Wetlands (2011) 31:251–261
DOI 10.1007/s13157-011-0157-8

ARTICLE

Influence of Bedrock Geology on Water Chemistry of Slope Wetlands and Headwater Streams in the Southern Rocky Mountains

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Received: 14 May 2010 / Accepted: 21 January 2011 / Published online: 18 February 2011

Abstract We characterized the water chemistry of nine slope wetlands and adjacent headwater streams in Colorado subalpine forests and compared sites in basins formed on crystalline bedrock with those formed in basins with a mixture of crystalline and sedimentary bedrock. The pH, Ca^{2+}, Mg^{2+}, NH_4^+, acid neutralizing capacity, and electrical conductivity of wetland porewater and streamwater were higher in the basins with mixed geology. Bryophyte cover was higher in lower pH, crystalline basins, and vascular plant cover was higher in the mixed bedrock basins. On average, wetland porewater had lower pH and higher concentrations of dissolved organic carbon (DOC) and nitrogen and several other ions than streamwater; however, because discharge from these small wetlands is low, their direct influence on stream solute concentrations was generally undetectable. Dilution altered stream solute concentrations during peak flow in both basin types, but had little effect on wetland chemistry. In contrast to other solutes, the concentration of DOC in streams increased marginally during peak runoff and its concentration in wetland porewater was stable throughout the year. These findings further knowledge of the influence of watershed characteristics on wetland and stream chemistry and will inform future decisions regarding conservation and management in headwater basins.

Keywords Biogeochemistry · Dissolved organic carbon · Groundwater-dependent ecosystems · Subalpine forests · Weatherable minerals

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Introduction

The complex terrain, climate, and underlying geology of the mountains of western North America contribute to diversity in wetland type, size, and biota (Bedford 1996; Winter 2001; Carsey et al. 2003). Slope wetlands are common on the sides or bases of hillslopes where sharp topographic gradients, bedrock fractures or faults, geologic disconformities, or stream down-cutting cause ground water to discharge to the surface (Brinson 1993; Bedford 1996; Johnson 2001). This type of minerotrophic wetland typically occurs at the interface between groundwater springs and streams, where they link upland and valley bottom topographic positions (Carsey et al. 2003). Like other wetland types, slope wetlands retain water, transform and store nutrients and carbon, and support local and regional biodiversity (Stein et al. 2004). Their close proximity and hydrologic connection with headwater streams differentiates them from other wetland types.

The shallow ground water that supports slope wetlands plays a fundamental role in the hydrology and hydrochemistry of mountainous regions. In subalpine forests of the Colorado Rockies, more than 95% of snowmelt infiltrates into soils and travels along subsurface pathways before entering streams (Troendle and Reuss 1997; Reuss et al. 1997). Ground water from springs and wetlands may provide the bulk of base flow in late summer (Hall et al. 2001; Chapman et al. 2003) and has been estimated to deliver 40%–80% of the total annual stream flow in some watersheds (Hill 1990; Meyer et al. 2003). The chemical composition of ground water entering wetlands is determined by contact with weatherable minerals as it passes through rock and soil layers (Hill 1990) and by organic matter and nutrients released from upslope soils and vegetation. In slope wetlands, plant and microbial nutrient uptake, nutrient transformation, and organic matter decomposition regulate carbon, nutrient, and elemental storage in peat and release to the atmosphere or streamwater (Hall et al. 2001; Chimner et al. 2002; Stein et al. 2004).

Slope wetlands are often peatlands that have been grouped based on underlying geology, porewater chemistry, and plant composition into poor, intermediate/transitional, rich, and extreme-rich classes (Sjörs 1950; Glaser et al. 1981; Karlin and Bliss 1984; Windell et al. 1986; Vitt and Chee 1990; Cooper 1991; Cooper and Andrus 1994; Almendinger and Leete 1998; Johnson 2001). Poor peatlands generally have pH below 5.5 and Ca^{2+} below 5 mg L^{-1}. Extreme-rich peatlands generally have pH values above 7.0 up to 8.5 and Ca^{2+} concentrations above 30 mg L^{-1}, sometimes in excess of 200 mg L^{-1}. There are numerous other classes intermediate to the rich and poor extremes. Owing to the complex underlying geology and faulting that mix igneous and metamorphosed crystalline material, sedimentary layers, calcite, and glacial till, intermediate wetland types are common to headwater basins throughout the Colorado Rocky Mountains (Cooper and Andrus 1994; Johnson 2001; Carsey et al. 2003).

