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Soil carbon and nitrogen storage in alluvial wet meadows of the Southern Sierra Nevada Mountains, USA

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Abstract

Purpose Wet meadows formed on alluvial deposits potentially store large amounts of soil carbon (C) but its stability is subject to the impacts of management practices. The objective of this study was to quantify and characterize soil organic carbon (SOC) and nitrogen (N) in mountain wet meadows across ranges of meadow hydrology and livestock utilization.

Materials and methods Eighteen wetlands in the southern Sierra Nevada Mountains representing a range of wetness and livestock utilization levels were selected for soil sampling. In each wetland meadow, whole-solum soil cores delineated by horizon were analyzed for total and dissolved organic C (DOC) total (TN) and mineral nitrogen and soil water content (SWC). Multiple regression and GIS analysis was used to estimate the role of wet meadows in C storage across the study area landscape.

Results and discussion Average solum SOC contents by wetland ranged from 130 to 805 Mg ha^{-1}. All SOC and TN components were highly correlated with SWC. Regression analyses indicated subtle impacts of forage utilization level on SOC and TN concentrations, but not on whole-solum, mass-per-area stocks of SOC and TN. Proportions of DOC and TN under seasonally wet meadows increased with increasing utilization. GIS analysis indicated that the montane landscape contains about 54.3 Mg SOC ha^{-1}, with wet meadows covering about 1.7% of the area and containing about 12.3% of the SOC.

Conclusions Results indicate that soil organic C and N content of meadows we sampled are resilient to current light to moderate levels of grazing. In seasonally wet meadows, higher proportions of DOC and N with increasing utilization indicate vulnerability to loss. Partial drying of the wettest and seasonally wet meadows could result in losses of over five % of landscape SOC.

Keywords Dissolved organic carbon and nitrogen · Livestock grazing · Montane and subalpine meadows · Soil organic carbon and nitrogen · Soil organic matter · Wetland soils

1 Introduction

Alluvial wet meadows store inordinate amounts of SOC compared with surrounding uplands. In addition, wet meadows are hotspots of biological productivity and diversity and it is important to understand how management practices affect accrual or loss of SOC from these small but biogeochemically important landscape locations. Forested mountain landscapes are dominated by steep slopes, often with shallow soils where most SOC is stored in biomass and forest-floor detritus, and therefore vulnerable to catastrophic events such as wildfires, over grazing, and storm water runoff (Kattelmann 1996; Choromanska and DeLuca 2001). Biologically and hydrologically intact alluvial wet meadows buffer losses of SOC and nutrients by capturing and cycling sediments rich in organic materials. Deposition of C from the surrounding landscape supports C sequestration and many other ecosystem services (Norton et al. 2011). Wet meadows provide crucial habitats for many wildlife species, including threatened and endangered ones (Kattelmann and Embury

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1996; Roche et al. 2012), sinks for nutrients and pollutants that could otherwise degrade downstream waters (Sickman et al. 2002), and forage for livestock (Sulak and Huntsinger 2002). Grazing is an intensive management practice that can compromise other ecosystem services leading to degradation of both wetlands and uplands (Fleischner 1994; Cao et al. 2004; Cole et al. 2004).

Warm summers and ample moisture drive high primary productivity with anaerobic soil conditions that lead to some of the highest SOC and TN densities of terrestrial ecosystems (Mitra et al. 2005; Kayranli et al. 2010). Suppressed decomposition causes accumulation of dissolved organic C (DOC) that rapidly mineralizes if climatic or hydrological conditions change (Loheide et al. 2009; Budge et al. 2010; Norton et al. 2011). Despite the importance of ecosystem services provided by mountain wetlands that store large amounts of C and N, as well as their potential vulnerability to environmental change and disturbance, few estimates for SOC and N storage in high elevation ecosystems in western North America have been published (Prichard et al. 2000).

Livestock can influence habitat, soil integrity, and hydrology of mountain wetlands both positively (e.g., Allen-Diaz and Jackson 2000; Jackson et al. 2006) and negatively (e.g., Cao et al. 2004; Cole et al. 2004). Direct removal of vegetation and preferential grazing has been shown to affect the quantity and quality of soil C inputs (Ganjegunte et al. 2005). Additionally, hoof compaction can decrease water infiltration and soil aeration (Trimble and Mendel 1995; Pietola et al. 2005), which changes soil processes and speeds movement of runoff through wetlands.

The upper montane belt of the central and southern Sierra Nevada Mountains in California contains a high density of hydrologically intact wetland meadows across a wide range of soil moisture conditions. Results reported here complement findings of Norton et al. (2011) on quantities and factors controlling SOC and TN in upper montane riparian wetlands. The objectives of this study were to (1) quantify and characterize soil C and N in closed-basin (non-riparian) montane wetlands across three classes of wetland hydrology, and (2) determine effects of current livestock management practices on soil C and N storage. We hypothesized that long-term summer livestock utilization would lead to changes in soil C and N stocks in ways that compromise key ecosystem services provided by upper montane wetlands. Defining relationships among soil moisture, livestock utilization levels, and soil C and N storage facilitates broad-scale estimates and predictions of C and N storage and flux in mountain wetlands during a time of rapidly changing temperature and moisture conditions. Furthermore, quantifying soil C stocks will provide a baseline for monitoring changes resulting from climate change and management.

