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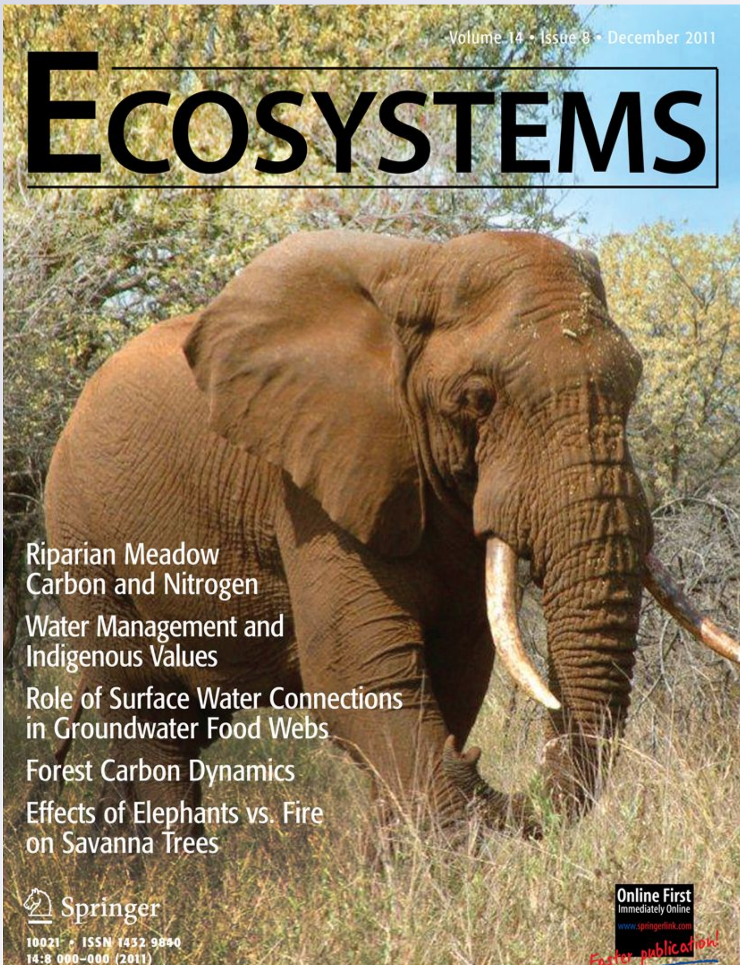

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Soil Carbon and Nitrogen Storage in Upper Montane Riparian Meadows

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Abstract

Though typically limited in aerial extent, soils of high-elevation riparian wetlands have among the highest density of soil carbon (C) and nitrogen (N) of terrestrial ecosystems and therefore contribute disproportionally to ecosystem services such as water retention, forage production, wildlife habitat, and reactive N removal. Because much soil C and N is stored in labile forms in anaerobic conditions, management activities or environmental changes that lead to drying cause mineralization of labile soil organic matter, and loss of C and N. Meadows are focal points of human activities in mountain regions, often with incised stream channels from historically heavy grazing exacerbated by extreme runoff events. To quantify soil C and N stores in montane riparian meadows across hydrologic conditions, 17 meadows between 1950- and 2675-m elevation were selected in the central Sierra Nevada Range, California, that were classified using the proper functioning condition (PFC) system. Results indicate that C and N density in whole-solum soil cores were equivalent at forest edge positions of properly functioning, functioning at-risk, and nonfunctioning condition. Soils under more moist meadow positions in properly functioning meadows have at least twice the C, N, dissolved organic C, and dissolved organic N (DON) than those under nonfunctioning meadows. Densities of total N and DON, but not C, of functioning at-risk meadows are significantly lower ($P < 0.05$) than those of properly functioning meadows at mid-slope and streambank positions, suggesting accelerated loss of N early in degradation processes. Though variable, the soil attributes measured correspond well to the PFC riparian wetland classification system.

Key words: soil organic matter; riparian meadows; wetlands; soil organic carbon; carbon and nitrogen storage; Sierra Nevada wet meadows.

Introduction

Although wetlands are typically small components of landscapes, they contribute disproportionally to biogeochemical processes that underlie key ecosystem services (Kayranli and others 2010; Mitra and others 2005). High-elevation riparian meadows have high C and N densities (Blank and others

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2006; Budge and others 2010), which provide important ecosystem services such as storing water, retaining potential pollutants, sustaining stream flows, and driving high primary productivity that creates valuable habitat for wildlife and seasonal livestock grazing (Cole and others 2004; Peterson and others 2001; Sulak and Huntsinger 2002).

High rates of anthropogenic N deposition in historically N-limited, high-elevation headwater systems (Beem and others 2010; Burcar and others 1997; Sickman and others 2002) require efficient N removal imperative for protection of downstream waters susceptible to eutrophication. In their review of the potential of wetlands to sequester reactive N, Jordan and others (2010) estimate that wetlands remove 20–21% of the total anthropogenic N load in the United States, and 17% worldwide. Peterson and others (2001) describe the very large capacity of properly functioning headwater streams to remove N. Sickman and others (2003) describe how properly functioning montane riparian meadows mitigate N flow from Sierra Nevada catchments impacted by elevated N deposition. The high potential of soils under riparian meadows for assimilation of reactive mineral N and dissolved organic N (DON) is a function of high soil organic C (SOC) content. For this reason, increased protection and restoration of wetlands is a key aspect to mitigate the effects of anthropogenic N deposition.

Soil organic C in cool and wet high-elevation meadows turns over much more slowly than in temperate environments (Budge and others 2010). High primary productivity generates large quantities of plant-residue-derived soil organic matter (SOM), which is partially decomposed and preserved as labile C and N in particulate and dissolved organic materials (Kayranli and others 2010). These labile materials are vulnerable to loss with changing management and environmental conditions. For example, Sigua and others (2009) report a 97% loss of total organic C (from 180 to 5.4 g kg^{-1}) with drainage of wetlands for conversion to beef cattle pastures. Global warming is expected to accelerate SOC turnover and may impact the ability to retain N.

Previously degraded or drained wetlands have proven to be resilient, however, and with improved management and restoration of wetland hydrology, represent an important opportunity for expanded habitat and forage production, increased C and N sequestration, and sustained stream flows (for example, Erwin 2009). Wetland restoration typically causes rapid recovery of SOC compared to restoration of upland ecosystems (for example, Foote and Grogan 2010). Loss of C and N from deteriorating wetlands, on the other hand, is a central source of greenhouse gases (Kayranli and others 2010) as well as reduced N retention, loss of habitat, declining water quality and supply, and other ecosystem services (Elmore and Kauffman 1994).