Compared to the rich and extreme-rich peatlands that support rare plant species and calciphilic plant communities (Cooper 1996; Chapman et al. 2003; Johnson and Steingraeber 2003), little is known about the water chemistry and plant communities of intermediate types (Johnson 2001, but see Cooper 1990; Johnson 1996). To increase understanding of the biogeochemistry of Rocky Mountain slope wetlands, we compared wetland porewater and streamwater chemistry in basins underlain entirely by crystalline bedrock with water chemistry in basins containing a mixture of crystalline and sedimentary bedrock. We also examined changes in wetland and stream chemistry between peak discharge during spring snowmelt and late summer low-flow periods.

Methods

Site Description

We studied nine slope wetlands located within subalpine forests of the Arapaho-Roosevelt National Forest in the Colorado Rocky Mountains. Study wetlands were located along tributaries of St. Louis Creek in the USDA Forest Service, Fraser Experimental Forest (39° 34′ N, 105° 30′ W), which drains to the Fraser River, and along tributaries of Keyser Creek (39° 54′N, 105° 59′ W), which drains to the Williams Fork River (Fig. 1). Both the Fraser and Williams Fork Rivers are headwater catchments in the upper Colorado River system. Study wetland elevations range from 2,700 to 3,100 m above sea level. Local climate is temperate and continental with long, cold winters and short, cool summers. Mean annual air temperature is 0.6°C with January and July average temperatures of −10°C and 12.2°C, respectively, at 2,740 m elevation (Elder and Porth unpublished data). Total annual precipitation averages 600 mm; snowfall received between October and May comprises 64% of precipitation, and summer rains contribute the balance.

Three slope wetlands were located in the headwater tributaries of Keyser Creek in basins formed entirely on crystalline materials. The bedrock of the Keyser Creek basin consists of Precambrian schist and biotite-hornblende gneiss associated with quartz diorite (Tweto 1957; Taylor 1975; Tweto 1979). Six wetlands were located on western tributaries of St. Louis Creek, in basins composed of a mixture of crystalline and sedimentary bedrock types. Complex geologic faulting within the basins draining from the west of St. Louis Creek thrust Jurassic and Cretaceous strata upon the matrix of crystalline rock. Interbedded shale, claystone, fine-grained sandstone, and limestone of the Morrison, Dakota, and Benton formations comprise the

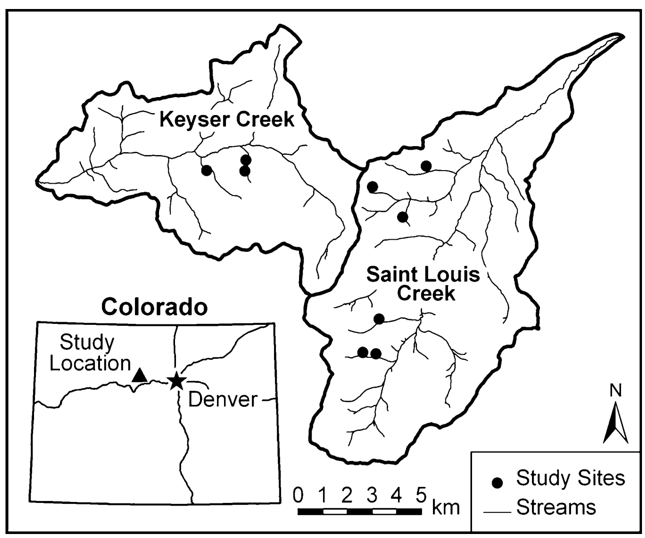

Fig. 1 Slope wetland study locations on the Arapaho-Roosevelt National Forest, Colorado. Sites 1–3 occur in the Keyser Creek drainage in basins comprised entirely of crystalline bedrock. Sites 4–9 occur in the St. Louis Creek watershed at the USDA Forest Service, Fraser Experimental Forest in basins comprised of a mixture of crystalline bedrock and sedimentary strata. Site numbers refer to wetland data in Table 2