2 Materials and methods

2.1 Site description

Study sites included 18 upper montane wetland meadows (2,115- to 2,535-m elevation) on the west slope of the central Sierra Nevada that are saturated to some extent for part of each year. Mean annual precipitation is approximately 900 mm, with most occurring as snow (Western Regional Climate Center 2011; Huntington Lake weather station, elev. 2,134 m). Mean annual temperature is approximately 7 °C, with a maximum monthly average of 23 °C in July, and a minimum of −6 °C in January and February. Although this area received 160% of normal annual precipitation during 2006, there was no precipitation at our study sites for over two months prior to September, when soils were sampled (Western Regional Climate Center 2011; Huntington Lake Weather Station). Dry summers are the norm for this region, and soil moisture is typically at base level conditions by September. The geologic substrate of the study area is Mesozoic granite overlain in some places by glacial deposits (Wood 1975) with sandy loam and loamy sand soil textures at all our study sites.

Typical vegetation of the study area includes stands of lodgepole pine (*Pinus contorta* Douglas ex Louden) and red fir (*Abies magnifica* A. Murray), with mixed forests of Jeffrey pine (*Pinus jeffreyi* Balf.), sugar pine (*Pinus lambertiana* Douglas), white fir (*Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr.), and incense cedar (*Calocedrus decurrens* (Torr.) Florin) at lower elevations (Potter et al. 1996). The wetlands are covered by herbaceous vegetation composed of sedges (*Carex* spp.), rushes (*Juncus* spp.), and other hydrophytic forbs, grasses, and occasional shrubs (*Salix* spp.) (Potter 2005). Wetlands selected for this study were dominated by obligate wetland species, with some facultative wetland species and bryophytes (see Table 1). The grazing allotments are stocked with cow–calf pairs at about 100 ha per animal unit between June 1 and September 15.

Wetland meadows we studied were described by Roche et al. (2012) to represent a cross-section of meadow hydrology and long-term livestock utilization. For that study, the meadows were placed into three hydrological groups based water table monitoring during 2006 to 2008: (1) wettest meadows where water tables stayed at or above the surface throughout the snow free season (six meadows); (2) seasonally wet meadows where water tables started at the surface after snow melt and dropped an average of 55 cm by September 15 (seven meadows); and (3) driest meadows where water tables started about 24 cm below the soil surface and dropped to about 75-cm depth by September 15 (five meadows). Livestock utilization levels determined by comparative yield methods (Interagency Technical Team 1999) during 2006 to 2008 were provided by Roche et al. (2012). Sierra National Forest records indicated that the

Table 1 Soil properties and dominant vegetation, from wettest to driest meadows. Forage utilization and soil properties are mean of three sample points per meadow

	Area	Elev.	Soil water	Ave. util.	OC	TN	C:N	Soil suborder			Dominant vegetation
	ha	m	%		kg m^{-2}			Pnt. 1	Pnt. 2	Pnt. 3	
1	1.78	2,330	251	26.3	52.9	3.8	14.9	Histosol	Histosol	Aquept	*Phalacroseris bolanderi*, *Moss*
2	2.87	2,535	214	42.0	80.5	4.8	16.4	Histosol	Histosol	Histosol	*Eleocharis pauciflora*, *Mimulus primuloides*, *Muhlenbergia filiformis*
3	2.67	2,130	185	39.3	51.8	3.5	15.1	Histosol	Udept	Histosol	*Eleocharis machrostachys*, *Carex simulata*, *Phalacroseris bolanderi*
4	0.57	2,180	123	34.7	57.9	4	14.7	Histosol	Aquept	Histosol	*Juncus oxymeris*, *Eleocharis machrostachys*, *Polygonum bistortoides*
5	2.71	2,320	121	22.0	36.4	2.9	13.2	Histosol	Aquept	Aquept	*Mimulus primuloides*, *Carex vesecaria*, *Carex simulata*, *Deschampsia caespitosa*
6	5.38	2,120	105	34.3	44.5	3	14.9	Aquoll	Histosol	Histosol	*Carex vesecaria*, *Carex simulata*, *Deschampsia caespitosa*
7	7.69	2,170	99.2	25.0	41.2	3.2	12.7	Aquoll	Aquept	Histosol	*Carex vesecaria*, *Deschampsia caespitosa*, *Danthonia californica*, *Eleocharis pauciflora*
8	2.27	2,460	90.7	37.3	48.0	3	16.5	Udept	Histosol	Udept	*Polygonum bistortoides*, *Muhlenbergia filiformis*
9	3.64	2,480	86.8	4.0	13.1	1	14.1	Aquept	Histosol	Histosol	*Phalacroseris bolanderi*, *Erigeron* spp., *Carex* spp.
10	2.14	2,405	84.1	37.0	41.6	2.4	17.4	Udept	Udept	Aquept	*Carex jonesii*, *Mimulus primuloides*, *Muhlenbergia filiformis*
11	1.46	2,310	80.0	26.3	36.5	2.3	15.8	Histosol	Histosol	Aquoll	*Mimulus primuloides*, *Phalacroseris bolanderi*, *Aster alpigenus*
12	0.65	2,415	69.6	31.7	23.5	1.4	16.4	Udoll	Udoll	Udoll	*Mimulus primuloides*, *Carex echinata*, *Moss*
13	1.78	2,120	56.8	41.0	32.8	2.3	14	Udept	Aquept	Udept	*Carex jonesii*, *Phalacroseris bolanderi*, *Eleocharis pauciflora*
14	2.27	2,115	55.7	46.7	24.0	1.4	17.3	Udoll	Udoll	Aquoll	*Mimulus primuloides*, *Hypericum anagalloides*, *Juncus oxymeris*
15	1.3	2,465	51.1	35.7	15.6	1.2	13.6	Udept	Udept	Aquept	*Polygonum bistortoides*, *Mimulus primuloides*, *Trifolium monanthum*
16	1.54	2,375	49.1	35.3	18.3	1.4	13.8	Aquoll	Aquoll	Aquoll	*Mimulus primuloides*, *Phalacroseris bolanderi*, *Muhlenbergia filiformis*
17	1.34	2,120	47.0	44.0	28.0	1.9	14.3	Aquept	Histosol	Udoll	*Juncus oxymeris*, *Carex integra*, *Trifolium sp.*
18	0.81	2,145	42.5	48.7	28.1	2.1	13.8	Udoll	Udoll	Udoll	*Polygonum bistortoides*, *Phalacroseris bolanderi*, *Juncus oxymeris*