The upper montane belt of the west slope of the Sierra Nevada range, between approximately 1800- and 2600-m elevation, contains extensive riparian meadows across a wide range of natural and land use-influenced variability (Potter 2005; Purdy and Moyle 2006). The objective of this study was to quantify total and labile soil organic C and N in upper montane riparian meadows of the central Sierra Nevada mountains in California. To sample across a spectrum of hydrological conditions, we chose meadows from a population evaluated using the properly functioning condition (PFC) system of Prichard (1998), which is used widely to assess potential for wetlands to fulfill habitat and hydrological functions. The magnitude of SOC and N retention or loss associated with different degradation conditions is not well known, however, nor is the potential for recovery with stream channel restoration. Linking soil characteristics and functions to PFC classes could improve broad-scale estimates for improved management or restoration.

Materials and Methods

Study Area

Study sites included upper montane riparian meadows at 1950- to 2675-m elevation in the Stanislaus National Forest (SNF) on the west slope of the Sierra Nevada range (Table 1; Figure 1). The climate is characterized by dry, warm summers and wet, cool or cold winters with mean annual precipitation of 1524 mm, 75–90% of which occurs as snow, and mean annual temperature of 2.7°C (Stanislaus Meadows weather station; 2362 m elevation, 38.5055°N 119.9373°W). Average minimum and maximum daily temperatures were −3.9 and 10°C, respectively. Snowfall occurs between September and May in most years (Potter 2005). Soil temperatures are frigid to cryic, ranging from 0 to 8°C (Retelas and others 1995).

Soils of the riparian meadows were classified broadly by Retelas and others (1995) as cryumbrepts with some endoaquolls (Soil Survey Staff 1994) derived from alluvium of granitic and volcanic rock. Surrounding uplands consist of large

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Table 1. Characteristics of Meadows Selected for Study

Meadow name	Condition class	Area (ha)	Elev. (m)	Soil suborder			Watershed and stream characteristics				
				Forest edge	Mid-slope	Stream-bank	Catchment area (ha)	Order[2]	Channel width (m)	Bank-full depth (m)	Width: depth
Bourland	Properly functioning	18	2,220	Xerept	Aquoll	Xeroll	238	1	1.31	0.19	6.79
Cooper west		10	2,553	Orthent	Aquept	Xeroll	351	2	3.81	0.26	14.6
Eagle upper south		18	2,304	Aquoll	Aquoll	Aquoll	16	1	0.76	0.12	6.58
Three meadows west		6	2,448	Cryept	Cryoll	Aquoll	121	1	2.59	0.15	17.1
Weed lower		4	2,204	Xeroll	Aquoll	Aquoll	45	1	1.25	0.12	10.6
							154				**11.1b**[3]
Beaver	Functioning at-risk	4	2,398	Cryept	Aquept	Aquept	1100	2	5.18	0.29	18.1
Disaster north		4	2,359	Xeroll	Xeroll	Xeroll	1228	1	6.77	0.19	34.8
Disaster south		4	2,318	Aquoll	Aquoll	Aquoll	1385	1	4.27	0.13	33.9
Milk ranch north		10	2,558	–[1]	–[1]	–[1]	21	2	2.10	0.29	7.31
Pacific valley lower		15	2,302	–[1]	–[1]	–[1]	1127	1	10.2	0.17	60.0
Pacific valley upper		6	2,496	–[1]	–[1]	–[1]	84	1	1.77	0.18	9.99
							489				**19.2ab**
Bell west/lower	Nonfunctioning	5	1,947	Xerept	Xerept	Xerept	304	1	3.81	0.12	31.5
Castle rock		17	2,675	Orthent	Cryept	Cryept	101	1	2.71	0.15	18.0
Cooper east		24	2,558	Xerept	Xerept	Xerept	760	2	11.3	0.12	96.7
Eagle upper east		4	2,301	Xeroll	Aquoll	Xerept	884	2	7.92	0.16	49.5
Hermit valley		12	2,156	Cryoll	Cryept	Cryoll	4754	3	17.7	0.60	29.6
Weed upper		8	2,243	Aquoll	Aquoll	Xeroll	19	1	0.43	0.06	7.64
							693				**25.4a**

[1] *Soil profiles not sampled.*
[2] *Stream order according the Strahler method (Strahler 1957).*
[3] *Mean width:depth ratio for condition class. Different letters following means indicate significant differences at $P < 0.05$.*
Condition class was assigned by the Stanislaus National forest based on the Proper Functioning Condition system of Prichard (1998).

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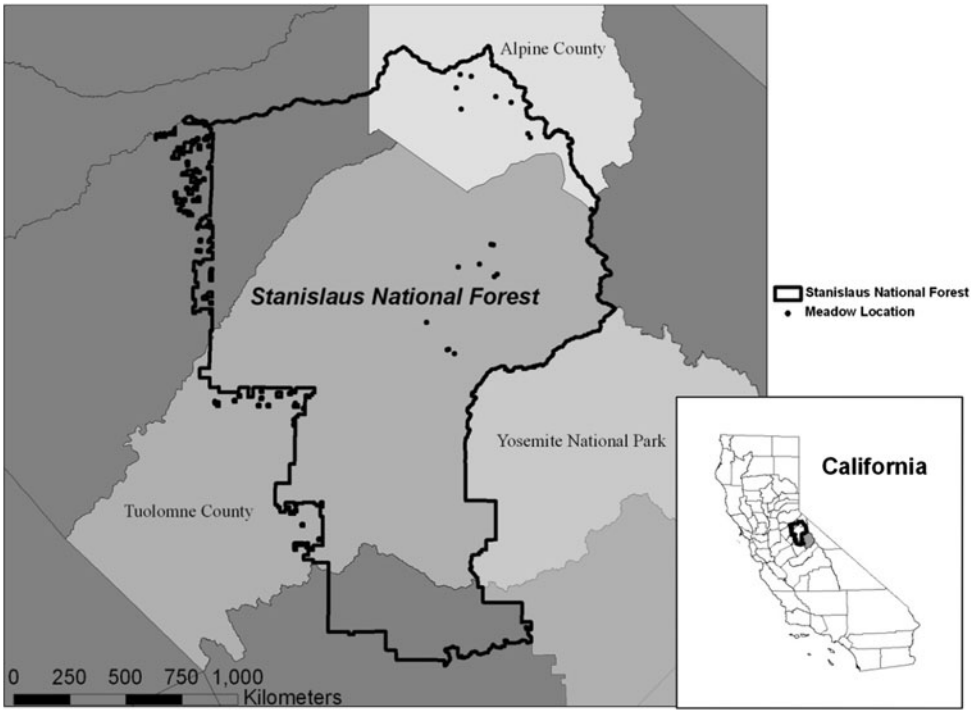

Figure 1. Study site locations in the central Sierra Nevada range, California.

areas of bare granitic and volcanic rocks and shallow forest soils of the Inville (frigid Ultic Haploxeralfs) and Gerle (frigid Humic Dystroxerepts) families ranging from 50 to 90 cm in depth (Soil Survey Staff 2011; Figure 2). Vegetation in the meadows consists of sedges (*Carex* spp.), and rushes (*Juncus* spp.), with other forbs, grasses, and shrubs (*Salix* spp.) (Ratliff 1985). Uplands are forested by lodgepole pine (*Pinus contorta* Louden spp. murrayana [Grev. & Balf.]), red fir (*Abies magnifica* A. Murray) and Jeffery pine (*Pinus jeffreyi* [Grev. & Balf.]) (Potter 2005).

