Biogeochemistry (2019) 145:161–175
https://doi.org/10.1007/s10533-019-00597-y

Hydrogeomorphic controls on soil carbon composition in two classes of subalpine wetlands

Ellen E. Daugherty · Georgina A. McKee · Robert Bergstrom · Sarah Burton · Céline Pallud · Robert M. Hubbard · Eugene F. Kelly · Charles C. Rhoades · Thomas Borch

Received: 19 October 2018 / Accepted: 6 September 2019 / Published online: 14 September 2019

Abstract Wetlands play a vital role in terrestrial carbon (C) sequestration, but the sensitivity of their C stocks to disturbance remains uncertain, requiring enhanced understanding of the processes that govern C storage and removal. The unique conditions in wetlands from different hydrogeomorphic (HGM) classes likely regulate the cycling, storage and vulnerabilities of wetland soil C stocks. To determine how differences in hydrogeomorphic setting influence soil organic carbon (SOC) processing, we compared C content and composition between depressional and slope wetlands located in the Colorado Rocky Mountains. Isolated depressional wetlands were characterized by seasonally declining water tables, slow discharge, high clay content, and thick organic horizons. Slope wetlands received perennial groundwater inputs and had coarser soil textures and thinner organic horizons. Seasonal snowmelt inputs coupled with low hydrologic discharge and higher clay content in depressional wetlands were predicted to sustain anoxic conditions, leading to high SOC content and chemically reduced C compounds. Depressional wetland soils had higher SOC content at depth and higher porewater DOC concentrations compared to slope wetland soils. Solid-state ^{13}C nuclear magnetic resonance spectroscopy demonstrated that aliphatic

Responsible Editor: Breck Bowden.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10533-019-00597-y) contains supplementary material, which is available to authorized users.

E. E. Daugherty · T. Borch (✉)
Department of Chemistry, Colorado State University, Fort Collins, CO 80523, USA
e-mail: thomas.borch@colostate.edu

G. A. McKee · R. Bergstrom · E. F. Kelly · T. Borch
Department of Soil and Crop Sciences, Colorado State University, Fort Collins, CO 80523, USA

R. Bergstrom
USDA Forest Service, Jackson, MS 39201, USA

S. Burton
Environmental Molecular Science Laboratory, Pacific Northwest National Laboratory, Richland, WA 99352, USA

C. Pallud
Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA 94720, USA

R. M. Hubbard · C. C. Rhoades (✉)
USDA Forest Service Rocky Mountain Research Station, Fort Collins, CO 80526, USA
e-mail: crhoades@fs.fed.us

compounds were the dominant SOC component in depressional wetlands compared to aromatic C forms in the slope wetlands. The higher prevalence of aliphatic carbon in depressional wetland soils suggests that stored SOC is protected by anaerobic conditions to a greater extent than in the slope wetlands, and that this SOC may be more vulnerable to drying and oxic conditions associated with wetland drainage and climate change.

Keywords ^{13}C NMR · Decomposition · Soil organic carbon · Wetlands

Introduction

Wetlands are important ecosystem control points that exert a strong influence on carbon cycling and water quality compared to the surrounding landscape (Bernhardt et al. 2017). They cover a small percentage of the earth's land surface but store substantial amounts of soil organic carbon (SOC) (Mitsch and Gosselink 2007; Lal 2008). North American wetlands make up 37% of the global wetland area and 36% of the global wetland C stock (Kolka et al. 2018). Frequent or permanently saturated conditions create oxygen-depleted soil environments where plant productivity often outpaces organic matter decomposition rates, favoring SOC accrual. Understanding wetland C cycling is critical for predicting changes to C storage as a result of environmental disturbances (e.g. climate and land-use change) and for effectively managing wetlands.

The flow paths that link wetlands with surrounding landscapes govern seasonal water table fluctuations and redox-related biogeochemical processes such as C cycling. The degree of hydrologic connectivity varies among wetland classes corresponding to different hydrogeomorphic (HGM) settings and can influence biogeochemical reaction rates and the supply and processing of C (Segnini et al. 2010, 2013; Bernal and Mitsch 2012; Covino 2017; Ameli and Creed 2017). Organic matter supply, decomposition, and removal rates are likely to differ across a gradient of hydrologic connectivity (Marton et al. 2015) and result in distinct soil C compositions among wetland HGM classes. In general, wetlands with features promoting prolonged anoxic conditions and low hydrologic discharge store more C and have a greater proportion of aliphatic C than wetlands that are minerotrophic or have shorter hydroperiods (Bernal and Mitsch 2008, 2012; Tfaily et al. 2014; Luan et al. 2014; Heller et al. 2015). However, it is unclear how the extent of hydrologic connectivity influences C storage and processing in undisturbed wetlands.

Wetlands with limited surface water connectivity make up an important fraction of mountain wetlands in North America. Small (< 1.5 hectares) and hydrologically unique, these wetlands are often excluded from or not distinguished in national-scale inventories (Johnston et al. 2012), though regional inventories document high densities of non-riverine wetlands in both the Sierra Nevada and Rocky Mountains (Chadde et al. 1998; Chimner et al. 2010; Johnston et al. 2012; Wolf and Cooper 2015). In addition to providing wildlife habitat and hosting diverse plant species (Carsey et al. 2003), high elevation wetlands can store C for several thousand years (Johnston et al. 2012). Cold temperatures in high elevations and northern latitudes prevent decomposition of plant material, allowing accumulation of deep peat layers. Changes in precipitation patterns and temperature due to climate change could have profound impacts on the hydrology regulating wetland C processing (Meixner et al. 2016), and are predicted to impact vulnerable SOC stocks in mountain wetlands (Chimner et al. 2002; Fissore et al. 2009).

In the Rocky Mountains of Colorado, wetlands located in isolated depressions co-occur in headwater forest watersheds with hydrologically connected slope wetlands (Carsey et al. 2003) and provide an opportunity to examine how C composition varies among HGM classes. Depressional wetlands are characterized by the accumulation of snowmelt discharge from the surrounding landscape, followed by a gradually dropping water table during the summer months (NRCS 2008). For most of the year, depressional wetlands lie above the water table and primarily lose water through evapotranspiration. In contrast, slope wetlands, a type of fen, receive continuous hydrologic inputs from emergent groundwater and discharge water downslope to adjacent streams. The topographically driven differences in hydrologic connectivity that regulate hydroperiod and hydraulic residence time are likely to result in distinct patterns of C storage and cycling in the two wetland types, resulting in

differential vulnerability to C remobilization caused by climate and land use change.

To determine the influence of HGM class on the processing of SOC, we compared the chemical composition and content of SOC in relation to key soil and porewater properties in slope and depressional subalpine wetlands in the Colorado Rocky Mountains. We used several techniques to assess C composition, including total C measurements, radiocarbon dating, and solid-state ^{13}C cross-polarization magic angle spinning (CP-MAS) nuclear magnetic resonance (NMR) spectroscopy. Solid-state NMR spectroscopy has been used to provide insight into the chemical composition of soil organic matter and the changes it undergoes during decomposition (Knicker and Ludemann 1995; Baldock et al. 1997; Kögel-Knabner 1997; Rumpel et al. 2002). We hypothesized that the seasonally pulsed hydrologic inputs and limited release from the depressional wetlands would promote anaerobic biogeochemical processes that favor accumulation of relatively persistent aromatic- and aliphatic-rich C compounds. By contrast, we expected the continuous hydrologic connectivity and recharge of the slope wetlands to favor more aerobic conditions, resulting in less accumulation of aliphatic and aromatic compounds.

Methods

Site description

We studied six wetlands in the Fraser Experimental Forest (FEF) (39° 34′ N, 105° 30′ W), a research area maintained by the U.S. Department of Agriculture (USDA) Forest Service. All wetlands form 0.1 to 1 ha openings within the subalpine conifer forest at comparable elevation (2700–3300 m) and climatic conditions (Fig. 1). Average air temperature ranges from −10 to 13 °C, and precipitation at 2725 m elevation is 58 cm, falling primarily as snow (Alexander et al. 1985). The three slope wetlands (S1, S2, S3) reside on hill sides with 15–20% slope gradients where groundwater emerges at the ground surface and passes along near-surface flow paths in hours to days, resulting in short hydraulic residence times (Fig. 2). One slope wetland (S1) is located in the Dead Horse watershed and the other two (S2 and S3) are located in the Fool Creek watershed. The three depressional wetlands (D1, D2, D3) formed within isolated topographic depressions that retain snowmelt water inputs for months. They are located adjacent to one another in the King Creek watershed. Wetland soils at FEF developed from Precambrian granite, schist and gneiss bedrock (Retzer 1962; Kellogg et al. 2008) and are classified as Histic Cryaquolls with 20–100 cm of peat accumulation (Alstatt and Miles 1983).