measured utilization levels, which ranged from zero to over 70% averaged by sampling point during the 3 years, are representative of longer term levels. Table 1 provides environmental information on the study meadows.

2.2 Soil sampling

Soils were described and sampled by horizon at sampling points selected to span the wettest to driest soils in each study wetland (three sample points per meadow) using a 3-cm diameter×45-cm length soil core. Cores were sampled to the C horizon and were laid out on a plastic tarp in the order they were extracted from the ground, taking care to maintain the proper depth by measuring the depth of the hole with a tape measure after each core was extracted. Soil horizons were then identified by noting differences in color (Munsell soil color chart), field texture by the feel method, organic horizon characteristics, and hydric soil features (Soil Survey Division Staff 1993). If necessary, a second or third core was collected to obtain an adequate amount of soil for laboratory analyses of each horizon. Cores were separated by horizon, bagged, and then placed on ice for transport to the laboratory. Whole-solum cores were also collected at each sample point for quantification of SOC and TN to a depth of up to 185 cm using a JMC Backsaver handle and extension with a 10-mm-diameter wet-soil core (Clements Associates, Inc., Newton, IA). Our objective was to sample to below the depth of appreciable SOM content as indicated by light-colored sandy C horizon material in order to estimate the total SOC and N contents. Two or more cores were collected and composited from each point and total depth and number of cores, as well as whether or not the core was suitable for bulk-density measurements, were noted. Cores deemed complete and suitable for accurate bulk-density analysis were bagged separately.

To preclude C and N transformations in sample bags, we homogenized and field extracted subsamples from full-solum cores immediately after collection by placing approximately 10 g from each sample into a pre-weighed vial that contained 30 ml of 0.5 M K_2SO_4 for determination of mineral N (nitrate-N (NO_3-N) and ammonium-N (NH_4-N)), DOC, and dissolved organic N (DON). Vials were immediately capped and stored on ice for transport to the laboratory.

2.3 Laboratory analyses

Composite samples were analyzed for gravimetric soil water content (SWC) (reported on a dry-weight basis; Gardner 1986), pH in H_2O by electrode (Thomas 1996), and bulk density by the core method (Blake and Hartge 1986). Soil texture was determined by the hydrometer method (Gee and Bauder 1986). Total SOC and TN were determined by Carlo Erba combustion on an NC2100 C/N analyzer (Carlo Erba Instruments, Italy). Total SOC was assumed to equal total C in these acidic systems (Nelson and Sommers 1996). Field extracts for DOC, inorganic N, and DON were reweighed to determine sample mass, shaken for 30 min, and filtered through Whatman # 40 paper. Soil remaining in the filters was 2-mm wet-sieved to determine gravel content for correction of initial soil sample weights. The SWC values were used to adjust soil weights for the field extracts. Extracts were analyzed for DOC using a UV-persulfate TOC Analyzer (Phoenix 8000, Tekman-Dorhmann, Cincinnati, OH). Total DON was measured by persulfate oxidation of the 0.5 M K_2SO_4 extracts (Cabrera and Beare 1993). Extracts were analyzed for NO_3-N using the single reagent method (Doane and Horwath 2003) and NH_4-N by the method of Weatherburn (1967). Extractable phosphorus was determined in 10-g subsamples by extraction with 0.5 M $NaHCO_3$ (Olsen and Sommers 1982).