Livestock grazing began in the Sierra Nevada in the 1860s and was unregulated until the Taylor Grazing Act of 1934 (Menke and others 1996; Purdy and Moyle 2006). Since then, stocking rates have gradually declined under U.S. Forest Service grazing management policies. Some meadows were foci of summer ranches and received heavy, continuous use by sheep, horses, and cattle, whereas others received lighter use. Legacy effects of unregulated heavy grazing are thought to remain in some meadows (Kattelmann and Embury 1996; Menke and others 1996) and may be a primary driver of hydrological degradation. Other factors may be exacerbated by the legacy effects of heavy grazing and include logging, recreational vehicle use, and intense rain-on-snow runoff events (Kattelmann 1996; Kattelmann and Embury 1996; Purdy and Moyle 2006).

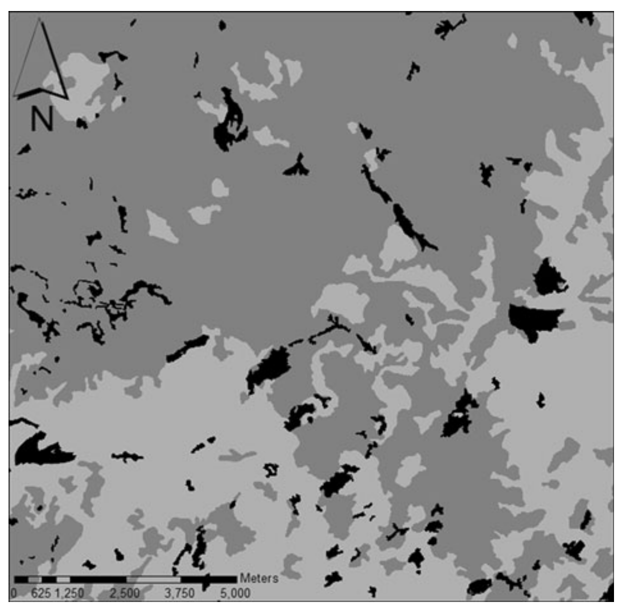

Figure 2. Portion of study area showing distribution of riparian meadow soil (*black*), forest soil (*dark gray*), and bare rock (*light gray*). Forest soils map units depicted here include Inville and Gerle rock outcrop complexes with 20–55% bare rock (Soil Survey Staff 2011).

Meadow Selection

Eighty-three prominent riparian meadows in the upper montane zone were rated by SNF staff for this study using the widely accepted PFC

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assessment guidelines of Prichard (1998). Twenty-seven of the rated meadows were classified as properly functioning, covering 406 ha, 31 as functioning at-risk, covering 410 ha, and 25 as nonfunctioning, covering 319 ha. To sample across a spectrum of hydrologic conditions, 17 meadows were randomly selected from the three condition classes (properly functioning, $n = 5$; functioning at-risk, $n = 6$; nonfunctioning, $n = 6$).

The National Riparian Service Team (2008) reports that by 2008 the PFC system was in use by all major state and federal land management agencies as well as communities across the western United States, with thousands of individuals having been trained on use of the technique. Although there are critical reviews of the PFC system (for example, Stevens and others 2002), Purdy (2010) found that the PFC method corresponded closely with other qualitative methods, but tended to overestimate condition compared to quantitative inventories. Ward and others (2003) found that rapid hydrological assessments like PFC were best used in combination with habitat-based techniques.

We chose this categorical approach to study site selection to ensure that we sampled across a spectrum of meadow conditions in a relatively small sample size that facilitated intensive sampling techniques. Our results would support simplified, focused analysis across a broader, completely random selection of meadows that would add precision to broad-scale estimates of meadow conditions, C and N stores, and other ecosystem services.

Sampling Design and Meadow Characterization

Six 30-m transects oriented parallel to the stream channel, each with four soil-vegetation sample points at 10-m intervals (24 points per meadow), were established in each selected meadow. Transects were placed at the midpoint of the stream-bank, mid-slope, and forest edge landforms on both sides of the stream (Figure 3). This geomorphic, landscape position-based sampling approach was chosen to facilitate extrapolation across wider areas with a manageable dataset. Though riparian meadows are highly variable and each is unique, these three landforms are characteristic, have distinct soil processes and hydrology, and are often used for meadow characterization and sampling (for example, Blank and others 2006; Potter 2005).

Prior to soil sampling, vegetation cover by species, soil morphology, and stream channel parameters were measured. Plant cover by species within a 35 × 70-cm quadrat was recorded at each sample

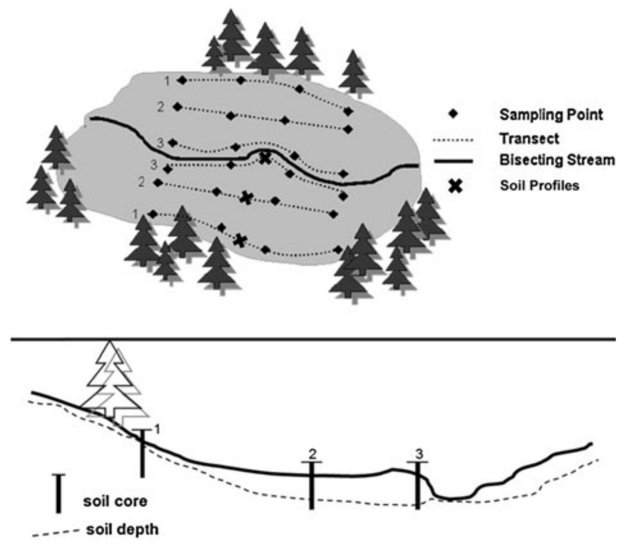

Figure 3. Conceptual diagram of sampling design within a meadow. Transects labeled as *1* are forest edge, *2* are mid-slope, and *3* are stream-bank positions.

point (Daubenmire 1968) and wetland status was noted for each species (Federal Interagency Committee for Wetland Delineation 1989). Soil profiles were described and sampled by horizon at the midpoint of each transect on one side of the stream (three profiles per meadow; Figure 3) using a 3-cm-diameter soil core. Channel width-to-depth ratio, defined as an index of cross-sectional shape measured at bank-full level (Rosgen 1996) was calculated from channel measurements. The location of each channel cross section, which represents the outlet of the contributing watershed, was recorded by GPS (Trimble Navigation Limited, Sunnyvale, CA). Watershed catchment area for each channel cross section was determined using the Automated Geospatial Watershed Assessment Tool 2.0 on a U.S. Geological Survey Digital Elevation Model base map in ARCmap (ESRI, San Diego, CA). All data were projected in NAD_1983_UTM_Zone_10 N.