Vegetation in the depressional wetlands is dominated by the grass and sedge species *Calamagrostis canadensis*, *Carex aquatilis*, and *Carex utriculata.* Quaking aspen (*Populus tremuloides*) grow immediately adjacent to the wetlands, with Engelmann spruce (*Picea engelmanni*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*) in the surrounding forest. Slope wetlands are dominated by sedges, but support a greater diversity of species than depressional wetlands, including a variety of forbs and bryophytes (Carsey et al. 2003; LaPerriere et al. 2011).

Soil sampling and analysis

In September and October of 2012, soil cores were extracted from two sites (located approximately 15 m apart) in three wetlands of each type, using a 6-cm diameter steel corer with polyethylene terephthalate liners (Giddings Machine Company, CO). Duplicate sets of six cores were collected—one set was used for physical and routine chemical analyses and the other was used for organic carbon characterization by NMR, carbon dating, and carbon isotope analysis. The cores ranged in length from 43 to 120 cm and were divided into 10-cm increments, weighed, air dried, sieved to 2 mm and ground using a ball mill prior to analyses. Soil texture was determined using the hydrometer method (Gavlak et al. 2003). Organic and mineral horizons were defined based on organic carbon and clay content (Soil Survey Staff 1999). Peak herbaceous biomass (annual graminoid and forb growth in August) was clipped from 1 m^2 sample quadrants, dried for 48 h at 60 °C, and weighed.

Soil Fe, Al, and Ca concentrations were measured using inductively-coupled plasma optical emission spectroscopy (ICP-OES). Samples were prepared as follows: 1 g of dried sample was digested with 5 mL concentrated HNO_3 and 5 mL concentrated $HClO_4$ at 125 °C until the volume was reduced to 5 mL, then at 200 °C for 2 h. Analysis was performed on a PerkinElmer Optima 7300 DV and data processed in

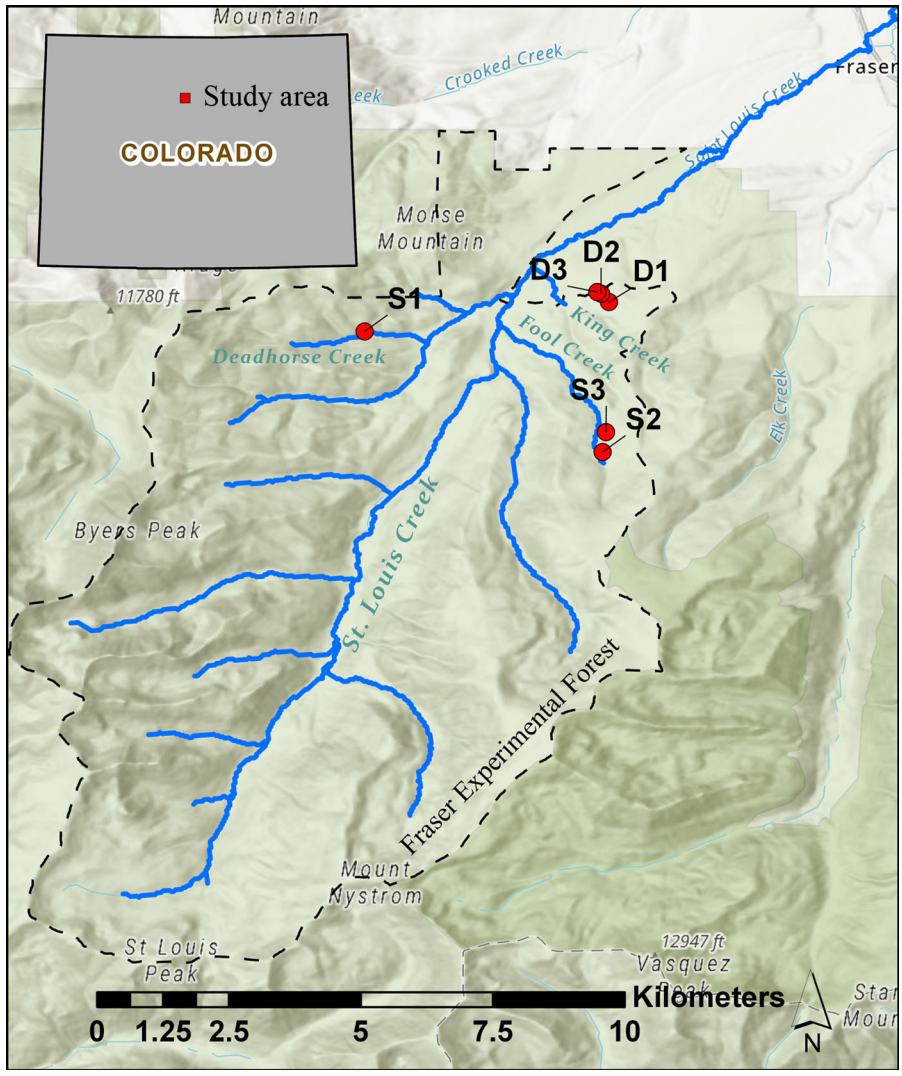

Fig. 1 Map of wetlands studied in Fraser Experimental Forest (FEF), Colorado, US. Wetlands are shown as red dots. The dashed line represents the FEF boundary. Blue lines represent major streams within FEF. (Color figure online)

Winlab32 software (PerkinElmer, Inc.). Total C and N were analyzed by dry combustion on a LECO Tru-Spec CN analyzer (Leco Corp.).

Water sampling and analysis

Groundwater wells were installed at both sampling sites in each wetland. Wells were constructed from slotted 2.54-cm diameter polyvinyl chloride (PVC) pipe, sealed at the base and inserted to a depth of 100 cm and 200 cm. The wells were capped to limit inputs from surface water and precipitation. Water table depth was recorded hourly using Hobo U20 Water Level Loggers (Onset Corp) from June through October, 2011, and data were corrected for local barometric pressure. Wetland porewater was sampled from wells approximately weekly from May to October of 2012. Water sampling was conducted in a similar method to that described in LaPerriere et al. (2011). Briefly, wells were purged with a hand pump and allowed to refill with fresh porewater for several minutes prior to sample collection and analysis. Reduction oxidation (redox) measurements were taken using a handheld meter immediately after sampling. Water samples were collected in clean, combusted glass bottles for DOC analyses and in clean plastic bottles for inorganic ion concentrations and pH. Samples were stored at 4 °C and filtered prior to analysis.

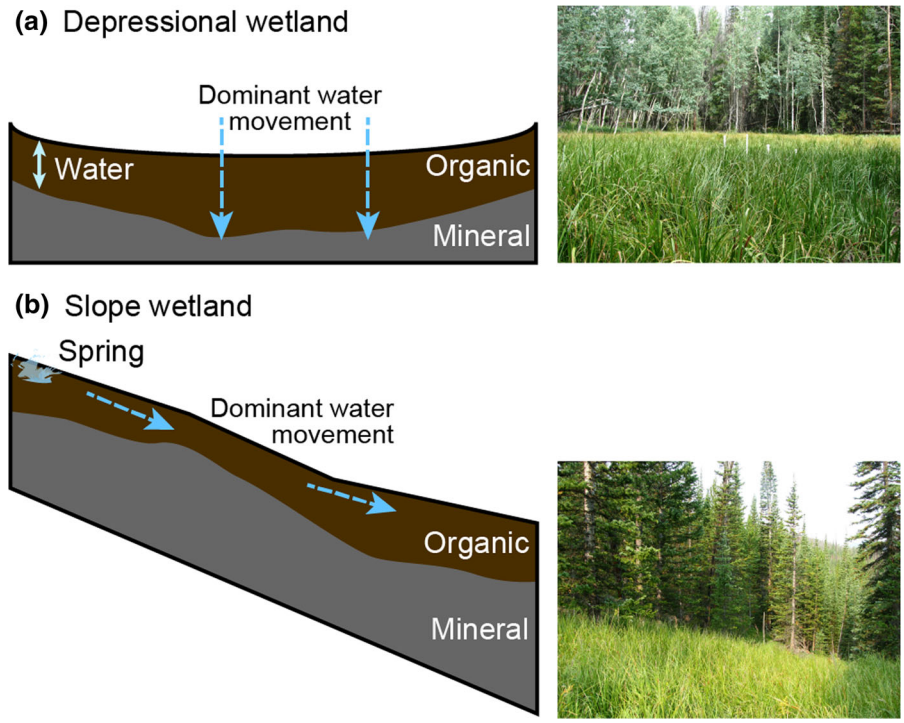

Fig. 2 Diagrams and photographs of representative depressional D3 (**a**) and slope S2 (**b**) wetlands, showing topography, dominant hydrodynamics, and relative soil horizon thickness

Anion concentrations were determined from ion chromatography using a Dionex AS12A anion-exchange column, an AG12A guard column, and conductivity detection. DOC and TDN concentrations were determined by high-temperature combustion catalytic oxidation using a Shimadzu TOC-V_{CPN} total organic carbon analyzer with a TNM-1 total nitrogen detection unit (Shimadzu Corporation). Dissolved organic nitrogen (DON) was calculated by subtracting the sum of NO_3^--N and NH_4^+-N from TDN.