sedimentary rocks (Tweto 1957; Taylor 1975; Tweto 1979; Eppinger et al. 1985) that are mixed with the schist, gneiss, and granite that predominate in these basins. Sedimentary layers represent a minor portion (<5%) of the mapped surface bedrock or are identified by isolated features (Eppinger et al. 1985). Quaternary morainal deposits, colluvium, and alluvium are distributed along the valleys of both the Keyser Creek and St. Louis Creek tributaries.

The study wetlands are shallow peatlands and consist of small openings (450–6,100 m^2) that occur on low to moderate slopes (<5–15%) near the base of valley hillsides adjacent to headwater streams. These groundwater-fed subalpine wetlands are classified as hydrogeomorphic slope wetland subclass 1 (Cooper 1998). The group includes saturated non-calcareous substrates commonly dominated by *Carex aquatilis* (Carsey et al. 2003) with a variety of forbs (e.g., *Cardamine cordifolia*, *Senecio triangularis*). Two sites have scattered Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (<50% overstory canopy cover) typical of Rocky Mountain forested wetlands (Johnson 1996, 1997; Lemly 2007).

Hillslope wetland soils are described as poorly drained inclusions within subalpine forest, both at the Fraser Experimental Forest (Retzer 1962) and nearby portions of the Arapaho-Roosevelt National Forest (Alstatt and Miles 1983; USDA 2001). The wetlands are defined by varying depth of peat (i.e., 25–60 cm) above deep to moderately deep strongly mottled silt and clay (Retzer 1962; Alstatt and Miles 1983). Current taxonomic description classifies the wetland soils as sloping Cryaquepts (Alstatt and Miles 1983; USDA 2001) found in association with forest soils formed from mixtures of metamorphic, igneous, and glacial parent materials (Dystric Cryochrepts and Pergelic Cryumbrepts). Similar to the geologic mapping described above, a small extent (95 ha) of soils associated with Cretaceous sedimentary rock are mapped at the Fraser Experimental Forest (Retzer 1962) in the basins comprised of a mixture of bedrock types that drain basins west of St. Louis Creek.

Streams adjacent to the study wetlands are confined, steep gradient, first and second order tributaries, ranging from 1 to 3 m in width. First and second order streams account for approximately 76% of the total stream length in the St. Louis Creek drainage (Retzer 1962). Average unit discharge in the region is 0.1 $m^3\ s^{-1}\ km^{-2}$ (Wohl and Merritt 2008). Typical hydrographs begin to rise from minimum flows in April and reach peak flows on the order of 0.1 $m^3\ s^{-1}$ in mid June, in response to high spring snowmelt. Streams maintain relatively stable base flow on the order of 0.01 $m^3\ s^{-1}$ from August through the winter, punctuated by summer precipitation events (Alexander et al. 1985; Elder 2006) (Fig. 2).

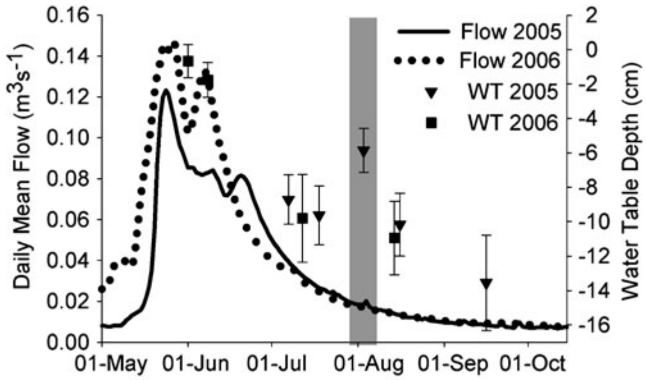

Fig. 2 Mean water table depth and standard error in nine slope wetlands (*n*=38 groundwater wells) and daily mean streamflow for a representative basin (Lexen Creek) at the Fraser Experimental Forest. The gray shaded region delineates a 4.4 cm rain event that occurred in 2005 and increased both stream discharge and the average wetland water table