Soil Sampling

Whole-solum cores were collected at each sample point for analysis of soil C and N pools 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). The goal was to sample to below the depth of appreciable SOC content as indicated by light-colored sandy C-horizon material. Two or more cores were collected and composited from each point and total depth, as well as whether or not the core was

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suitable for bulk-density measurements, were noted. Cores selected for bulk-density analysis were bagged separately from bulk samples.

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 nitrate-N (NO_3-N), ammonium-N (NH_4-N), dissolved organic C (DOC), and DON. Vials were immediately capped and stored on ice for transport to the laboratory.

Laboratory Analyses

Composite samples were analyzed for gravimetric water content (Gardner 1986), pH in H_2O by electrode (Thomas 1996), and bulk density by the core method (Blake and Hartge 1986). Total C and TN were determined by Carlo Erba combustion on an NC2100 C/N analyzer (Carlo Erba Instruments, Italy). Total C was assumed to equal SOC 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.

Extracts were analyzed for DOC using a UV-persulfate TOC Analyzer (Phoenix 8000, Tekman-Dorhmann, Cincinnati, OH). Total dissolved N was measured by persulfate oxidation of the 0.5 M K_2SO_4 extracts (Cabrera and Beare 1993). Extracts were analyzed by flow injection for NO_3-N using the single reagent method (Doane and Horwath 2003) and NH_4-N by the method of Weatherburn (1967).

Density fractionation (Sohi and others 2001) was used to separate and quantify organic C (OC) and total N (TN) in free and aggregate-occluded light SOM fractions known to respond differently to changing management conditions, and in the more stable mineral-associated fraction. Following separation, the three SOM fractions were dried at 105°C for 24 h and analyzed on an EA1100 Soil C/N analyzer (Carlo Erba Instruments, Milan Italy) to determine light fraction organic C (LFOC) and N (LFN) in the free and occluded light fractions, as well as mineral-associated OC and N.

Data Analysis

The data from this study were as analyzed as a split–split plot in space set in a completely randomized design, which was excerpted from the linear model of Milliken and Johnson (1992). Analysis was conducted to test the effects of meadow hydrologic condition on multiple soil characteristics. The experimental unit was the meadow and the sub plots were transects within each landscape position. Landscape position within each meadow was fixed and repeated as a variable nested within each replicated meadow across all three hydrologic conditions. The effect of meadow side was examined statistically, but was not significant, so data were composited from both transects for each landscape position. Also, preliminary analyses indicated that soils under the forest edge position did not vary significantly by hydrological condition class, and those of the mid-slope and stream-bank positions were statistically similar, so we excluded forest edge soils and grouped the other two positions for analysis of OC and TN parameters by condition class. SAS software running a general linear model (Proc GLM) was used with an alpha of 0.05 selected to determine statistical significance of comparisons between hydrologic condition and landscape position as determinants of soil characteristics (SAS 9.1.3, SAS Institute, Cary, NC). The ANOVA and LSD functions in PASW Statistics 18 (IBM Corporation, Somers, NY) were used for comparison of soil depth and horizon thickness (alpha = 0.05) and the correlation function was used for correlation of soil water content with SOC and TN densities. For vegetation cover analysis, each species was categorized by lifeform, including trees, shrubs, forbs, grasses (members of Poaceae family), and sedges and rushes (members of Cyperaceae and Juncaceae families).

Results

Hydrological Characteristics, Vegetation, and Soil Morphology

Stream channel and watershed measurements confirmed that channels through properly functioning meadows were deeper and narrower (lower width:depth ratios) than those through nonfunctioning meadows (Table 1). Linear regression of channel depth by catchment area (Figure 4) indicated that channel depth increases with catchment size for properly functioning meadows but not for nonfunctioning meadows.

Soils and vegetation of the forest edge landscape position are transitional, with mixed upland and wetland plants dominated by forbs and grasses (Table 2). Pedons were mostly characterized by dark colored A and Bw horizons of Mollisols,

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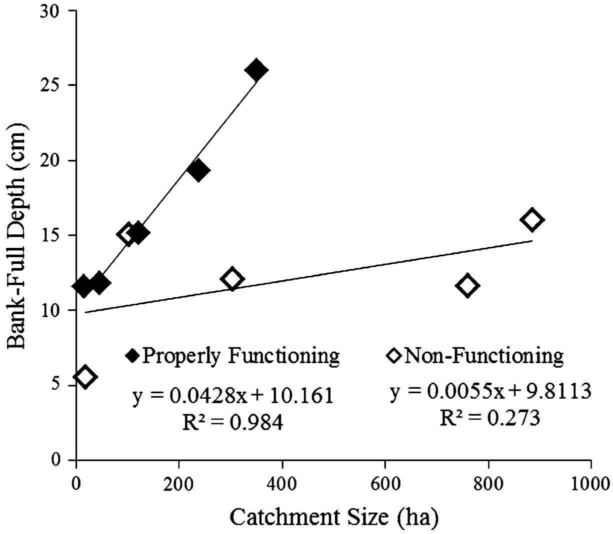

Figure 4. Linear regression of bank-full depth versus catchment area for properly functioning and nonfunctioning meadows. Hermit Meadow was excluded because it is the only order 3 stream in the study and has a much larger catchment area than the others (see Table 1).

indicating aerobic soil-forming conditions dominated by incorporation of organic material. Seven of the 14 forest-edge pedons classified reflect the dynamic erosional and depositional process of less developed Entisols and Inceptisols. Most of the meadows had distinct boundaries between mid-slope and forest-edge positions as indicated by the change in soil suborder (Table 1), but three of the meadows had low relief so that aquic moisture regimes (Aquolls) extended into the forest edge.

Soil properties under mid-slopes and stream-banks were similar, so these two landscape positions are considered together for most analyses. Mid-slopes and stream-banks of properly functioning meadows were covered by wetland forbs, sedges, and rushes that were typically most dense on stream-bank positions (Table 2). Pedons were classified as Aquolls with very dark thick A horizons, sometimes under highly decomposed organic Oa horizons up to 10 cm thick, and over gleyed Bg horizons that extend to depths of 155 cm underlain by sandy, light-colored Cg material. Buried A and O horizons were identified in three pedons at depths of 15, 40, and 50 cm.