^{13}C nuclear magnetic resonance (NMR) spectroscopy

Soil samples taken from 0 to 50 cm depth at one site per wetland were analyzed using solid state ^{13}C cross polarization magic angle spinning (CP-MAS) NMR spectroscopy. These samples contained sufficient C for NMR analysis without prior treatment to remove paramagnetic minerals, and pilot spectra from hydrofluoric acid (HF) treated and untreated samples yielded similar integration results. Samples were dried and ground prior to analysis.

Tree litter and fresh grass and sedge leaves were dried, ground and analyzed using the same instrumental methods as the soil samples (Supplementary Fig. 1).

All soils were analyzed at the Environmental Molecular Sciences Laboratory (EMSL) at the Pacific Northwest National Laboratory. 1-D CP-MAS experiments were performed on a 300 MHz Varian VNMRS spectrometer operating with a ^{13}C frequency of 75.4 MHz and a ^{1}H frequency of 299.9 MHz. Between 30 and 90 mg of sample was packed in a 4-mm zirconia rotor and spun at 14 kHz. A ramped cross-polarization pulse of 1 ms was applied after the 4 µs proton pulse before transfer to the ^{13}C nuclei. During the 20 ms acquisition time, a 62.5 kHz H decoupling field was applied and 2000 points were recorded. The recycle delay was optimized for each sample between 1 and 10 s dependent on the proton relaxation. The spectra were processed using the Varian vnmrj software where 50 Hz line broadening, zerofilling, and appropriate base line corrections were applied.

Chemical shifts were calibrated with an adamantane external standard. The cross-polarization experiment was optimized and monitored using glycine. Chemical shift regions were integrated to correspond to broad functional group classifications of 0–45 ppm

for alkyl C, 45–110 ppm for O-alkyl C, 110–160 ppm for aromatic C and 160–190 ppm for carbonyl and amide C (Supplementary Fig. 2; Knicker 2011).

Carbon dating and $\delta^{13}C$ analysis

We selected soil samples from surface (0–20 cm), intermediate (20–50 cm), and deep (70–120 cm) profile depths from two slope wetland sites (S3-1 and S3-2) and one depressional wetland site (D2-1) to measure ^{14}C age and $\delta^{13}C$. Radiocarbon dating was completed at Beta Analytic (Miami, FL) using accelerator mass spectrometry (Fifield 1999). Prior to analysis, samples were air dried and sieved to 2 mm, roots were removed manually, and samples were ground using a ball mill. Samples were then sieved to < 180 µm and the remaining bulk organic fraction was acid washed to remove carbonates. Spectra from accelerator mass spectrometry analysis were corrected using tree-ring data (Talma and Vogel 1993). We used OxCal 4.3 (Bronk Ramsey et al. 2013) to calibrate samples using the IntCAL13 (Reimer et al. 2013) calibration curve. We report uncalibrated age, $^{13}C/^{12}C$ ratio, 95.4% probability range, mean and median calibrated age, and 1 sigma error on mean calibrated age in years before present (yr BP) for each sample.

Statistical analyses

Statistical comparisons via Wilcoxon rank sum tests were performed using the R statistical package (R Core Team 2018). Group sample size for each test is given in Table 1. Reported p-values less than 0.01 were considered significant.

Results

Site, soil, and water properties

The hydrologic regime differed substantially between the wetland types. Depressional wetlands accumulated standing water during spring snowmelt (April and May), followed by a dropping water table from July through October (Fig. 3). By contrast, slope wetlands received continuous groundwater inputs, which resulted in limited water table fluctuations. These hydrologic differences did not translate into distinct trends in redox potential measurements. Redox

Table 1 Mean (and 1 standard deviation shown in parentheses) for soil texture, soil and water chemistry, and plant biomass values from three wetlands of each class

	Soil texture			Soil chemistry				Aqueous chemistry						C input
	Sand[a] (%)	Silt[a] (%)	Clay[a] (%)	Fe^b (g kg^{-1})	Al^b (g kg^{-1})	Ca^b (g kg^{-1})	N^b (g kg^{-1})	pH[c]	NO_3^- [c] (mg L^{-1})	SO_4^{2-} [c] (mg L^{-1})	NH_4^+ [c] (mg L^{-1})	Ca^{2+c} (mg L^{-1})	DON[c] (mg L^{-1})	DOC[c] (mg L^{-1})	Plant biomass[d] (g m^{-2})
Depressional	44.3 (10.1)	26.6 (9.5)	29.7 (10.1)	17.5 (3.8)	54.1 (18.6)	6.10 (1.1)	1.11 (0.57)	6.04 (0.40)	0.154 (0.169)	2.69 (7.09)	0.818 (0.985)	12.6 (4.57)	1.75 (0.996)	44.4 (20.9)	514 (165)
Slope	56.7 (6.9)	24.6 (4.4)	18.6 (5.2)	20.6 (5.1)	36.2 (15.4)	11.9 (7.4)	0.574 (0.702)	6.71 (0.44)	0.0437 (0.426)	3.26 (4.38)	0.114 (0.0387)	20.7 (8.31)	0.173 (0.135)	5.58 (4.48)	167 (83)
p value	0.0003	> 0.01	< 0.0001	0.0052	< 0.0001	0.0003	< 0.0001	< 0.0001	> 0.05	> 0.05	< 0.0001	0.0003	< 0.0001	< 0.0001	< 0.0001

[a] n = 46 and 32 soil samples from depressional and slope wetlands, respectively

[b] n = 40 and 39 soil samples from depressional and slope wetlands, respectively

[c] n = 34 and 23 well water samples from depressional and slope wetlands, respectively. Means represent averaged values from measurements collected from May to October, 2012

[d] n = 12 and 12 for depressional and slope wetlands, respectively

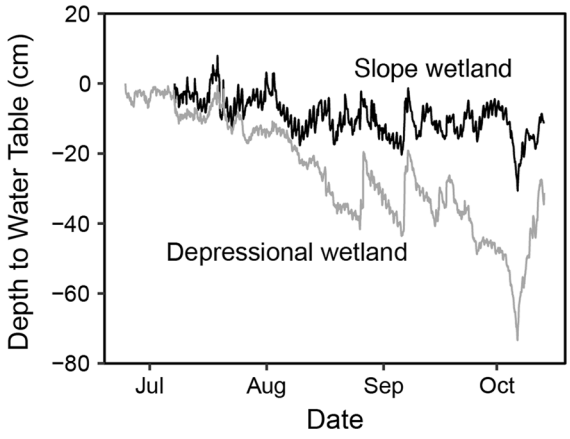

Fig. 3 Relative change in seasonal water table height of representative depressional (D2) and slope (S2) wetlands, from July to October, 2011

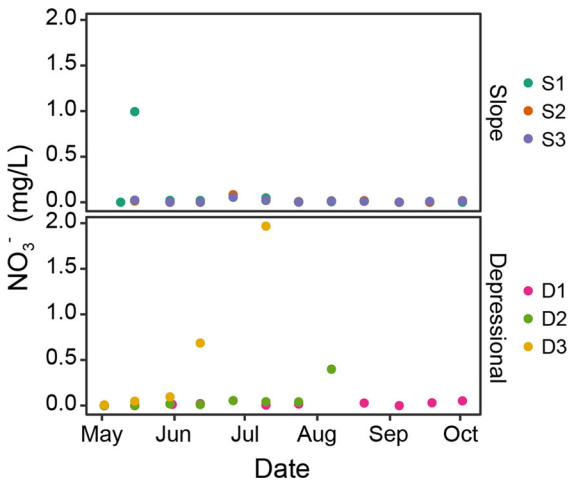

Fig. 4 Nitrate (NO_3^-) concentrations from well water samples collected from slope and depressional wetlands, May–October, 2012

potential in porewater sampled at 50–100 cm depth varied between − 425 and 350 mV in both wetland classes (Supplementary Fig. 3). Ninety percent of measurements in depressional wetlands and 100% of measurements in slope wetlands were below 300 mV, indicating generally suboxic and anoxic conditions.