Due to difficulties obtaining volumetric cores in saturated conditions, we were able to calculate accurate bulk density for less than half of our soil samples. In the samples for which we did obtain intact cores, bulk density was found to relate strongly to SOC concentration by a second-order polynomial equation: $[(\text{bulk density})^{1/2} = 1.32411 - 0.24918(\text{SOC})^{1/2} + 0.01929(\text{SOC})]$ ($r^2 = 0.66$), which we used to estimate bulk density for the remaining samples. This approach has been used by many researchers to estimate bulk density where volumetric samples cannot be obtained (e.g., Adams 1973; Alexander 1980; Manrique and Jones 1991; Franzluebbers 2010; Albaladejo et al. 2013).

2.4 Statistical analyses

Analyses of relationships among SWC, forage utilization level, and soil properties were conducted first by simple ANOVA comparing soil properties among the three hydrologic groups, and then by simple linear regression of values from all sample points ($n = 54$) (PROC REG; SAS Institute 2010). The considerable variation among the meadows (Table 1) was accounted for in the regressions by assigning dummy variables that represent arbitrary y intercepts (Weisberg 1982), nesting the sample points by meadow. Next, for variables where significant relationships were detected, multiple linear regressions and partial regressions (Neter et al. 1990; SAS Institute 2010) were conducted to determine whether the relationships remained when the other source was included in the model. Partial regressions (sometimes referred to as sequential or partial sum of squares) helped us determine the influence of forage utilization level when SWC was already accounted for in the model, as well as the influence of SWC when forage utilization was already in the model (Neter et al. 1990). These tests were applied for whole-solum, surface horizons, and uppermost mineral horizons for the meadows. Only results of the multiple linear regression analyses are presented.

2.5 Estimation of landscape carbon storage

To extrapolate our measured SOC storage values in the context of landscape SOC across the montane wet meadows and forests of our study area we utilized GIS (ARCmap 10.1, ESRI, San Diego, CA) with a wetland layer provided by the Sierra National Forest and the Sierra National Forest soil survey (Soil Survey Staff 2013a), in which associations of soil series are mapped and estimates of the extent of each soil series within each map unit are provided. A publicly available digital elevation model was used to confine our analysis to 2,115–2,535 m elevation. Soil organic C content by soil series was gathered by averaging soil pedon data available from the National Soil Characterization Database (NSCD) (Soil Survey Staff 2013b). Map unit SOC content was estimated by weighted average Mg SOC ha^{-1} from the soil survey and NSCD values and then grouped into six levels of SOC content. Soil organic C values for wet meadows across the study area were determined based on weighted average by hydrological group of the meadows we sampled.

3 Results

3.1 Soil morphology and whole-solum soil properties

Nineteen of the 54 pedons were classified as Histosols, 16 as Mollisols, and 19 as Inceptisols (Table 1). Table 2 shows soil characteristics and vertical distribution of SOC in pedons representative of wettest, seasonally wet, and driest meadows. In general, horizons high in SOC concentration increased in thickness with increasing soil moisture. Soil organic C content decreased constantly with depth in 28 of the 54 pedons (as in

Table 2 Representative soil profile descriptions from one pedon within wet (number 2 from Table 1), seasonally wet (number 10), and driest (number 18) meadows

Meadow	Soil suborder	Hor.	Depth	Dominant color (moist)	Rock frags	Texture			Text. class	C conc.	SWC	pH
						Sand	Silt	Clay				
			cm			%				%		
2	Histosol[a]	O1	0–8	10 YR 2/2	–	–	–	–	–	35.7	118	–
		O2	8–21	10 YR 2/2	–	–	–	–	–	24.5	118	–
		O3	21–58	10 YR 2/2	–	76	20	4	ls	41.3	465	4.8
		O4	58–125	10 YR 2/2	–	69	25	6	sl	36.6	404	4.9
		Bg	125–134+	10 YR 3/2	–	–	–	–	–	2.05	58.2	5.7
10	Aquept	O	0–8	10 YR 2/1	–	–	–	–	–	20.1	78.0	5.0
		A	8–26	2.5 Y 3/2	–	76	20	4	sl	4.40	36.3	5.2
		Ab	26–37	10 YR 2/1	–	–	–	–	–	8.91	122	5.2
		Ab	37–78	10 YR 3/2	–	49	41	10	–	6.26	59.1	5.2
		C	78–164+	10 YR 3/2	4.9	78	16	6	ls	2.12	53.6	5.5
18	Udoll	O	0–12	10 YR 2/2	–	–	–	–	–	17.3	316	–
		A	12–39	10 YR 2/1	–	68	26	6	sl	6.04	74.3	5.5
		Bg	39–106	10 YR 2/1	1.0	70	22	8	sl	1.78	40.0	5.8
		BC	106–137	2.5 Y 3/2	1.0	71	19	10	sl	1.12	43.9	6.1
		C	137–160+	2.5 Y 4/2	1.2	73	18	9	sl	0.47	45.4	6.1

Abk angular blocky, *Cl* clear, *Co* coarse (5 to <20 mm), *Di* diffuse, *F* few, *Fi* fine (<2 mm), *Gr* granular, *l* loam, *ls* loamy sand, *Med* medium (2 to <5 mm), *Mod* moderate, *Rm* dense mass of fine roots, *sl* sandy loam, *s* sand

[a] Histosols were not classified to suborder

meadow number 18, Table 2) and fluctuated with depth in the other 29 pedons (as in meadows 2 and 10, Table 2), indicating buried surface horizons or organic deposits.