Functioning at-risk mid-slope and stream-bank positions had the most diverse vegetation (Table 2), with equivalent representation of wetland and upland forbs, sedges/rushes, and grasses. Soils beneath mid-slope and stream-bank positions in functioning at-risk meadows were similar in thickness to those of properly functioning meadows, but

Table 2. Vegetation Cover by Life Form Within Meadow Landscape Positions and Condition Classes and Plant Species Richness by Meadow

Condition class	Landscape position	Forbs Cover (%)	Sedges/rushes	Grasses	Shrubs	Trees	Mixed bryophytes	Species richness whole meadow
Properly functioning	Stream-bank	23.2 (10.8)	76.6 (8.88)a	19.9 (10.9)	3.90 (2.95)ab	0	0	25.4 (1.94)b
	Mid-slope	58.1 (12.7)	38.7 (8.35)bc	13.7 (4.18)	23.1 (17.2)a	0	2.84 (2.38)	
	Forest edge	70.8 (4.16)	17.1 (3.20)cd	15.3 (9.22)	4.75 (4.75)ab	8.05 (7.47)	3.71 (3.71)	
Functioning at-risk	Stream-bank	46.3 (10.4)	33.8 (11.8)bc	20.0 (4.14)	2.48 (1.81)b	1.65 (1.63)	1.84 (1.84)	32.8 (1.20)a
	Mid-slope	33.7 (7.67)	30.0 (11.9)bc	31.1 (6.62)	12.0 (6.96)ab	0.86 (0.86)	0.32 (0.32)	
	Forest edge	49.3 (6.05)	16.4 (4.07)cd	17.3 (7.73)	0.15 (0.16)cd	9.41 (6.00)	0.86 (0.78)	
Nonfunctioning	Stream-bank	56.9 (16.8)	16.7 (5.98)cd	14.5 (8.94)	13.4 (10.2)ab	1.38 (1.38)	0.32 (0.32)	27.0 (1.37)b
	Mid-slope	74.6 (16.0)	6.16 (2.75)d	15.8 (3.34)	3.10 (2.46)ab	1.58 (1.58)	0	
	Forest edge	50.5 (11.2)	6.56 (2.63)d	17.3 (8.70)	13.6 (6.88)ab	11.0 (7.05)	1.66 (0.41)	
All meadows		51.5 (4.13)	25.9 (3.64)	22.1 (2.39)	8.10 (2.31)	3.84 (1.37)	1.11 (0.48)	

Standard errors are in parentheses. Different letters following sedges/rushes, shrubs, and species richness values indicate significant differences within columns.

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Table 3. Representative Pedon Descriptions in Riparian Meadows

Horizon	Depth (cm)	Munsell color Moist	Structure			Sand (%)	Silt (%)	Clay (%)	BD (g cm^{-3})	TOC (%)	TN (%)	CF (%)	pH
			Grade	Size	Type								
Forest edge soil													
A	0–9	10YR 3/3	2	M	GR	72	22	6	1.19	3.74	0.27	8.3	5.37
Bw	9–18	10YR 3/3	1	M	SBK-GR	71	21	8	1.29	2.72	0.21	9.5	5.44
Bw2	18–38	10YR 3/3	0	F	SGR	83	11	6	1.43	1.34	0.11	20	5.62
Mid-slope/stream-bank soil—properly functioning condition													
Oa	0–10	10YR 2/1	2	M	SBK	62	34	4	0.56	16.2	1.21	0.52	4.99
Bg	10–40	10YR 3/4	2	CO	SBK	–	–	–	1.19	3.52	0.28	0.70	5.42
Bg2	40–80	10YR 3/3	2	CO-M	SBK	63	29	8	1.37	1.77	0.15	11	5.58
Bg3	80–117	10YR 3/3	2	CO-M	SBK	55	35	10	1.38	1.62	0.13	3.5	5.24
Mid-slope/stream-bank soil—functioning at-risk condition													
Ag1	0–11	10YR 2/2	1	M	GR	54	39	7	1.45	4.09	0.29	0.23	5.11
Ag2	11–57	10YR 3/2	2	M	SBK	73	20	7	0.73	1.43	0.11	5.6	5.24
Bw	57–98	10YR 3/3	2	M	SBK	–	–	–	1.19	1.16	0.08	7.3	5.49
Mid-slope/stream-bank soil—nonfunctioning condition													
A	0–20	10YR 3/3	–		SGR	52	33	15	1.43	1.42	0.11	5.8	6.07
Bw1	20–80	10YR 3/3	1	M	SBK	–	–	–	1.44	1.43	0.11	3.3	6.13
Bw2	80–110	10YR 4/4	2	M	SBK	59	29	12	1.48	1.04	0.07	5.7	6.06

TOC total organic carbon; TN total nitrogen; TC textural class; BD bulk density; 0 structureless; 1 weak; 2 medium; CO coarse; M medium; F fine; VF very fine; GR granular; SBK subangular blocky; SGR single grain.

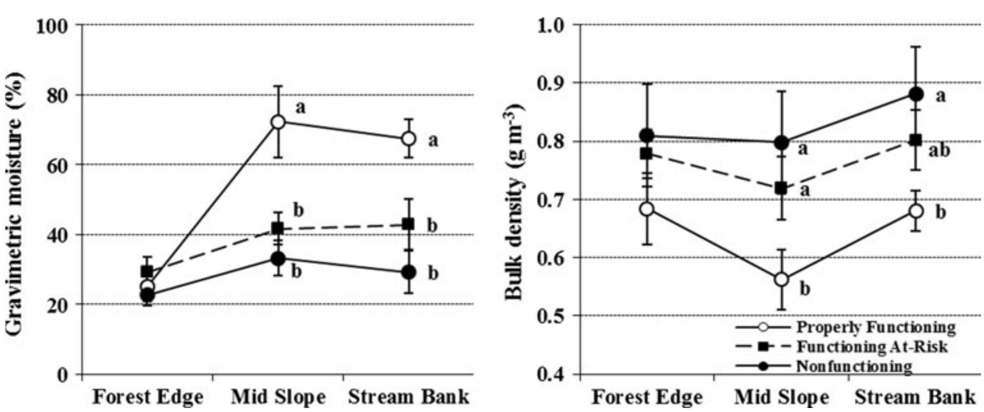

Figure 5. Soil properties averaged by condition classes within slope positions, whole-core analyses. Different letters within slope positions indicate significant differences among means at $P < 0.05$. *Error bars* represent standard error of each mean.