Sample Collection and Analysis

Wetland porewater and adjacent streamwater were sampled and analyzed from July to September of 2005 and from June to August of 2006. Streamwater grab samples were collected 20 m upstream and 20 m downstream of the wetland-stream confluence. In each wetland, porewater was sampled from shallow groundwater wells installed at 10 m intervals along longitudinal transects extending from the point of groundwater emergence, down slope to the wetland–stream confluence (3–6 wells per site). Shallow groundwater wells were constructed from slotted 2.54 cm diameter polyvinyl chloride (PVC) pipe that was sealed at the base and inserted to an impermeable layer (mean depth: 1.3 m); bore holes were backfilled with local soil. The slotted portions of the wells were inserted below the wetland surface and the wells were capped to limit inputs from surface water and precipitation. The depth to the water table was measured in each well prior to sample collection. Wells were then purged with a hand pump and allowed to refill with fresh porewater. The pump apparatus and sample bottles were triple-rinsed with deionized water and then sample water prior to sampling. Wetland porewater and streamwater samples were collected in pre-combusted, amber glass bottles for total dissolved nitrogen (TDN) and dissolved organic carbon (DOC) analyses and in plastic bottles for inorganic ion concentrations, pH, electrical conductivity (EC), and acid neutralizing capacity (ANC). Samples were kept at approximately 4°C, transported in coolers to the laboratory, and filtered within 48 hours. Aliquots were filtered through 0.45 μm mesh polyvinylidene fluoride (PVDF) membrane filters for ion analysis and through 0.7 μm mesh glass-fibre pre-filters for DOC and

TDN analysis (Millipore Corp., Billerica, MA). Acid neutralizing capacity, EC, and pH were analyzed on unfiltered subsamples.

Anion and cation concentrations were determined by ion chromatography (Waters Co. Milford, MA.) and conductivity detection with a Dionex AS12A anion exchange column, an AG12A guard column, and Waters IC-Pak cation M/D column (APHA 1998) using EZChrom Elite software (Scientific Software Inc., Pleasanton, CA). Detection limits were 0.01 mg L^{-1} for Na^+, NH_4^+, and Cl^-; 0.02 mg L^{-1} for Ca^{2+}, Mg^{2+}, K^+, and NO_3^-; and 0.05 mg L^{-1} for SO_4^{2-}. Acid neutralizing capacity was measured by Gran titration (Gran 1952) to a 3.2 pH endpoint using 0.01 N HCL. Electrical conductivity and pH were analyzed with PC Titrate sensors (Man-Tech Co.). Dissolved organic carbon and TDN 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 Columbia, MD). Dissolved organic nitrogen (DON) was calculated by subtracting the sum of NO_3^--N and NH_4^+-N from TDN. Detection limits for DOC and TDN were 0.05 mg L^{-1}.

Redox potential was measured using platinum electrode probes installed at the center of each wetland opening and inserted to approximately half the depth of the peat layer (30–50 cm). Electrodes were allowed to equilibrate for 1 h following installation and then for 20 min while attached to a voltmeter affixed to a saturated Ag/Cl reference electrode (Bohn 1971; Mueller et al. 1985) before recording measurements. Readings were adjusted to express Eh with respect to a hydrogen electrode (correction factor: 214 mV) at neutral pH (correction factor: −59/pH).

Herbaceous and woody understory plant cover was estimated visually within 1 m^2 quadrats (Daubenmire 1959) distributed along one transect extending downslope through the center of each wetland and along 2–4 equally spaced lateral transects (6–14 quadrats per site). We summed the total number of vascular species observed in sample quadrats in each wetland, and used quadrat estimates of absolute plant cover to calculate mean percent cover for each vascular species within each wetland; total cover summed to >100% in many quadrats. Nomenclature follows the U.S. Department of Agriculture, Natural Resources Conservation Service PLANTS database (2010). The total cover of bryophytes was recorded for each quadrat, and the dominant moss species were identified.