Soils of all the meadows we evaluated were covered by organic (O) horizons that ranged from 3 cm to over 164 cm thick. Sandy, light-colored C horizons were over one m below the surface in 34 of the 54 pedons. Soil pH of all horizons ranged from extremely acidic (4.4) to slightly acidic (6.5), and increased with depth. Soils were mostly sandy loams and loamy sands, with 35 to 92% sand and 2 to 20% clay.

Soil properties in whole-solum cores averaged by meadow hydrology (Table 3) indicate distinct differences among the three hydrologic groups, with the wettest meadows storing over twice as much C and N on an area basis than the driest meadows. Concentrations of dissolved organic C and N, mineral N, and extractable P, did not vary substantially with meadow hydrology. Levels of extractable P and mineral N were very low in all the meadow soils. As proportions of SOC and total N, DOC, DON, and mineral N each varied significantly with meadow hydrology, with the driest meadows having the highest values and the wettest meadows the lowest values (Table 3). Average grazing utilization was about 30% in meadows of all the hydrologic groups but was most variable in the wettest meadows.

3.2 Soil C and N across ranges of utilization and soil moisture

Simple linear regression with arbitrary intercepts (nesting sample points by meadow) across all the data from all meadows indicated strong relationships among utilization level, SWC, and SOM components ($P<0.05$). However, partial regression of utilization against whole-solum soil properties normalized for SWC indicated that forage utilization explained no additional variation in the size of soil C and N pools ($P>0.10$). Multiple linear regression analysis indicated that livestock utilization did not significantly impact SOC independent of SWC across all the meadows ($P>0.10$). Considering only surface and uppermost mineral horizons, relationships of utilization level and SWC to SOC parameters were weaker, with utilization level having no influence when normalized for SWC by partial linear regression (not presented).

Multiple linear regression applied separately to hydrological groups indicated that, with SWC in the model, SOC and TN concentrations (milligrams per kilogram) dropped significantly with increasing forage utilization in soils beneath seasonally wet meadows (Table 4), but were not related to utilization beneath the wettest and driest meadows. Total SOC and TN stocks (mass per area) were not impacted by utilization, but were strongly related to SWC in each hydrological group. Soil organic C stocks beneath

Table 3 Average whole-solum soil properties and grazing utilization for meadows divided into three hydrologic groups. Standard deviations are in parentheses. Different letters following values indicate significant differences at $P<0.10$ by simple ANOVA

Hydrologic group[a]	N	Soil bulk density			Forage utilization			Soil water content			C/N		
		g cm^{-3}			%								
Wettest	18	0.64	(0.29)	b	29.8	(26.2)		167	(113)	a	14.9	(1.57)	a
Seasonally wet	21	0.81	(0.18)	a	29.8	(23.6)		83.6	(32.0)	b	15.2	(2.54)	ab
Driest	15	0.91	(0.15)	a	31.3	(17.6)		49.3	(15.0)	c	13.9	(1.09)	b
All	54	0.78	(0.24)		30.2	(22.7)		102	(82.9)		14.7	(1.96)	
Hydrologic group	N	Soil organic C			Soil total N			Soil organic C			Soil total N		
		%						kg m^{-2}					
Wettest	18	11.1	(9.21)	a	0.738	(0.549)	a	54.0	(26.0)	a	3.65	(1.65)	a
Seasonally wet	21	4.96	(2.69)	b	0.343	(0.210)	b	33.8	(15.0)	b	2.27	(1.04)	b
Driest	15	3.12	(1.28)	c	0.225	(0.096)	c	22.8	(10.0)	c	1.76	(0.67)	b
All	54	6.49	(6.46)		0.442	(0.403)		37.5	(17.0)		2.59	(1.42)	
Hydrologic group	N	Dissolved organic C			Dissolved organic N			NH_4-N			NO_3-N		
		mg kg^{-1}											
Wettest	18	105	(48.6)		12.0	(4.09)		3.88	(1.67)		0.0055	(0.0011)	a
Seasonally wet	21	91.8	(36.8)		10.0	(3.21)		3.74	(2.02)		0.0046	(0.0015)	b
Driest	15	92.4	(59.1)		10.6	(5.42)		4.80	(2.09)		0.0047	(0.0017)	ab
All	54	96.4	(47.2)		10.8	(4.22)		4.08	(1.95)		0.0049	(0.0015)	
Hydrologic group	N	Extractable phosphorus			DOC/SOC			DON/TN			Mineral N/TN		
		mg kg^{-1}			%								
Wettest	18	0.162	(0.189)		0.196	(0.197)	b	0.31	(0.258)	b	0.04	(0.061)	c
Seasonally wet	21	0.132	(0.145)		0.245	(0.172)	ab	0.40	(0.224)	ab	0.14	(0.149)	b
Driest	15	0.167	(0.185)		0.335	(0.218)	a	0.53	(0.328)	a	0.27	(0.176)	a
All	54	0.152	(0.169)		0.254	(0.198)		0.41	(0.277)		0.14	(0.161)	