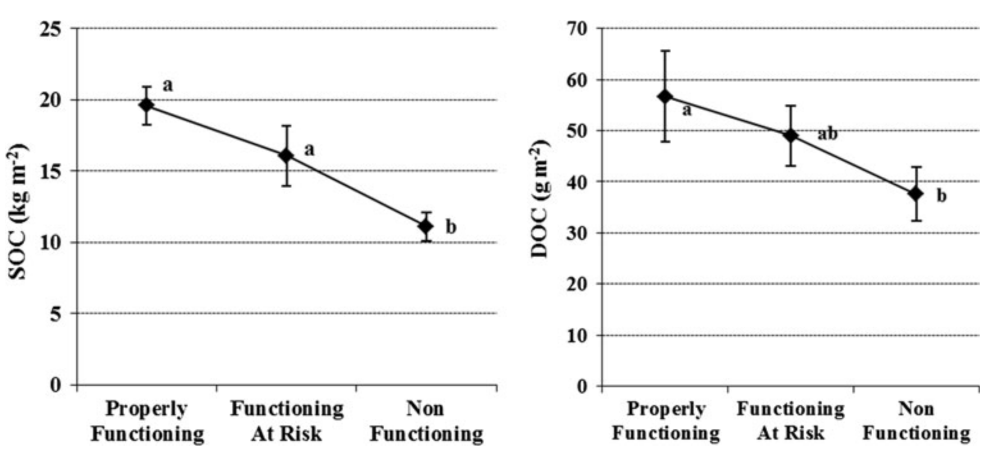

Figure 6. Soil OC and DOC from mid-slope and stream-bank whole-solum samples averaged across meadow condition classes. $N = 20$, 24, and 24 for functional, functional at-risk, and nonfunctional, respectively. Different letters indicate significant differences among condition classes at $P < 0.05$. *Error bars* represent standard error.

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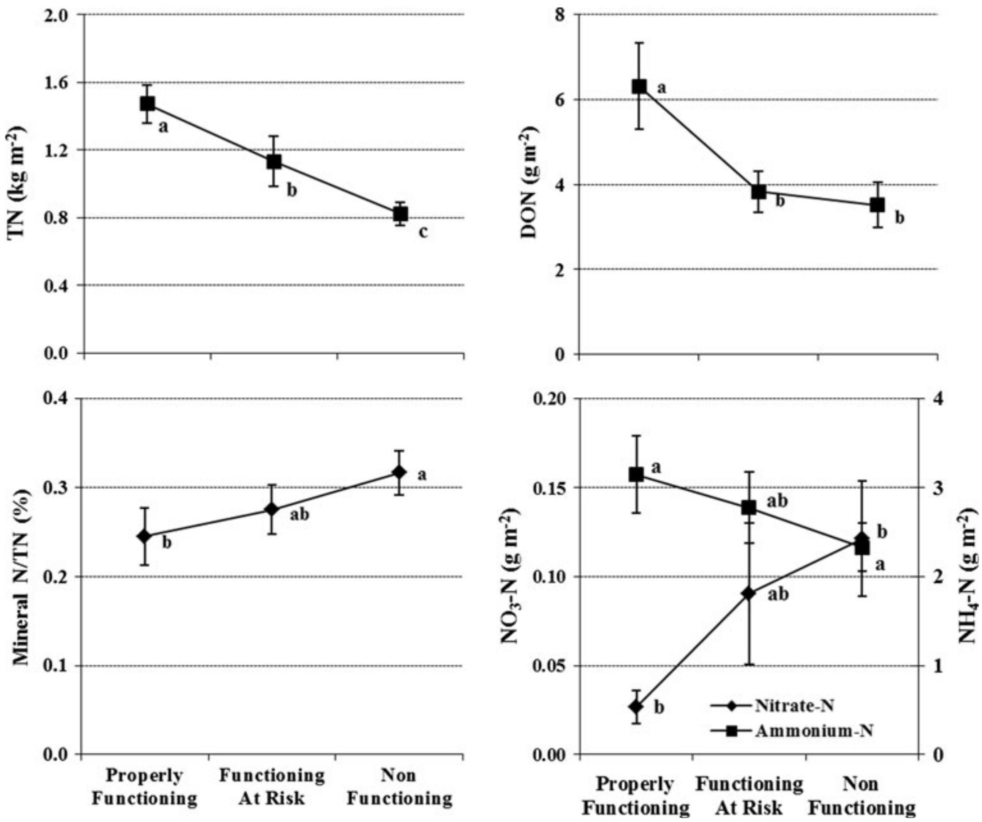

Figure 7. Soil *N* components from mid-slope and stream-bank whole-solum samples averaged across meadow condition classes. $N = 20$, 24, and 24 for functional, functional at-risk, and nonfunctional, respectively. Different letters indicate significant differences among condition classes at $P < 0.05$. *Error bars* represent standard error.

Table 4. Pearson Correlation Coefficients for Gravimetric Moisture Content versus SOC and TN Density in Soils of Mid-slope and Stream-Bank Landscape Positions, Based on all Whole-solum Soil Samples Analyzed

Condition class	*N*	SOC *R* value	TN *R* value
All mid-slope and stream-bank	272	0.538*	0.554*
Properly functioning	80	0.642*	0.587*
Functioning at-risk	96	0.673*	0.639*
Nonfunctioning	96	0.087	0.192

**Significant correlation at $P < 0.0001$.*
$n = 16$ per meadow.

commonly had weakly developed Bw horizons (chroma of three) under O and A horizons. Chroma of three or higher on the Munsell soil color chart indicates nonhydric conditions as used for jurisdictional wetland delineation (Federal Interagency Committee for Wetland Delineation 1989).

Vegetation in nonfunctional mid-slope and stream-bank positions was dominated by forbs, with the lowest representation of sedges and rushes and of wetland species. Soil development was similar in thickness to meadows of other condition classes, but most pedons were classified as Inceptisols, with more strongly developed Bw horizons (chromas of three and four). Representative pedon descriptions are presented in Table 3.

Whole-Solum C and N

Statistical analysis of soil properties in whole-solum cores revealed a significant meadow condition by landscape position interaction. Soils of nonfunctioning meadows are similar across all meadow landscape positions, whereas those of properly functioning and functioning at-risk classes change markedly, with soils under the forest edge having lower soil water content, higher bulk density, and lower amounts of SOM in different fractions than soil under mid-slopes and stream-banks (Figure 5).

Soils beneath properly functioning meadows contain an average of 19.6 kg SOC m^{-2}, compared to 16.1 kg SOC m^{-2} beneath functioning at-risk meadows and 11.1 kg SOC m^{-2} beneath nonfunctioning meadows (Figure 6). Total N followed a similar trend, with nearly twice as much N in soils under properly functioning than nonfunctioning meadows (Figure 7). Soil C:N ratios (data not presented) do not vary among condition classes and

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Table 5. Average Horizon and Solum Thickness, and Average Concentration of SOC and TN by Horizon for Hydrological Condition Classes

Horizon	Properly functioning	Functioning at-risk	Nonfunctioning
		Thickness (cm)	
Surface	10.0 (1.70)	11.0 (2.65)	13.5 (2.94)
Subsurface 1	36.6 (16.4)	58.7 (33.9)	24.4 (10.9)
Subsurface 2	49.8 (13.8)	49.0 (10.0)	48.8 (16.6)
Total	96.4 (12.1)a	119 (8.11)a	86.7 (18.7)a
		Organic C (g kg^{-1})	
Surface	113 (19.7)a	97.8 (50.8)ac	41.3 (10.7)b
Subsurface 1	39.2 (12.5)b	31.9 (6.57)b	48.5 (17.4)bc
Subsurface 2	29.4 (8.14)b	13.8 (8.01)b	20.1 (5.93)b
		Total N (g kg^{-1})	
Surface	9.29 (1.10)a	7.53 (3.85)ac	4.18 (1.15)bc
Subsurface 1	3.51 (1.11)bc	1.86 (0.43)b	4.11 (1.10)bc
Subsurface 2	2.25 (0.563)b	0.955 (0.51)b	2.05 (0.86)b

Different letters indicate significant differences among all means for each variable at $P < 0.05$. Error bars represent standard error.