Soil texture varied between the two wetland classes, with more clay ($p < 0.0001$) and less sand ($p < 0.0005$) in the depressional wetlands compared to slope wetlands (Table 1). Soil chemical composition also differed, with higher Al and N content in depressional wetlands ($p < 0.0001$ and $p < 0.0001$) and higher Fe and Ca content in slope wetlands

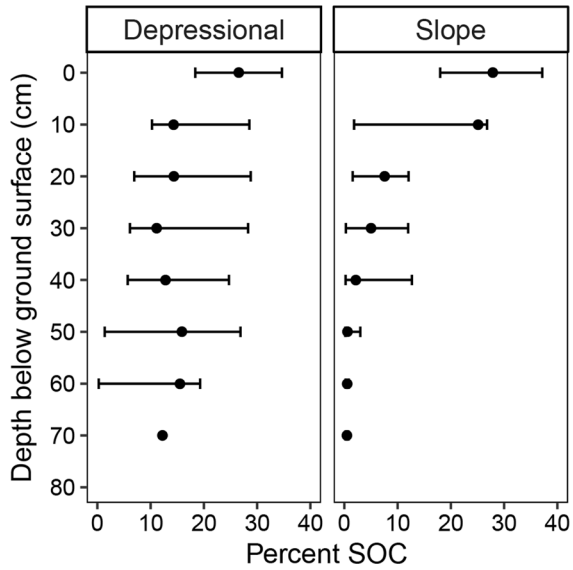

Fig. 5 Means (dots) and ranges (error bars) of percent soil organic carbon (SOC) by depth from two sites per wetland in three wetlands of each class

($p < 0.01$ and $p < 0.0005$, respectively). Mottling was observed in mineral horizons of both wetland types.

Pore water chemistry also varied between wetland types (Table 1). Depressional wetlands had higher mean DOC concentrations (44.4 vs. 5.6 mg L^{-1}, $p < 0.0001$). The porewater in depressional wetlands was also more acidic (pH 6.0 vs 6.7, $p < 0.0001$), perhaps due to the higher concentration of organic acid-containing DOC. In all but one wetland, sulfate (SO_4^{2-}) concentrations remained below 5 mg/L for most of the summer. Nitrate (NO_3^-) values were very low, often below 0.01 mg/L. In depressional wetlands D2 and D3, NO_3^- concentrations rose temporarily before the wetlands and wells dried (Fig. 4). Ammonium (NH_4^+) and dissolved organic nitrogen (DON) concentrations were significantly higher in the depressional wetlands ($p < 0.0001$). Phosphate concentrations were low, usually less than 0.01 mg/L in all wetlands. Aqueous Ca^{2+} concentrations were significantly higher in slope wetlands, consistent with greater Ca content in slope wetland soils (Table 1).

Biomass production differed significantly between wetland types ($p < 0.0001$, Table 1). On average, the depressional wetlands produced about three times as much plant biomass per square meter as the slope wetlands during our study period.

Table 2 $^{13}C/^{12}C$ ratio, uncalibrated ^{14}C age, 95.4% probability range, mean and median calibrated age, and corresponding horizons of soil samples from depressional wetland D2 and slope wetland S3

Site	Depth (cm)	Soil Horizon	$^{13}C/^{12}C$ (‰)	Uncalibrated ^{14}C age (yr BP)	95.4% range (yr BP)	Mean calibrated age (error)[b] (yr BP)	Median calibrated age (yr BP)
D2-1	0–10	Organic	− 27.4	101.8 ± 0.4 pMC[a]	Modern	Modern	Modern
	40–50	Organic[c]	− 26.9	1163 ± 30	1178–983	1087 (56)	1087
	90–100	Mineral	− 26.3	2945 ± 30	3207–2998	3100 (51)	3104
S3-1	10–20	Organic	− 26.4	175 ± 30	294–modern	160 (88)	179
	20–30	Mineral	− 25.0	1471 ± 30	1406–1306	1357 (30)	1356
	70–80	Mineral	− 24.7	3882 ± 30	4417–4193	4322 (58)	4326
S3-2	10–20	Organic	− 25.4	105 ± 30	269–13	132 (78)	113
	40–50	Mineral	− 24.8	3006 ± 30	3331–3076	3196 (59)	3194
	110–120	Mineral	− 24.9	3984 ± 30	4525–4410	4465 (39)	4473

Median calibrated age is used to represent the age of each sample

[a]pMC = percent modern carbon

[b]1 sigma error on mean calibrated age

[c]Buried organic horizon

Soil organic carbon content

For both wetland types, C content averaged about 25% in organic soil horizons and 7% in mineral soil horizons (Fig. 5). Organic horizons were deeper on average but more variable in depressional wetlands (10–70 cm thick) relative to slope wetlands (10–20 cm thick). Carbon content declined more rapidly with depth in slope wetlands—by 50 cm below the surface, SOC declined to about 1%. In the depressional wetlands, SOC content was generally higher at depth, with as much as 20% SOC at 60–70 cm below the surface.

Soil carbon age

Radiocarbon dates of mineral soils were older than for organic soils in both wetland types. Median ^{14}C ages ranged from 0 to 180 years before present (yr BP) in organic soils (0–10 or 10–20 cm depths) in both wetland types (Table 2), consistent with rapid decomposition of organic inputs. Mineral soil C in the slope wetland (20–30 and 40–50 cm depths) was substantially older (1356 and 3194 yr BP) than in surface organic soils. In the depressional wetland, the 40–50 cm depth sample was taken from a buried organic horizon, which despite its low mineral content, contained quite old C (1087 yr BP). Carbon in this buried organic horizon was, however, still younger than the C sampled from mineral soil at similar depths below the organic layer in the slope wetland. Samples from deeper within the slope wetland soil profile (70–80 and 110–120 cm depths) had median ^{14}C ages around 4400 yr BP, about 1000 years older than C in soil from a similar depth in the depressional wetland.

Soil organic carbon composition

Distributions of carbon functional groups derived from ^{13}C CP-MAS NMR spectra showed distinct trends with depth (Fig. 6). In most profiles, C chemistry changed markedly 20 cm below the ground surface, so integrations of NMR spectra are averaged separately for "surface" samples (0–20 cm) and "deep" samples (20–50 cm). The organic C in surface soil of both wetland classes is dominated by O-alkyl C, which includes carbohydrate compounds such as cellulose and hemicellulose (34–39% total C by integration). O-alkyl C content decreased with depth and the relative proportion of aromatic C increased. Aromatic C groups in soils commonly include lignin and tannins. The switch in dominance of O-alkyl C and aromatic C with increasing depth was consistent across all slope wetlands and depressional wetlands D1 and D2. In depressional wetlands, alkyl C