Data Analyses

We analyzed streamwater and wetland porewater chemistry at nine sites in the mixed and crystalline basins during the 2005 and 2006 growing seasons. Analysis of variance was used to evaluate differences between wetlands and adjacent streams, basin geology, and the interactions between the main effects (wetland/stream and basin geology). Site replicates were nested within basin types and analyses were performed with GLIMMIX mixed model procedures after checking assumptions of normality and equal variance (SAS 2002, Version 9.1). Where main effects were statistically significant, we used Tukey's multiple range tests to separate differences among means.

In 2006, stream and wetland chemistry were compared during the peak snowmelt runoff period in June (referred to as peak flow), and the falling limb of the hydrograph from July to August (referred to as low flow). We used paired t-tests to compare samples collected upstream and downstream of the wetland-stream confluence as an evaluation of the influence of wetland inputs on stream chemistry. Similarly, we compared porewater chemistry between the uppermost and lowest wells to assess longitudinal changes in porewater chemistry within individual wetlands. Significance is reported at the α=0.05 critical value except where noted otherwise.

Understory plant species cover and richness were summarized for each wetland individually and compared between wetlands in the crystalline and mixed geology basins. Overlap in species occurrence between the two basin types was evaluated using Sörensen's similarity coefficients (Magurran 1988). Basin type effects on species number and cover were tested using multi-response permutation procedures (MRPP) using Sörensen's distance measure (Mielke and Berry 2001; McCune and Grace 2002).

Results

Water Table and Anoxic Indicators

Wetland water table tracked the seasonal pattern of stream runoff (Fig. 2). At peak snowmelt discharge in June 2006, for example, the water table was 0.3 cm above the wetland surface, on average (range: −7.5 cm to 2.4 cm); in two-thirds of the wells, the water level was at or above the soil surface. By mid-July, as streamflow declined, the average water table height dropped to −12.5 cm (range: −26.5 to −0.5 cm), and only two of the 38 wells had water at or above the soil surface. The water table continued to decline from July to September along the descending limb of the hydrograph, but wells went completely dry only in the two steepest wetlands. In early August 2005, stream discharge and wetland water table depth responded to a 4.4 cm precipitation event (Fig. 2); water table depth responded at all sites, and reached or exceeded the wetland soil surface at 10 of 38 wells.

Anoxic soil indicators were present at all slope wetland sites (Faulkner and Patrick 1992). Mineral soil horizons were very dark gray or black (5Y 3/1–10YR 3/1) with distinct bands and patches of olive-gray gleying and mottling (e.g., 5Y 4/1, 2.5Y 4/2). Redox potential averaged 145 and 44 mV in July and September, respectively, indicating that reducing conditions (i.e., <300 mV) persisted throughout the growing season. Organic surface horizons are present at all sites; layers measured 40 cm on average (range: 20–110 cm) and typically contained organic matter in excess of 60% (Dwire unpublished data).

Influence of Bedrock Geology

The concentrations of the dominant cations and anions differed substantially between wetlands and streams located in basins with crystalline geology and those in basins with mixed sedimentary and crystalline geology (Table 1). The mean Ca^{2+} concentration in wetlands in mixed geology basins was 17.6 mg L^{-1}, more than 2.5 times the mean concentration of wetlands in crystalline basins; likewise, stream Ca^{2+} concentrations averaged 15.6 mg L^{-1}, more than twice the mean concentration of streams in crystalline basins. Porewater and streamwater Mg^{2+} and NH_4^+-N concentrations were 1.8–4.0-fold higher in the mixed basins and K^+ (p=0.07) and SO_4-S (p=0.06) were also higher. In the mixed basins, porewater ANC (primarily comprised of bicarbonate) and EC were twice as high, and mean porewater pH was 0.4 units higher than wetlands in crystalline basins. The EC and ANC of streamwater in mixed geology basins averaged 105.4 µS cm^{-1} and 889.7 µeq L^{-1}, respectively, and were almost twice the value of crystalline basin streams. Dissolved organic nitrogen was the only constituent of wetland porewater that was significantly higher in the crystalline basins.