[a] 1, wettest meadows (water table at or above surface all season); 2, seasonally wet meadows (water table started at surface in spring and dropped to 55-cm depth by Sept 15); 3, driest meadows (water table started 24 cm below surface in spring and dropped to 75-cm depth by Sept 15). Assigned via water table monitoring during 2006–2008 by Roche et al. (2012)

wettest and driest meadows dropped by about 13 and 4 g m^{-2}, respectively, for each percent increase in SWC, and, beneath seasonally wet meadows, increased about 270 g m^{-2} for each percent increase in SWC. Total N followed a similar pattern but dropped more steeply with increases in SWC in the wettest and driest meadows. Concentrations of SOC increased with SWC in all three hydrologic wet meadow groups, while concentrations of TN increased with SWC under seasonally wet meadows, but decreased under the wettest and driest meadows (Table 4).

Dissolved organic C per unit SOC increased significantly with increasing utilization level in the seasonally wet and driest meadows, while DON per unit TN increased with increasing utilization in the wettest meadows (Table 4). Dissolved organic C levels per unit SOC decreased with increasing SWC in the seasonally wet and driest meadows, but not the wettest meadows. The DOC/DON ratios were lower than SOC/TN ratios, ranging from 8.14 to 12.6, and averaging 8.83.

Mineral N per unit TN showed a strong negative relationship with SWC across all meadows, but no relationship with utilization (Table 4). Extractable P contents were also very low and showed no relationship with utilization or SWC. A low variance inflation factor indicates that these results were not caused by collinearity between forage utilization and soil water content (Weisberg 1982).

3.3 Landscape carbon storage estimates

GIS analysis indicated that 13% of our study area has been mapped as bare, glacier-scoured granite that contains less than 10 Mg C ha^{-1} (Fig. 1). Shallow entisol–lithic complexes cover 37.7% of the area and contain 10–40 Mg C ha^{-1}. Somewhat deeper forest soils cover 37.8% of the area and contain 40–90 Mg C ha^{-1}. Deep forest soils cover about 11% of the area and contain 90–160 Mg C ha^{-1} (Soil Survey Staff 2013b), while wet meadows cover 1.8% of the area and contain a weighted average of 394 Mg C ha^{-1} based on our analysis.

Table 4 Slope and P values for multiple linear regression of whole-solum soil properties regressed against forage utilization level and soil water content. All regressions were conducted with each meadow being an arbitrary y-intercept in the model

	Hydro:[a]	Utilization			Soil water content		
		Wettest	Seasonally wet	Driest	Wettest	Seasonally wet	Driest
	N:[b]	6	7	5	6	7	5
SOC (mg kg^{-1})	Slope	ns[c]	−0.025	ns	0.007	0.074	0.007
	R^2	0.0003	0.1515	0.0712	0.4105	0.8559	0.4521
	P	ns	0.073	ns	0.003	0.000	0.004
TN (mg kg^{-1})	Slope	ns	−0.002	ns	−0.185	0.006	−0.047
	R^2	0.0124	0.2421	0.0004	0.3503	0.8809	0.3504
	P	ns	0.020	ns	0.008	0.000	0.016
Mineral N/TN	Slope	ns	ns	ns	ns	−0.003	ns
	R^2	0.0736	0.0645	0.0232	0.0652	0.7759	0.0129
	P	ns	ns	ns	ns	0.000	ns
DOC/OC	Slope	ns	0.001	0.094	ns	−0.001	−0.008
	R^2	0.0212	0.1888	0.3018	0.0034	0.2256	0.3846
	P	ns	0.043	0.028	ns	0.026	0.010
DON/TN	Slope	0.010	ns	ns	0.000	0.000	ns
	R^2	0.1879	0.0741	0.0231	0.1439	0.3817	0.0021
	P	0.064	ns	ns	0.109	0.002	ns

[a] Hydro group: wettest, saturated to surface all season; seasonally wet, saturated to surface in spring dropping to 55 cm by fall; driest, saturated to 24 cm in spring dropping to 75 cm by fall. Depth values are averages over three years based on Roche et al. (2012)

[b] N number of meadows with three points per meadow

[c] *ns* not significant at $P=0.1$

Extrapolating across this portion of the upper montane zone, meadows currently contain an estimated 12.3% of SOC stores and other soils 87.7%, totaling about 54.3 Mg C ha^{-1} across this landscape. Soils beneath the six wettest meadows we evaluated contain an average of 540 (±150) Mg C ha^{-1}, while those beneath the seven seasonally wet meadows contain 338 (±120) Mg C ha^{-1}, and those beneath the five driest meadows contain 228 (±56.7) Mg C ha^{-1} (standard deviation in parentheses).