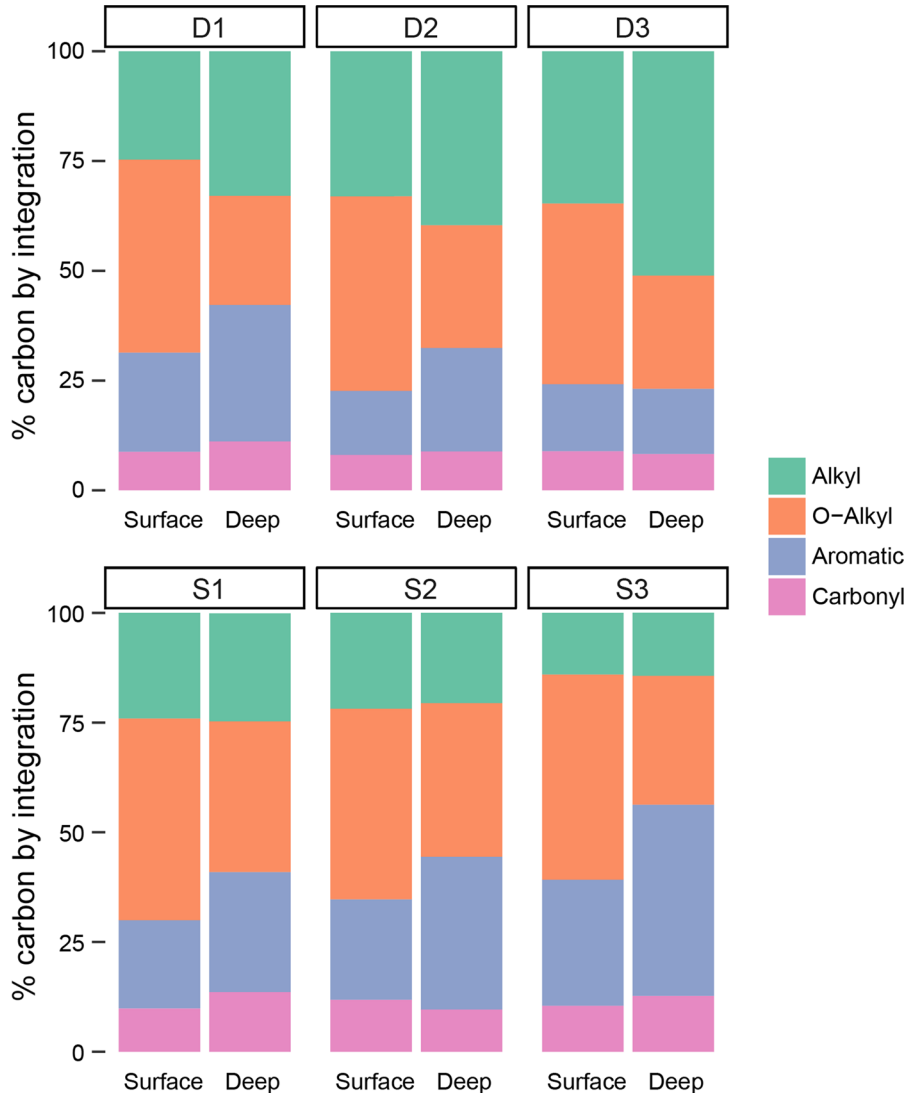

Fig. 6 Distribution of C species (determined by integration of ^{13}C CP-MAS NMR spectra) in surface (0–20 cm) and deep (20–50 cm) soil samples collected from each of six wetlands (D = depressional wetland and S = slope wetland). Integration regions are alkyl C (0–45 ppm), O-alkyl C (45–110 ppm), aromatic C (110–160 ppm), and carbonyl C (160–190 ppm)

constituted a larger proportion throughout the soil profile and increased with depth. This group represents primarily aliphatic compounds such as cutins and suberins found in leaf and root waxes (Nierop 1998; Simpson et al. 2008), but can also include microbial membrane lipids (Lorenz et al. 2007). Carbonyl C, which includes amides and carboxylic groups in organic and amino acids, represented much lower proportions (< 15%) of total C and represented a slightly larger fraction of total carbon in slope wetlands, especially at depth.

Discussion

In this study, we compared the SOC content and composition in isolated depressional wetlands and hydrologically connected slope wetlands in the Colorado Rocky Mountains. Our results demonstrate distinct patterns in SOC storage and chemistry between the two wetland types, suggesting different processes governing SOC processing and stabilization.

Soil organic carbon stabilization

SOC content is a function of physical and chemical stabilization, dissolved and gaseous C losses, and

organic matter decomposition. Clays and Al and Fe oxides have high surface areas that can adsorb and occlude SOC, protecting it from decomposition (Oades 1988; Schimel et al. 1994; Sposito et al. 1999; Rasmussen et al. 2018). The HGM setting of depressional wetlands promotes deposition and retention of fine sediments (e.g. clays) transported from upland soils (Rosenbloom et al. 2001). Indeed, the soils in depressional wetlands had over 1.5 times more clay (Table 1), as well as higher Al content, which may have promoted SOC retention throughout the mineral soil profile. The slope wetlands in our study had coarser soil textures compared to the depressional wetlands, but slightly higher Fe content (Table 1). Fe oxides can also contribute to C stabilization, as evidenced by positive correlations between Fe oxide and SOC concentrations in many soils and sediments (Kaiser and Guggenberger 2000; Lalonde et al. 2012) and between Fe oxide content and SOC age (Torn et al. 1997; Eusterhues et al. 2003). Although our data do not distinguish Fe oxidation state or speciation, we observed mottling in the mineral horizons of some soil cores extracted from both wetland types, providing visual indication of the presence of Fe oxides. Sorption or co-precipitation of SOC with these minerals could contribute to the relatively high SOC content of some mineral layers in the slope wetlands, which represents up to 11% of soil mass in samples from 10 to 50 cm depth (Fig. 5).

While sorption likely plays a role in C stabilization in both wetland types, it may be especially important for SOC retention in slope wetlands, where DOC that is not stabilized by minerals can be decomposed by microbes and transported downslope. In depressional wetlands, where hydraulic residence time is likely longer, DOC may have greater opportunity to accumulate and exchange with soil. Vertical water table fluctuations may also translocate DOC deeper into depressional wetland soils (Fig. 2a), where it can associate with soil minerals (Kögel-Knabner et al. 2010).

In many soils, long-term C stabilization occurs in mineral layers, where sorption, co-precipitation and physical occlusion of organic matter deter microbial decomposition (Eusterhues et al. 2003; Kleber et al. 2005; Sollins et al. 2009). Carbon dating of soils from a depressional and a slope wetland showed that mineral layers contained older C compared to organic soil horizons, even buried ones. In addition, carbon from mineral soil sampled at about 1 m depth was approximately 1000 years older in the slope wetland compared to the depressional wetland. A number of factors could contribute to the younger age of deep C in the depressional wetland. One possibility is that higher organic C inputs and the seasonally declining water table promote transport of young DOC to greater depths within the soil profile, reducing the median age of the deep SOC. In slope wetlands, downhill subsurface flow dominates hydrodynamics, likely limiting vertical translocation of DOC and removing any SOC that is not protected by minerals. However, SOC interacting with minerals such as Fe oxides may become stabilized for long periods of time. This may explain the small but stable C fraction found in deeper soils of slope wetlands (Fig. 5; Table 2).

Potential drivers of soil organic carbon composition

Organic matter decomposition pathways, which depend on soil redox conditions, influence SOC composition (Kögel-Knabner et al. 2010; Boye et al. 2017). Measures of redox conditions suggest soils in both wetland types remained anaerobic for most of the study period. However, the increasing nitrate concentrations corresponding with the seasonal drying of depressional wetland soils implies denitrification maintained low NO_3^- levels under saturated conditions but diminished when the water table dropped and oxygen penetrated the soil profile. Water table fluctuations in depressional wetlands thus appear to create a more dynamic redox environment. Numerous studies have shown fluctuating redox conditions enhance organic matter decomposition (Aller 1994; Fierer and Schimel 2002; Rezanezhad et al. 2014), though most have investigated the effects of short term drying-rewetting cycles (hours to weeks). The depressional wetlands characterized in this study experienced long term fluctuations in water table levels (over months-long timescales) and are likely dominated by different microbial communities than soils experiencing frequent redox fluctuations (Pett-Ridge and Firestone 2005). In spite of seasonal water table fluctuations, depressional wetlands appeared to maintain predominately anaerobic conditions that limit the decomposition of recalcitrant organic compounds.

Several factors may contribute to a greater degree of anaerobic C processing and resulting accumulation

of aliphatic C compounds in depressional wetlands. Their high clay content likely limits oxygen infiltration, and along with the long hydraulic residence time and high organic matter content (Boye et al. 2017), prolongs anoxic conditions. Although the water table declines over the course of the season, anoxic microsites persist in fine textured, high-SOC depressional wetland soils. Both of these soil characteristics are correlated with reducing conditions, the fraction of pore volume that is anoxic, and decreased C mineralization rates (Boye et al. 2017; Keiluweit et al. 2017, 2018; Noël et al. 2017). Wetland plants, such as the *Carex* species found in the FEF wetlands, leak O_2 into the rhizosphere from aerenchyma tissue and create oxic microsites (Armstrong 1979; Fagerstedt 1992), but they can also contribute to anoxic microsite formation through root respiration (Bidel et al. 2000), stimulation of microbial respiration (Keiluweit et al. 2015a), and the release of organic reductants (Fimmen et al. 2008). In depressional wetlands, persistence of anoxic microsites may sustain anaerobic decomposition during the dry season and explain higher proportions of aliphatic compounds.