Table 6. Soil OC and C:N Ratios in Density-Based Soil Organic Matter Fractions

Fraction	Horizon	Properly functioning	Functioning at-risk	Nonfunctioning
			OC in fraction (g kg^{-1})	
Free light	Surface	69.6 (26.7)a	68.4 (54.9)ab	9.46 (1.59)def
	Subsurface 1	6.06 (2.41)efg	2.18 (0.51)fg	4.49 (1.54)fg
	Subsurface 2	2.93 (1.12)fg	1.39 (0.62)fg	3.00 (0.89)fg
Occluded light	Surface	6.34 (2.11)efg	5.44 (1.50)efg	4.02 (1.94)fg
	Subsurface 1	4.35 (2.77)fg	1.71 (0.20)g	0.667 (0.21)g
	Subsurface 2	2.47 (1.47)fg	1.50	2.33 (0.35)fg
Mineral-associated	Surface	41.4 (7.40)ab	27.1 (1.23)bc	27.9 (7.16)bc
	Subsurface 1	29.2 (9.12)bc	21.2 (5.63)bcde	37.2 (12.9)abc
	Subsurface 2	23.7 (6.51)bcd	11.2 (8.81)cdefg	22.7 (7.49)bc
			C:N	
Free light	Surface	18.0 (1.62)e	17.6 (2.50)def	16.2 (1.40)eg
	Subsurface 1	28.3 (4.34)abc	36.2 (8.00)ab	23.0 (2.59)cd
	Subsurface 2	28.1 (3.95)abc	38.2 (21.1)abd	20.5 (2.96)cde
Occluded light	Surface	17.9 (0.83)de	23.3 (5.55)bcde	13.9 (2.29)efh
	Subsurface 1	25.8 (2.10)bc	27.8 (3.44)abc	39.6 (6.71)a
	Subsurface 2	35.3 (6.09)ab	22.6	32.5 (4.62)abc
Mineral-associated	Surface	11.1 (0.97)fghi	10.7 (1.78)fghij	5.81 (1.46)ijk
	Subsurface 1	9.59 (2.65)hijk	6.97 (1.09)hijk	4.98 (1.31)jk
	Subsurface 2	6.56 (1.27)hijk	8.56 (1.36)hijk	3.79 (1.14)k

Different letters indicate significant differences among means in all fractions at $P < 0.05$. Error bars represent standard error.

range between 13.5 and 15. Pearson correlation coefficients for SOC and TN densities as functions of soil moisture content for soils at mid-slope and stream-bank positions show highly significant relationships across all meadows combined and for both classes of functioning meadows individually, but no relationship was found for nonfunctioning meadows (Table 4).

Similar to SOC and TN, labile forms of organic C and N (DOC and DON) were higher beneath properly functioning than nonfunctioning meadows. Overall, DOC and DON made up approximately 0.3–0.4% of total whole-solum SOC and TN. However, DOC content is 15% higher beneath properly functioning than functioning at-risk meadows, and 17% higher in functioning at-risk

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than nonfunctioning meadows, resulting in an overall difference of approximately 33% between soils of properly functioning and nonfunctioning meadows. Similarly, DON is approximately 41% higher beneath properly functioning than nonfunctioning meadows, with the greatest difference of 38% between properly functioning and functioning at-risk meadows (Figure 7).

Overall, soil mineral N contributed about 0.28% to the soil TN pool (Figure 7). Soil TN under properly functioning meadows contains 28% less mineral N, at 0.25%, than soil TN beneath nonfunctioning meadows, at 0.32%. Quantities of different forms of mineral N varied strongly with meadow condition class, with about 20% less NH_4-N and 80% more NO_3-N in soils under nonfunctioning than properly functioning meadows (Figure 7).

Vertical Distribution of SOC and TN

Pedon measurements at mid-slope position showed constant overall soil development (whole-solum) thickness at about one meter (Table 4). Surface horizons of both functioning classes had much higher concentrations of SOC and TN than subsurface horizons (Table 5). Concentrations are much lower in nonfunctioning meadows and do not vary significantly with depth.

Separation of light and mineral-associated SOC fractions in mid-slope soils revealed high concentrations of free LFOC in both functioning classes (Table 6). Average free LFOC concentrations exceeded but were statistically similar to concentrations of mineral-associated OC, making up over 50% of SOC. In nonfunctioning meadows, free LFOC concentrations in surface horizons were much lower than in the other condition classes and much lower than mineral-associated OC, which is more typical of upland ecosystems. Concentrations of occluded LFOC are statistically similar among depths and condition classes. Mineral-associated OC, which is the largest SOC and TN fraction in most forest and agricultural soils (for example, Rasmussen and others 2005; Veenstra and others 2007), is the largest fraction we measured in surface SOC of nonfunctional meadows and in all subsurface SOC.

Carbon:N ratios in both free and occluded light SOM fractions range from 14 to 33 and are significantly lower on average than those of subsurface horizons (Table 5). C:N values in mineral-associated SOM are very low and do not vary significantly by condition class or depth, ranging from about 2 to 16.

Discussion

Organic C in the Upper Montane Zone

Our study area covers upper montane portions of the SNF, including parts of the Emigrant and Carson-Iceberg wilderness areas, where about 65% of areal cover is bare, glacier-scoured granite and volcanic rocks, 28% is shallow forest soils, and 7% is riparian meadows (Soil Survey Staff 2011; Figure 2). Soils in the spruce-fir dominated forest here are mostly 20–70 cm deep and contain around 90 t C ha^{-1} (National Cooperative Soil Survey 2011), whereas the meadows we evaluated contain an average of about 156 t C ha^{-1} in their current condition. Extrapolating across this portion of the upper montane zone, meadows currently contain an estimated 31% of SOC stores and forest soils 69%, totaling about 36 t C ha^{-1} across this landscape. Restoration of all the riparian meadows to properly functioning conditions would increase SOC stores in meadows by 25%, to nearly 200 t C ha^{-1}, and over the entire study area by about 8%, to just over 39 t C ha^{-1}.

Although this represents a substantial increase in regional C sequestration for global warming mitigation, it may be much more important in terms of other, more regional ecosystem services provided by C-rich soils in properly functioning riparian meadows, such as reactive N removal, sustained stream flows, wildlife habitat, and forage production. In many soils in upper montane headwaters catchments of this area, riparian meadows have nearly the only soil cover, and are therefore crucial for capture of N in runoff from uplands.