4 Discussion

Our results indicate that upper montane meadow wetlands of the southern Sierra Nevada Range store high densities of SOC in deep soil horizons, many of which are buried by sediment deposits (Table 2). Long-term meadow utilization by livestock affected C and N concentrations in soils beneath seasonally wet meadows, but did not affect overall SOC and TN stocks. High density of SOC results from high primary productivity combined with influx of deposited organic materials from forested slopes under cool, anaerobic conditions that retard decomposition (Kayranli et al. 2010). The high surface SOC contents along with buried organic horizons we observed indicate that both in situ production and influx of forest-floor materials contribute high SOC densities in these meadows. Roche et al. (2012) noted strong negative correlation between forage quality and meadow wetness, which not only deters utilization by livestock in the wettest meadows, but also facilitates accumulation because indicators of low forage quality also indicate resistance to decomposition (e.g., acid detergent fiber).

Although the meadow wetlands evaluated in this study do not show signs of hydrological degradation, degradation stemming from changing land use that increases runoff from uplands or damages meadow resistance to erosion, for instance, could cause substantial loss of SOC and related ecosystem services provided by upper montane wetlands (Norton et al. 2011). If, for example, degradation changed meadow hydrology of the wettest and seasonally wet meadows in our study to be similar to the driest meadows, with water tables below the surface all season and about 245 Mg SOC ha^{-1}, landscape-scale C storage would drop from 54 to 51 Mg C ha^{-1}, and the proportion stored beneath wetland meadows would drop from 12.3 to 7.8%. Drying would also lead to increased livestock utilization and further changes to SOC and N pools.

While organic-matter-rich soils of wetland meadows represent substantial C storage for global warming mitigation, they may be more important in terms of other ecosystem services, such as reactive N removal, flood mitigation, sustained stream flows, wildlife habitat, and forage production. In large parts of upper montane catchments in this area, wetland meadows contain nearly the only soil cover, and are therefore crucial buffers between high alpine runoff zones and downstream aquatic habitats, mitigating erosive power and capturing sediments, forest debris, and N from uplands.

As global climate change scenarios continue to take effect, increases in temperature, with rain replacing more and more