Under anoxic conditions, highly reduced aliphatic compounds are thermodynamically unfavorable electron donors for microbial respiration (Keiluweit et al. 2016, 2017; Boye et al. 2017). Microbes may be unable to couple reduction of Fe(III) or SO_4^{2-} terminal electron acceptors with oxidation of reduced aliphatic substrates, leading to the selective preservation of these compounds. In all three depressional wetlands, the proportion of total C comprised of alkyl C (the dominant form of C in aliphatic compounds) increased with depth. This spatial pattern is consistent with thermodynamic predictions for anaerobic decomposition and observations of aliphatic compounds persisting in saturated soils (Tfaily et al. 2014; Heller et al. 2015; Noël et al. 2017).

Lower SOC concentrations, coarser soil textures, and perennial water flow should favor more oxic conditions in slope wetlands, despite their consistently high water tables. Consistent with these conditions, alkyl C represented a smaller proportion of total C in slope wetland soils and remained fairly constant with depth. The carbonyl C fraction was also slightly higher in the slope wetlands. Lower alkyl C and higher carbonyl C contents have been associated with oxygen infiltration, such as following peatland drainage (Leifeld et al. 2012; Heller et al. 2015).

The surface horizons of both subalpine wetland types contained high proportions of O-alkyl C, associated with cellulose and hemicellulose present in fresh plant litter. Predominance of these carbohydrate compounds has been observed elsewhere in wetland and upland soils (Rumpel et al. 2002; Jokic et al. 2003; Grover and Baldock 2010, 2013; Luan et al. 2014). These components typically decompose relatively quickly (Berg and McClaugherty 2014; McKee et al. 2016), even in anoxic environments with thermodynamic limitations (Keiluweit et al. 2016). Their abundance in upper soil horizons of the studied wetlands suggests that input of new plant material exceeded decomposition losses. The relative contribution of the O-alkyl fraction to the total organic carbon pool decreased with depth, suggesting it decomposed prior to translocation deeper into the profile (Kaiser and Kalbitz 2012; Cotrufo et al. 2015; Leinemann et al. 2018).

In all but one wetland (D3), the relative proportion of the aryl C region, which includes aromatic compounds such as lignins, tannins, and pyrolyzed organic matter, increased with depth. In general, aromatic compounds take longer to decompose, accumulating in deeper soils (Leifeld et al. 2012; Grover and Baldock 2013; Berg and McClaugherty 2014; Tfaily et al. 2014). Carbon isotope measurements generally support the overall trend of increasingly decomposed organic material with depth. For the three profiles measured, $\delta^{13}C$ values increased by 0.5–1.7‰ (Table 2), suggesting an increase in microbial biomass relative to plant biomass between surface and deep soil layers (Taylor et al. 2003; Tfaily et al. 2014).

Differences in vegetation between the slope and depressional wetlands likely influence SOC content and chemistry. Greater above-ground litter inputs in depressional wetlands may contribute to the higher SOC content found in those soils. The depressional wetlands have higher aqueous and soil N content than slope wetlands, which may explain their greater biomass production.

Variations in litter chemistry based on vegetation type influence the decomposition rates of litter inputs (Keiluweit et al. 2015b) and soil organic matter content and chemistry (Quideau et al. 2000, 2001; Ussiri and Johnson 2003). Depressional wetlands were dominated by grasses and sedges, with aspen at the wetland the perimeter. Slope wetlands hosted a greater

diversity of herbaceous plants species including forbs and bryophytes, but lacked aspen (LaPerriere et al. 2011). The distinct plant communities likely create differences in the quantity and chemical composition of above- and belowground organic matter inputs (Supplementary Fig. 1). For example, depressional wetland soils contained large quantities of C in the alkyl region, even in the top 10 cm, consistent with leaf cutin and root suberin inputs to surface soils (Nierop 1998; Simpson et al. 2008). Aspen litter contains slightly higher proportions of alkyl C than conifer needles or graminoid leaves (Supplementary Fig. 1). Though we cannot directly link the SOC composition of the two wetland types to specific vegetation inputs, the C composition of litter inputs for various plant species agree with the wetland SOC composition we observed.

Conclusions and implications

Our findings demonstrate distinct patterns in SOC content and chemistry with depth between depressional wetlands that remain hydrologically isolated for most of the year and slope wetlands that receive continuous hydrologic inputs. Depressional wetlands had higher litter inputs and greater SOC concentrations deeper into the soil profile compared to slope wetlands. However, radiocarbon dates suggested this C was younger than that in slope wetland soils at similar depths. This implies the C in depressional wetlands may turn over faster and represent a less stable SOC pool than in slope wetlands. Surface soil horizons of slope wetlands were dominated by labile carbohydrate compounds while those of depressional wetlands contained large proportions of aliphatic C more resistant to decomposition. Aromatic C dominated total SOC of deeper slope wetland soils, whereas aliphatic C increased with depth in depressional wetlands. These patterns are consistent with persistent and extensive anoxic conditions in the depressional wetlands. The finer soil texture, higher organic C content, and long residence time of seasonal hydrologic inputs in depressional wetlands should favor anoxic conditions. Detailed analyses of chemical composition of plant inputs, microbial community structure and activity, redox gradients, concentrations of electron acceptors, extent of mineral sorption and physical protection, and hydrologic and gaseous C export could help elucidate the biochemical and physical pathways responsible for the differences in SOC chemistry observed in these wetland types.

Mountain wetlands are subject to disturbances from road development, logging, mining, grazing, and climate change, which can alter local hydrology and soil temperatures (Covington 1981; Chimner et al. 2002, 2010; Johnston et al. 2012). The vulnerability of wetland SOC stocks to re-mobilization depends on soil redox conditions, temperature, and SOC composition. In surface layers, labile O-containing compounds such as carbohydrates are especially vulnerable to decomposition due to drainage, drying, or warming (Leifeld et al. 2012; Wilson et al. 2016). However, it has been suggested that the older, more recalcitrant C typically found in aromatic and aliphatic compounds is more sensitive to warming under oxic conditions compared to younger, more labile C (Hilasvuori et al. 2013). More oxic conditions may disproportionately decrease C storage in depressional wetlands, which contain a larger proportion of anaerobically protected C. These scenarios demonstrate the need to consider the effect of HGM class on the sensitivity of wetland soil carbon to changing climate and hydrologic conditions.

Acknowledgements We would like to thank Dr. Tom Wietsma for the access to the TOC analyzer, Ryan Taylor for his contribution to bulk soil analyses, Kelsey Dean for extensive field work, and Dr. Daniel Scott for assistance with carbon age calibrations, statistical analyses, and mapping. Funding was provided by USDA NIFA AFRI postdoctoral fellowship no. 2012-01330, and the Agriculture and Food Research Initiative Competitive Grant no. 2013-67019-21359 from the USDA National Institute of Food and Agriculture. A portion of the research was performed using EMSL, a DOE Office of Science User Facility sponsored by the Office of Biological and Environmental Research and located at Pacific Northwest National Laboratory.