Stream and Meadow Morphology

Pedon and stream channel measurements support the assumption that nonfunctioning and functioning at-risk meadows are degraded states of previously properly functioning meadows. Similar soil thicknesses (Table 4), along with fluvial strata and buried A and O horizons suggest similar developmental processes and conditions. Weak development of soil colors beneath meadows of the two degraded condition classes suggests seasonally dry conditions that likely developed after meadow degradation. Montagne and others (2009) reviewed soil morphological changes after wetland drainage and found that such color changes can occur within decades.

In our randomly selected sample, nonfunctioning and functioning at-risk meadows had larger catchments than properly functioning meadows

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(Table 1), which suggests that watershed-scale sediment movement and discharge may be important drivers of meadow degradation. Our data show that meadow degradation corresponds with channel widening (Table 1; Figure 4), which is likely the result of combined watershed-scale fluvial processes and meadow-scale resistance to bank erosion. Changes in watershed sediment yield or sudden erosive events can increase channel bedloads in depositional zones, which forces channel widening (Kattelmann 1996). Within meadows, heavy grazing, recreational use, or other activities can reduce resistance to bank erosion (Cole and others 2004; Trimble and Mendel 1995). Whatever combinations of forces cause wider, higher capacity channels, the outcome is decreased residence time of runoff water in meadows.

Such decreased hydrological connectivity between stream channels and riparian meadows begins a degradation feedback in which drier soils result in lower primary productivity and a shift from dominance by sedges and rushes toward grasses and forbs (Table 2). All three factors—drying, reduced productivity, and plant species shift from lignin-rich sedges and rushes to more decomposable grasses and forbs—contribute to declining SOC contents (Figure 5) that increase soil bulk density and reduce water holding capacity (Figure 5), resulting in further drying.

Soil Organic Matter Processes

Properly functioning meadows are characterized by high densities of SOC, TN, DOC and DON and free LFOC compared to those of both degraded condition classes (Figures 6, 7). These soil characteristics represent SOC accumulation and N occlusion processes that are functions of interactions among anoxic soil conditions, cold temperatures, and inputs of relatively recalcitrant, lignin-rich plant biomass from sedges and rushes (Kayranli and others 2010). Very low NO_3-N content and mineral N per unit TN suggests a high assimilative capacity for N, probably driven by the very high proportion of SOC stored as free LFOC (Table 5). The high content of free LFOC with relatively low C:N ratios indicates both active N occlusion and vulnerability to rapid loss of SOC and N with drying hydrological conditions.

The rapid decline in DON and the increase in mineral N per unit TN (Figure 7) in functioning at-risk meadows demonstrate how hydrological processes are responsible for exporting labile forms of N. With changing hydrologic conditions, both LFOC and DON can become substrates for N mineralization, leading to leaching and removal. Plant-derived inputs are predominantly more decomposable residues of grasses and forbs. Soil water content likely fluctuates as flooding occurs, but soils dry out more rapidly than soils of properly functioning meadows. Frequent wetting and drying is known to increase turnover rates and contributions of mineral N to the total N pool (for example, Cabrera 1993; Cui and Caldwell 1997). Highly variable free LFOC may reflect the high species richness as well as overall variable conditions among functioning at-risk meadows, which we evaluated.

Nonfunctioning meadows have drier conditions than the two hydrologically functional condition classes, with eroded stream channels disconnected from former flood plains. Vegetation is dominated by forbs with a much smaller component of sedges and rushes than the meadows in the two functioning condition classes (Table 2). Some degraded nonfunctioning meadows are impacted by springs that maintain moist soils. But channel widening and SOC loss lowers water tables, narrowing the spatial and temporal influence of springs. This likely leads to relatively intense wetting–drying cycles. Loheide and others (2009) described how the common occurrence of springs in Sierra Nevada meadows confounds attempts to relate soil moisture directly to meadow degradation. This altered, more spatially and temporally variable environment, probably facilitates rapid decomposition of relatively labile, forb-derived plant residues, which may prime mineralization of artifact SOC and N accumulated prior to meadow degradation. Significantly higher mineral N per unit TN, along with loss of TN, DON, and free LFOC compared to properly functioning meadows suggests increased mineralization rates and a shift from sink to source for reactive N, as was also described by Jordan and others (2010) for degraded wetlands and by Peterson and others (2001) for small headwater stream ecosystems.

Studies of N fluxes through upper montane catchments in the southern Sierra Nevada describe how properly functioning riparian meadows effectively remove anthropogenic N from runoff. The bulk of N deposition accumulates in snowpack and is released as a pulse of NO_3-N during early spring snow melt (Williams and others 1995). Most N released in this early phase is assimilated by meadow soils, even in high-elevation catchments with very little soil cover. Sickman and others (2003) defined mechanisms where early season snow melt flushes microbial N from well-drained upland soils that is assimilated

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by robust microbial communities in C-rich riparian meadow soils. Isotopic studies confirm that N exported in streams is microbially transformed during rapid immobilization in N-limited soils beneath the snowpack (Sickman and others 2003). In later stages of snowmelt, microbial N can be flushed from meadow soils, but this late spring pulse was small or absent in watersheds with more extensive, intact riparian meadows.

Sickman and others (2003) also measured a late summer pulse of inorganic N and DON as meadow soils dry out, plants senesce, and assimilated N is mineralized and lost. Riparian meadows that retain high SWC late in summer assimilate and retain more N than meadows that dry out.

In related findings, Walker and others (2009) found that N assimilation processes recovered rapidly in riparian meadows restored after decades of overgrazing. They measured lower mineralization rates, nitrification, and N trace gas emissions in restored meadows than in adjacent ones with continued simulated overgrazing.

Conclusions

In this study, we sought to quantify and determine factors controlling SOC and TN in upper montane zone riparian meadows across a spectrum of hydrological functionality. Our results suggest that degraded hydrological condition leads to loss of nearly half the SOC and TN stored in properly functioning meadows, most of it coming from near-surface labile pools stored as free LFOC. Degradation shifts soil conditions from immobilizing environments with low quantities of mineral N and apparently high capacity for reactive N assimilation, to mineralizing environments where reservoirs of labile SOC and N are rapidly lost, as are capacities for OC storage, N occlusion, water retention, and productivity. The PFC rapid assessment approach appears to be a reasonable indicator of riparian soil functions, although simple observations of such parameters as soil depth and water content would likely improve it for this purpose.

Our results underscore a need for maintenance of properly functioning riparian meadows and restoration of degraded ones. Nearly two-thirds of the riparian meadows in our study area are degraded, which represents a huge potential for increases in SOC and N storage and the water quality, water quantity, habitat, forage production, and other ecosystem services supported by healthy, organic matter-rich meadows.

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