About half the vascular taxa identified were shared between slope wetlands in the mixed and crystalline basin types (Sörensen's similarity coefficient=0.67) (Table 2). Bedrock type and hydrochemistry may have influenced the number of vascular species per wetland (i.e., 23 vs. 31 species per wetland in the crystalline and mixed bedrock basins, respectively; p=0.02). Bryophytes were common in all wetlands (i.e., 25%–75% cover), and total bryophyte cover was significantly higher in the crystalline bedrock basins (p=0.01). Most common were the mosses *Brachythecium erythrorrhizon* Schimp., *Rhizomnium pseudopunctatum* (Bruch & Schimp.) T. Kop., and *Aulacomnium palustre* (Hedw.) Schwägr. (Weber and Wittmann 2007). In contrast, total graminoid cover (p=0.01) and cover of several forb species, including *Symphyotrichum foliaceum* (p=0.02), *Geranium richardsonii* (p=0.01), and *Parnassia fimbriata* (p<0.01) were higher in wetlands in the mixed geology basins.

Table 1 Mean water chemistry of nine slope wetlands and adjacent streams in basins with crystalline and mixed crystalline and sedimentary bedrock in the Rocky Mountains of northern Colorado (with pooled SE)

	Units	pH no unit	EC µS cm^{-1}	ANC µeqL^{-1}	Ca^{2+} mg L^{-1}	Mg^{2+} mg L^{-1}	Na^+ mg L^{-1}	K^+ mg L^{-1}	Cl^- mg L^{-1}	SO_4^{2-}-S mg L^{-1}	NO_3^--N mg L^{-1}	NH_4^+-N mg L^{-1}	DON mg L^{-1}	DOC mg L^{-1}
Crystalline Bedrock Basins	Wetland	6.96 (0.09)	56.76 (12.8)	508.48 (96.9)	6.65 (2.0)	2.01 (0.4)	2.85 (0.2)	0.84 (0.4)	0.29 (0.04)	0.56 (0.5)	0.00 (0.05)	0.02 (0.01)	0.15 (0.02)	3.45 (0.5)
	Stream	7.60 (0.07)	54.49 (12.8)	449.29 (96.9)	7.06 (2.0)	1.49 (0.4)	2.24 (0.2)	0.82 (0.4)	0.16 (0.04)	0.83 (0.5)	0.01 (0.05)	0.01 (0.01)	0.08 (0.02)	2.01 (0.5)
Mixed Bedrock Basins	Wetland	7.40 (0.09)	120.38 (9.0)	1101.70 (68.5)	17.60 (1.4)	3.54 (0.3)	2.56 (0.1)	1.82 (0.3)	0.34 (0.03)	1.26 (0.3)	0.01 (0.04)	0.05 (0.01)	0.10 (0.02)	2.69 (0.4)
	Stream	7.83 (0.07)	105.43 (9.0)	889.69 (68.5)	15.58 (1.4)	2.80 (0.3)	1.83 (0.1)	1.24 (0.3)	0.20 (0.03)	1.96 (0.3)	0.10 (0.04)	0.04 (0.01)	0.04 (0.02)	1.48 (0.4)
P values														
Main Effects	1 Basin Geology	0.004**	0.001**	<0.0001**	0.005**	0.005**	0.073	0.069	0.265	0.063	0.322	0.017*	0.053	0.186
	2 Wetland or Stream	<0.0001**	0.463	0.150	0.670	0.121	0.005**	0.387	0.006**	0.286	0.327	0.195	0.014*	0.020*
	3 Site (Basin)	0.214	0.096	0.018*	0.103	0.121	0.009**	0.146	0.022*	0.484	0.532	0.137	0.772	0.116
Interaction	1 X 2	0.230	0.585	0.393	0.270	0.823	0.736	0.416	0.920	0.623	0.342	0.768	0.629	0.810

Symbols indicate significant p-values (* p<0.05; ** p<0.01)

Table 2 Plant cover (mean and SE) measured in 1 m^2 quadrats at nine slope wetlands in the Rocky Mountains of northern Colorado