References

Alexander RR, Troendle CA, Kaufmann MR et al (1985) The Fraser Experimental Forest, Colorado: Research program and published research 1937–1985. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins

Aller RC (1994) Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chem Geol 114:331–345

Alstatt D, Miles RL (1983) Soil survey of Grand County area, Colorado. USDA Soil Conservation Service and Forest Service and Colorado Agriculture Experiment Station, U.S. Government Printing Office

Ameli AA, Creed IF (2017) Quantifying hydrologic connectivity of wetlands to surface water systems. Hydrol Earth Syst Sci 21:1791–1808. https://doi.org/10.5194/hess-21-1791-2017

Armstrong W (1979) Aeration in higher plants. In: Woodhouse HW (ed) Advances in botanical research. Academic Press, London, pp 225–332

Baldock JA, Oades JM, Nelson PN et al (1997) Assessing the extent of decomposition of natural organic materials using solid-state 13C NMR spectroscopy. Soil Res 35:1061–1084. https://doi.org/10.1071/s97004

Berg B, McClaugherty C (2014) Plant litter: decomposition, humus formation, carbon sequestration, 3rd edn. Springer, Berlin

Bernal B, Mitsch WJ (2008) A comparison of soil carbon pools and profiles in wetlands in Costa Rica and Ohio. Ecol Eng 34:311–323. https://doi.org/10.1016/j.ecoleng.2008.09.005

Bernal B, Mitsch WJ (2012) Comparing carbon sequestration in temperate freshwater wetland communities. Glob Chang Biol 18:1636–1647. https://doi.org/10.1111/j.1365-2486.2011.02619.x

Bernhardt ES, Blaszczak JR, Ficken CD et al (2017) Control points in ecosystems: moving beyond the hot spot hot moment concept. Ecosystems 20:665–682

Bidel LPR, Renault P, Pagès L, Rivière LM (2000) Mapping meristem respiration of *Prunus persica* (L.) Batsch seedlings: potential respiration of the meristems, O_2 diffusional constraints and combined effects on root growth. J Exp Bot 51:755–768. https://doi.org/10.1093/jexbot/51.345.755

Boye K, Noël V, Tfaily MM et al (2017) Thermodynamically controlled preservation of organic carbon in floodplains. Nat Geosci 10:415–419. https://doi.org/10.1038/ngeo2940

Bronk Ramsey C, Scott EM, van der Plicht J (2013) Calibration for archaeological and environmental terrestrial samples in the time range 26–50 ka cal BP. Radiocarbon 55:2021–2027

Carsey K, Kittel G, Decker K et al (2003) Field guide to the wetland and riparian plant associations of Colorado. Colorado National Heritage Program, Colorado State University, Fort Collins

Chadde SW, Shelly JS, Bursik RJ et al (1998) Peatlands on National Forests of the Northern Rocky Mountains: ecology and conservation. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO

Chimner RA, Cooper DJ, Parton WJ (2002) Modeling carbon accumulation in rocky mountain Fens. Wetlands 22:100–110. https://doi.org/10.1672/0277-5212(2002)022%5b0100:mcairm%5d2.0.co;2

Chimner RA, Lemly JM, Cooper DJ (2010) Mountain Fen distribution, types and restoration priorities, San Juan Mountains, Colorado, USA. Wetlands 30:763–771. https://doi.org/10.1007/s13157-010-0039-5

Cotrufo MF, Soong JL, Horton AJ et al (2015) Formation of soil organic matter via biochemical and physical pathways of litter mass loss. Nat Geosci 8:776–779. https://doi.org/10.1038/ngeo2520

Covington WW (1981) Changes in forest floor organic matter and nutrient content following clear cutting in Northern Hardwoods. Ecology 62:41–48. https://doi.org/10.2307/1936666

Covino T (2017) Hydrologic connectivity as a framework for understanding biogeochemical flux through watersheds and along fluvial networks. Geomorphology 277:133–144

Eusterhues K, Rumpel C, Kleber M, Kögel-Knabner I (2003) Stabilisation of soil organic matter by interactions with minerals as revealed by mineral dissolution and oxidative degradation. Org Geochem 34:1591–1600. https://doi.org/10.1016/j.orggeochem.2003.08.007

Fagerstedt K (1992) Development of aerenchyma in roots and rhizomes of *Carex rostrata* (Cyperaceae). Nord J Bot 12:115–120

Fierer N, Schimel JP (2002) Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. Soil Biol Biochem 34:777–787. https://doi.org/10.1016/S0038-0717(02)00007-X

Fifield LK (1999) Accelerator mass spectrometry and its applications. Rep Prog Phys 62:1223–1274

Fimmen RL, de Richter D, Vasudevan D et al (2008) Rhizogenic Fe–C redox cycling: a hypothetical biogeochemical mechanism that drives crustal weathering in upland soils. Biogeochemistry 87:127–141. https://doi.org/10.1007/s10533-007-9172-5

Fissore C, Giardina CP, Kolka RK, Trettin CC (2009) Soil organic carbon quality in forested mineral wetlands at different mean annual temperature. Soil Biol Biochem 41:458–466. https://doi.org/10.1016/j.soilbio.2008.11.004

Gavlak R, Hornek R, Miller RO, Kotuby-Amacher J (2003) Soil, plant and water reference methods for the western region. WREP-125

Grover SPP, Baldock JA (2010) Carbon decomposition processes in a peat from the Australian Alps. Eur J Soil Sci 61:217–230. https://doi.org/10.1111/j.1365-2389.2009.01220.x

Grover SPP, Baldock JA (2013) The link between peat hydrology and decomposition: beyond von post. J Hydrol 479:130–138. https://doi.org/10.1016/j.jhydrol.2012.11.049

Heller C, Ellerbrock RH, Roßkopf N et al (2015) Soil organic matter characterization of temperate peatland soil with FTIR-spectroscopy: effects of mire type and drainage intensity. Eur J Soil Sci 66:847–858. https://doi.org/10.1111/ejss.12279

Hilasvuori E, Akujärvi A, Fritze H et al (2013) Temperature sensitivity of decomposition in a peat profile. Soil Biol Biochem 67:47–54. https://doi.org/10.1016/j.soilbio.2013.08.009

Johnston BC, Stratton BT, Young WR et al (2012) Inventory of Fens in a Large Landscape of West-Central Colorado: Grand Mesa, Uncompahgre, and Gunnison National Forests. U.S. Forest Service, Delta

Jokic A, Cutler JN, Ponomarenko E et al (2003) Organic carbon and sulphur compounds in wetland soils: insights on structure and transformation processes using K-edge XANES and NMR spectroscopy. Geochim Cosmochim Acta 67:2585–2597. https://doi.org/10.1016/S0016-7037(03)00101-7

Kaiser K, Guggenberger G (2000) The role of DOM sorption to mineral surfaces in the preservation of organic matter in