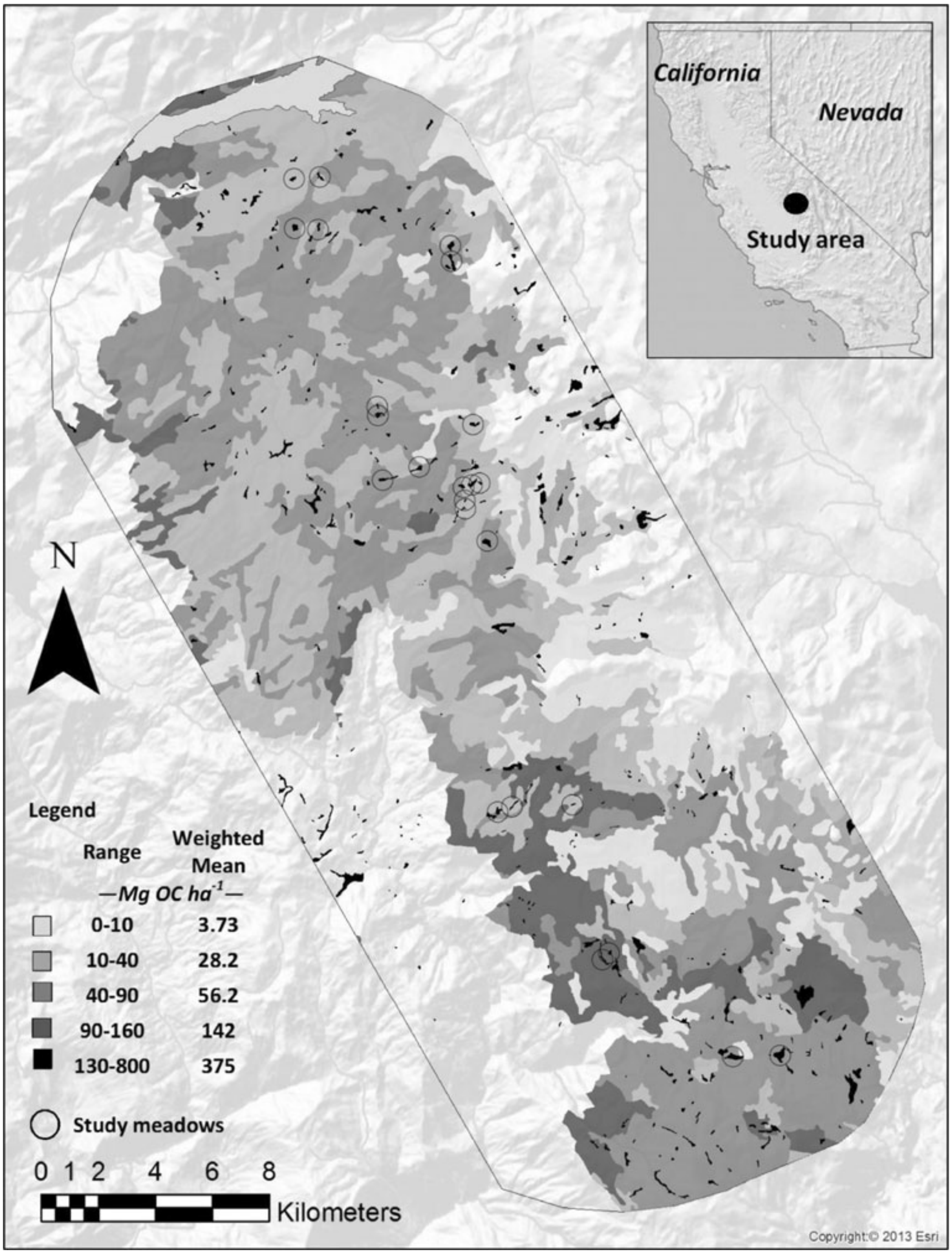

Fig. 1 Distribution of wetland meadows and soils in the study area. Area of mapped soils represents the upper montane zone (2,115- to 2,535-m elevation) in this portion of the west slope of southern Sierra Nevada Mountains. Meadow soil organic carbon values are based on results of this study. Other values are based on weighted means by area of soil map units and organic carbon contents from the Sierra Nevada soil survey (Soil Survey Staff 2013a) and the National Soil Characterization Database (Soil Survey Staff 2013b)

high elevation snowfall (Hayhoe et al. 2004), will cause increased runoff intensity and stream power (Kattelmann 1996). This means that, for meadows to continue to function properly and resist hydrological degradation, they need optimal plant cover and productivity.

4.1 Soil water content and forage utilization interactions

Relationships between grazing utilization, SWC, and other factors did not correlate to SOC levels across meadows indicating that current management protocols, with forage utilization levels generally below 50%, have subtle impacts on SOC (Table 4). Soil organic C and TN concentrations that decline with increasing forage utilization under seasonally wet meadows are consistent with changes due to livestock utilization observed by other authors. In a study of pack stock impacts on subalpine Sierra Nevada meadows, Cole et al. (2004) found that consistent utilization levels over 35% caused marked declines in productivity of meadows in Yosemite National Park. Though they did not measure SOC levels, feedbacks between biomass productivity and SOC would, with time, cause declines in SOC. Walker et al. (2009) found that soils of restored Appalachian mountain wetlands assimilated reactive N more rapidly in than wetlands degraded by heavy livestock utilization. Shan et al. (2011), recorded significant negative impacts of moderate to heavy sheep utilization on N cycling and storage in Mongolian grasslands. They concluded that livestock had indirect effects by decreasing snow retention due to less residual biomass, reducing soil moisture and biomass production while increasing soil temperature in strongly seasonal patterns.

A combination of moist soil and palatable forage may make the seasonally wet meadows more vulnerable to late-season grazing activity than either the wettest group, with low quality forage, or driest group, with relatively resistant soils due to lower moisture content. Lack of influence of utilization level on C and N stocks on a mass-per-area basis in any of the hydrological groups underscores the subtlety of the effect and is likely due to variability in soil density that overwhelms effects on C and N concentration. Increases in DOC per unit OC with increasing utilization in the drier meadows (Table 4) are consistent with disturbance effects noted in many environments (Norton et al. 2004, 2011). Wetland soils also commonly have high proportions of DOC compared to drier soils due to inhibited mineralization and immobilization (Budge et al. 2010; Norton et al. 2011). Our results from multiple regression analysis indicate that, at given levels of SWC in seasonally wet and driest meadows, DOC accumulates as utilization level increases. Such proportional increases in DOC often result from soil disturbance and may indicate a shift toward a more open, less conservative SOC cycling (DeLuca and Keeney 1993; Norton et al. 2004, 2011, 2012). Increases in mineral N, both in absolute terms and per unit TN, also often result from disturbance, but in this case, only correspond to drier meadow hydrology and not to utilization levels. Roche et al. (2012) noted very low concentrations of dissolved mineral N in pools of standing water located in our study meadows, regardless of livestock utilization intensity, suggesting conservative N cycling characteristic of undisturbed plant–soil systems.

5 Conclusions

High mountain wetland meadows represent important regional C sinks with some of the highest measured SOC densities of any soils. Soils of the non-riparian, hydrologically intact wetlands we evaluated are apparently resistant to impacts of low to moderate livestock utilization levels that are often noted in other settings. Our data show that the high densities of SOC have relatively high proportions of DOC and total N such that accumulation and preservation is highly dependent upon maintenance of saturated conditions. Indeed, SWC is so highly correlated with SOC and DOC that it is difficult to detect whether other potential impacts, such as livestock utilization, have any influence. However, the exceptionally strong connection between SWC and SOC indicates that any change in hydrology of the wetlands will lead to losses of soil C and likely deterioration of ecosystem services. Under predicted climate change, with reduced total precipitation and less snowpack to maintain anaerobic conditions, these wetlands may lose their resilience and their ability to retain soil C and N. Our work reported here emphasizes that C and N storage supports many of the important ecosystem services gained through proper use, management, and restoration of upper montane wetlands.

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