2005.03.005

Moore, C.A., and W.W. McCaughey. 1997. Snow accumulation under various forest stand densities at Tenderfoot Creek Experimental Forest. Proceedings of the 65th Annual Western Snow Conference, Banff, Canada. 4–9 May 1997. Colorado State Univ., Fort Collins.

Morgan, M.D. 1969. Ecology of aspen in Gunnison County, Colorado. Am. Midl. Nat. 82:204–228. doi:10.2307/2423831

Moukoumi, J., C. Munier-Lamy, J. Bethelin, and J. Ranger. 2006. Effect of species substitution on organic matter biodegradability and mineral nutrient availability in a temperate topsoil. Ann. For. Sci. 63:763–771. doi:10.1051/forest:2006057

Mueggler, W.F. 1985. Forage. In: N.V. DeByle and R.P. Winokur, editors, Aspen: Ecology and management in the Western United States. Gen. Tech. Rep. RM-119. USDA Forest Serv., Rocky Mountain Forest and Range Exp. Stn., Fort Collins, CO. p. 129–134.

Müller, M., C. Alewell, and F. Hagedorn. 2009. Effective retention of litter-derived dissolved organic carbon in organic layers. Soil Biol. Biochem. 41:1066–1074. doi:10.1016/j.soilbio.2009.02.007

Olsen, H.R., and H. Van Miegroet. 2010. Factors affecting CO_2 release from forest and rangeland soils in northern Utah. Soil Sci. Soc. Am. J. 74:282–291. doi:10.2136/sssaj2009.0095

O'Neill, K.P., E.S. Kapsischke, and D.D. Richter. 2002. Environmental controls on soil CO_2 flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. Can. J. For. Res. 32:1525–1541. doi:10.1139/x02-077

Paré, D., and Y. Bergeron. 1996. Effect of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Can. J. For. Res. 26:1022–1031. doi:10.1139/x26-113

Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci. Soc. Am. J. 51:1173–1179. doi:10.2136/sssaj1987.03615995005100050015x

Paul, E.A., S.J. Morris, and S. Bohm. 2001. The determination of soil C pool sizes and turnover rates: Biophysical fractionation and tracers. In: R. Lal et al., editors, Assessment methods for soil carbon. Lewis Publ., Boca Raton, FL. p. 193–206.

Prescott, C.E., L.M. Zabek, C.L. Staley, and R. Kabzems. 2000. Decomposition

of broadleaf and needle litter in forests of British Columbia: Influences of litter type, forest type, and litter mixtures. Can. J. For. Res. 30:1742–1750. doi:10.1139/x00-097

Rehfeldt, G.E., D.E. Fergusin, and N.L. Crookston. 2009. Aspen, climate and sudden decline in western USA. For. Ecol. Manage. 258:2353–2364. doi:10.1016/j.foreco.2009.06.005

Rogers, P.C. 2002. Using forest health monitoring to assess aspen cover change in the Southern Rockies region. For. Ecol. Manage. 155:223–236. doi:10.1016/S0378-1127(01)00560-6

Rogers, P.C., A.J. Leffler, and R.J. Ryel. 2010. Landscape assessment of a stable aspen community in Southern Utah, USA. For. Ecol. Manage. 259:487–495. doi:10.1016/j.foreco.2009.11.005

Rovira, P., and V.R. Vallejo. 2003. Physical protection and biochemical quality of organic matter in mediterranean calcareous forest soils: Density fractionation approach. Soil Biol. Biochem. 35:245–261. doi:10.1016/S0038-0717(02)00257-2

SAS Institute. 2003. SAS user's guide: Statistics. Release 9.1. SAS Inst., Cary, NC.

Saxton, K.E., W.J. Rawls, J.S. Romberger, and R.I. Papendick. 1986. Estimating generalized soil-water characteristics from texture. Soil Sci. Soc. Am. J. 50:1031–1036. doi:10.2136/sssaj1986.03615995005000040039x

Schimel, D.S., B.H. Braswell, E.A. Holland, R. McKeown, D.S. Ojima, T.H. Painter et al. 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Global Biogeochem. Cycles 8:279–293. doi:10.1029/94GB00993

Schimpf, D.J., J.A. Henderson, and J.A. MacMahon. 1980. Some aspects of succession in the spruce-fir forest zone of northern Utah. Great Basin Nat. 40:1–26.

Shakespeare, B. 2006. Linking quantified lateral flow gains to catchment attributes in a paired watershed study. M.S. thesis. Dep. Watershed Sci., Utah State Univ., Logan.

Sims, Z.R., and G.A. Nielsen. 1986. Organic carbon in Montana soils as related to clay content and climate. Soil Sci. Soc. Am. J. 50:1269–1271. doi:10.2136/sssaj1986.03615995005000050037x

Six, J., P. Callewaert, S. Lenders, S. De Gryze, S.J. Morris, E.G. Gregorich, E.A. Paul, and K. Paustian. 2002a. Measuring and understanding carbon storage in afforested soils by physical fractionation. Soil Sci. Soc. Am. J. 66:1981–1987. doi:10.2136/sssaj2002.1981

Six, J., R.T. Conant, E.A. Paul, and K. Paustian. 2002b. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. Plant Soil 241:155–176. doi:10.1023/A:1016125726789

Skujins, J., and B. Klubek. 1982. Soil biological properties of a montane forest sere- corroboration of Odum postulates. Soil Biol. Biochem. 14:505–513. doi:10.1016/0038-0717(82)90111-0

Soil Survey Division Staff. 1993. Soil survey manual. Agric. Handb. 18. U.S. Gov. Print. Office, Washington, DC.

Tew, R.K. 1968. Properties of soil under aspen and herb-shrub cover. USDA Forest Serv. Res. Note INT-78. Intermountain Forest and Res. Exp. Stn., Ogden, UT.

Trofymow, J.A., T.R. Moore, B. Titus, C. Prescott, I. Morrison, M. Siltanen et al. 2002. Rates of litter decomposition over 6 years in Canadian forests: Influence of litter quality and climate. Can. J. For. Res. 32:789–804. doi:10.1139/x01-117

Van Miegroet, H., J.L. Boettinger, M.A. Baker, J. Nielsen, D. Evans, and A. Stum. 2005. Soil carbon distribution and quality in a montane rangeland-forest mosaic in northern Utah. For. Ecol. Manage. 220:284–299. doi:10.1016/j.foreco.2005.08.017

Van Miegroet, H., M.T. Hysell, and A. Denton Johnson. 2000. Soil microclimate and chemistry of spruce-fir tree islands in Northern Utah. Soil Sci. Soc. Am. J. 64:1515–1525. doi:10.2136/sssaj2000.6441515x

von Lützow, M., I. Kögel-Knabner, K. Ekschmitt, H. Flessa, G. Guggenberger, E. Matzner, and B. Marschner. 2007. SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. Soil Biol. Biochem. 39:2183–2207. doi:10.1016/j.soilbio.2007.03.007

Washington-Allen, R.A., T.G. Van Niel, R.D. Ramsey, and N.E. West. 2004. Remote sensing based piosphere analysis. GIScience Remote Sensing 41(2):136–154. doi:10.2747/1548-1603.41.2.136

Woldeselassie, M. 2009. Soil organic carbon and site characteristics in aspen and evaluation of potential effects of conifer encroachment on soil properties in Northern Utah. M.S. thesis. Dep. Wildland Resources, Utah State Univ., Logan.