soils. Org Geochem 31:711–725. https://doi.org/10.1016/S0146-6380(00)00046-2
Kaiser K, Kalbitz K (2012) Cycling downwards-dissolved organic matter in soils. Soil Biol Biochem 52:29–32. https://doi.org/10.1016/j.soilbio.2012.04.002
Keiluweit M, Bougoure JJ, Nico PS et al (2015a) Mineral protection of soil carbon counteracted by root exudates. Nat Clim Chang 5:588–595. https://doi.org/10.1038/nclimate2580
Keiluweit M, Nico P, Harmon ME et al (2015b) Long-term litter decomposition controlled by manganese redox cycling. Proc Natl Acad Sci USA 112:E5253–E5260. https://doi.org/10.1073/pnas.1508945112
Keiluweit M, Nico PS, Kleber M, Fendorf S (2016) Are oxygen limitations under recognized regulators of organic carbon turnover in upland soils? Biogeochemistry 127:157–171. https://doi.org/10.1007/s10533-015-0180-6
Keiluweit M, Wanzek T, Kleber M et al (2017) Anaerobic microsites have an unaccounted role in soil carbon stabilization. Nat Commun 8:1771. https://doi.org/10.1038/s41467-017-01406-6
Keiluweit M, Gee K, Denney A, Fendorf S (2018) Anoxic microsites in upland soils dominantly controlled by clay content. Soil Biol Biochem 118:42–50. https://doi.org/10.1016/j.soilbio.2017.12.002
Kellogg KS, Shroba RR, Bryant B, Premo WR (2008) Geologic Map of the Denver West 30′ × 60′ Quadrangle, North-Central Colorado
Kleber M, Mikutta R, Torn MS, Jahn R (2005) Poorly crystalline mineral phases protect organic matter in acid subsoil horizons. Eur J Soil Sci 56:717–725
Knicker H (2011) Solid state CPMAS 13C and 15 N NMR spectroscopy in organic geochemistry and how spin dynamics can either aggravate or improve spectra interpretation. Org Geochem 42:867–890. https://doi.org/10.1016/j.orggeochem.2011.06.019
Knicker H, Ludemann HD (1995) 15 N and 13 C CP-MAS and solution NMR-studies of 15 N enriched plant material during 600 days of microbial degradation. Org Geochem 23:329–341
Kögel-Knabner I (1997) 13C and 15 N NMR spectroscopy as a tool in soil organic matter studies. Geoderma 80:243–270. https://doi.org/10.1016/S0016-7061(97)00055-4
Kögel-Knabner I, Amelung W, Cao Z et al (2010) Biogeochemistry of paddy soils. Geoderma 157:1–14. https://doi.org/10.1016/j.geoderma.2010.03.009
Kolka R, Trettin C, Tang W et al (2018) Chapter 13: Terrestrial wetlands. In: Cavallaro N, Shrestha G, Birdsey R et al (eds) Second State of the Carbon Cycle Report (SOCCR47): a sustained assessment report, USA. U.S. Global Change Research Program, Washington, D.C., pp 507–567
Lal R (2008) Carbon sequestration. Philos Trans R Soc Lond B Biol Sci 363:815–830. https://doi.org/10.1098/rstb.2007.2185
Lalonde K, Mucci A, Ouellet A, Gelinas Y (2012) Preservation of organic matter in sediments promoted by iron. Nature 483:198–200. https://doi.org/10.1038/nature10855
LaPerriere Nelson M, Rhoades CC, Dwire KA (2011) Influence of bedrock geology on water chemistry of slope wetlands and headwater streams in the southern rocky mountains. Wetlands 31:251–261. https://doi.org/10.1007/s13157-011-0157-8
Leifeld J, Steffens M, Galego-Sala A (2012) Sensitivity of peatland carbon loss to organic matter quality. Geophys Res Lett 39:L14704
Leinemann T, Preusser S, Mikutta R et al (2018) Multiple exchange processes on mineral surfaces control the transport of dissolved organic matter through soil profiles. Soil Biol Biochem 118:79–90. https://doi.org/10.1016/j.soilbio.2017.12.006
Lorenz K, Lal R, Preston CM, Nierop KGJ (2007) Strengthening the soil organic carbon pool by increasing contributions from recalcitrant aliphatic bio(macro)molecules. Geoderma 142:1–10. https://doi.org/10.1016/j.geoderma.2007.07.013
Luan J, Cui L, Xiang C et al (2014) Soil carbon stocks and quality across intact and degraded alpine wetlands in Zoige, east Qinghai–Tibet Plateau. Wetl Ecol Manag 22:427–438. https://doi.org/10.1007/s11273-014-9344-8
Marton JM, Creed IF, Lewis DB, Lane CR, Basu NB, Cohen MJ, Craft CB (2015) Geographically isolated wetlands are important biogeochemical reactors on the landscape. BioScience 65:408–418
McKee GA, Soong JL, Caldéron F et al (2016) An integrated spectroscopic and wet chemical approach to investigate grass litter decomposition chemistry. Biogeochemistry 128:107–123. https://doi.org/10.1007/s10533-016-0197-5
Meixner T, Manning AH, Stonestrom DA et al (2016) Implications of projected climate change for groundwater recharge in the western United States. J Hydrol 534:124–138
Mitsch WJ, Gosselink JG (2007) Wetlands, 4th edn. Wiley, Hoboken
Nierop KGJ (1998) Origin of aliphatic compounds in a forest soil. Org Geochem 29:1009–1016. https://doi.org/10.1016/S0146-6380(98)00165-X
Noël V, Boye K, Kukkadapu RK et al (2017) Understanding controls on redox processes in floodplain sediments of the Upper Colorado River Basin. Sci Total Environ 603–604:663–675. https://doi.org/10.1016/j.scitotenv.2017.01.109
NRCS (2008) Hydrogeomorphic wetland classification system: an overview and modification to better meet the needs of the natural resources conservation service. Technical note no. 190-8-76
Oades JM (1988) The retention of organic matter in soils. Biogeochemistry 5:35–70. https://doi.org/10.1007/BF02180317
Pett-Ridge J, Firestone MK (2005) Redox fluctuation structures microbial communities in a wet tropical soil. Appl Environ Microbiol 71:6998–7007. https://doi.org/10.1128/AEM.71.11.6998-7007.2005
Quideau SA, Anderson MA, Graham RC et al (2000) Soil organic matter processes: characterization by 13C NMR and 14C measurements. For Ecol Manag 138:19–27. https://doi.org/10.1016/S0378-1127(00)00409-6
Quideau SA, Chadwick OA, Benesi A et al (2001) A direct link between forest vegetation type and soil organic matter composition. Geoderma 104:41–60. https://doi.org/10.1016/S0016-7061(01)00055-6

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for statistical computing, Vienna

Rasmussen C, Heckman K, Wieder WR et al (2018) Beyond clay: towards an improved set of variables for predicting soil organic matter content. Biogeochemistry. https://doi.org/10.1007/s10533-018-0424-3

Reimer PJ, Bard E, Bayliss A et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1869–1887. https://doi.org/10.2458/azu_js_rc.55.16947

Retzer JL (1962) Soil survey of Fraser Alpine area, Colorado. U.S. Department of Agriculture, Washington, D.C.

Rezanezhad F, Couture R-M, Kovac R et al (2014) Water table fluctuations and soil biogeochemistry: an experimental approach using an automated soil column system. J Hydrol 509:245–256. https://doi.org/10.1016/j.jhydrol.2013.11.036

Rosenbloom NA, Doney SC, Schimel DS (2001) Geomorphic evolution of soil texture and organic matter in eroding landscapes. Glob Biogeochem Cycles 15:365–381. https://doi.org/10.1029/1999GB001251

Rumpel C, Kögel-Knabner I, Bruhn F (2002) Vertical distribution, age, and chemical composition of organic carbon in two forest soils of different pedogenesis. Org Geochem 33:1131–1142. https://doi.org/10.1016/S0146-6380(02)00088-8

Schimel DS, Braswell BH, Holland EA et al (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Glob Biogeochem Cycles 8:279–293. https://doi.org/10.1029/94GB00993

Segnini A, Posadas A, Quiroz R et al (2010) Spectroscopic assessment of soil organic matter in wetlands from the high Andes. Soil Sci Soc Am J 74:2246–2253. https://doi.org/10.2136/sssaj2009.0445

Segnini A, Souza D, Alves A et al (2013) Characterization of peatland soils from the high Andes through 13 C nuclear magnetic resonance spectroscopy. Soil Sci Soc Am J 77:673–679. https://doi.org/10.2136/sssaj2012.0291

Simpson MJ, Otto A, Feng X (2008) Comparison of solid-state carbon-13 nuclear magnetic resonance and organic matter biomarkers for assessing soil organic matter degradation. Soil Sci Soc Am J 72:268–276. https://doi.org/10.2136/sssaj2007.0045

Soil Survey Staff (1999) Differentiae for mineral and organic soils. In: Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys, 2nd edition. U.S. Department of Agriculture Natural Resources Conservation Service, pp 19–20

Sollins P, Kramer MG, Swanston C et al (2009) Sequential density fractionation across soils of contrasting mineralogy: evidence for both microbial- and mineral-controlled soil organic matter stabilization. Biogeochemistry 96:209–231. https://doi.org/10.1007/s10533-009-9359-z

Sposito G, Skipper NT, Sutton R et al (1999) Surface geochemistry of the clay minerals. Proc Natl Acad Sci USA 96:3358–3364. https://doi.org/10.1073/pnas.96.7.3358

Talma AS, Vogel JC (1993) A simplified approach to calibrating 14C dates. Radiocarbon 35:317–322

Taylor AFS, Fransson PM, Högberg P et al (2003) Species level patterns in 13C and 15 N abundance of ectomycorrhizal and saprotrophic fungal sporocarps. New Phytol 159:757–774. https://doi.org/10.1046/j.1469-8137.2003.00838.x

Tfaily MM, Cooper WT, Kostka JE et al (2014) Organic matter transformation in the peat column at Marcell Experimental Forest: humification and vertical stratification. J Geophys Res Biogeosci 119:661–675. https://doi.org/10.1002/2013JG002492

Torn MS, Trumbore SE, Chadwick OA et al (1997) Mineral control of soil organic carbon storage and turnover. Nature 389:170–173. https://doi.org/10.1038/38260

Ussiri DAN, Johnson CE (2003) Characterization of organic matter in a northern hardwood forest soil by 13C NMR spectroscopy and chemical methods. Geoderma 111:123–149. https://doi.org/10.1016/S0016-7061(02)00257-4

Wilson RM, Hopple AM, Tfaily MM et al (2016) Stability of peatland carbon to rising temperatures. Nat Commun 7:13723. https://doi.org/10.1038/ncomms13723

Wolf EC, Cooper DJ (2015) Fens of the Sierra Nevada, California, USA: patterns of distribution and vegetation. Mires Peat 15:1–22