		Crystalline bedrock basins			Mixed bedrock basins					
		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9
Bryophytes and others[a]	Bryophytes	71 (11)	38 (15)	75 (13)	35 (7)	59 (8)	55 (12)	50 (10)	24 (9)	58 (12)
	Equisetum arvense L.	7 (2)	1 (1)	10 (3)	15 (6)	5 (2)	5 (1)	8 (2)	2 (1)	10 (2)
Graminoids[a]	*Calamagrostis canadensis* (Michx.) P. Beauv.	0	0	0	1 (1)	<1	1 (1)	12 (7)	10 (3)	0
	Carex aquatilis Wahlenb.	0	8 (5)	25 (9)	12 (4)	17 (4)	12 (4)	16 (4)	17 (4)	1 (1)
	Carex disperma Dewey	0	0	0	1 (1)	4 (3)	<1	6 (4)	1 (<1)	0
	Carex utriculata Boott	0	0	0	0	0	13 (4)	12 (4)	0	0
Forbs[a]	*Cardamine cordifolia* A. Gray	2 (1)	6 (5)	1 (1)	5 (1)	3 (1)	1 (1)	0	0	<1
	Fragaria spp.[b]	0	<1	0	0	1 (1)	1 (1)	0	0	6 (3)
	Geranium richardsonii Fisch. & Trautv.	0	1 (1)	0	1 (1)	2 (1)	1 (1)	1 (<1)	10 (3)	3 (2)
	Heracleum maximum Bartram	6 (4)	0	0	0	0	<1	5 (3)	3 (3)	0
	Maianthemum stellatum (L.) Link	0	0	0	0	0	8 (3)	0	0	0
	Mitella pentandra Hook.	8 (3)	6 (1)	2 (1)	5 (1)	7 (2)	4 (1)	<1	5 (2)	4 (2)
	Oxypolis fendleri (A. Gray) A. Heller	1 (1)	0	0	3 (2)	7 (2)	1 (1)	4 (2)	1 (1)	3 (2)
	Parnassia fimbriata K. D. Koenig	0	1 (1)	1 (1)	0	4 (2)	7 (3)	15 (2)	1 (1)	8 (4)
	Saxifraga odontoloma Piper	7 (2)	3 (2)	26 (7)	9 (4)	16 (3)	13 (4)	<1	8 (4)	12 (4)
	Senecio triangularis Hook.	11 (2)	2 (1)	9 (2)	6 (2)	8 (2)	19 (8)	5 (2)	13 (5)	7 (2)
	Streptopus amplexifolius (L.) DC.	8 (3)	5 (2)	0	4 (1)	4 (2)	2 (2)	1 (1)	4 (2)	1 (1)
	Symphyotrichum foliaceum (Lindl. ex DC.) G. L. Nesom	0	10 (4)	3 (2)	3 (1)	3 (1)	7 (2)	10 (4)	7 (2)	8 (2)
	Trollius laxus Salisb.	2 (1)	7 (2)	0	9 (4)	7 (4)	7 (2)	0	<1	17 (2)
Shrubs[a]	*Alnus incana* (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung	6 (5)	11 (10)	0	0	0	0	3 (2)	0	0
	Vaccinium scoparium Leiberg ex Coville	1 (1)	6 (3)	3 (2)	5 (2)	0	2 (2)	0	4 (2)	1 (1)
	Wetland Area (m^2)	1,225	900	800	6,100	1,600	3,000	1,800	600	450
	Vascular Species Observed (#)	23	24	22	27	31	34	33	26	32
	Sample Quadrats (n)	10	7	8	11	14	10	11	6	8

Wetlands are located either in basins formed entirely on crystalline bedrock or a mixture of crystalline and sedimentary bedrock. The taxa included represented >5% cover in one or more wetlands. Site numbers refer to locations on Fig. 1

[a] Nomenclature from USDA Natural Resources Conservation Service PLANTS database (2010)

[b] *Fragaria vesca* L. and *F. virginiana* Duchesne ssp. *glauca* (S. Watson) Staudt are both common to the study area but were not differentiated

Comparisons of Wetland and Stream Chemistry

For several analytes, solute concentrations were significantly higher in wetlands than streamwater for both basin types (Table 1). Wetland porewater pH averaged 0.6 and 0.4 units lower than streamwater in crystalline and mixed basins, respectively. Porewater Na^+, Cl^-, DON, and DOC concentrations were consistently higher than streamwater. Wetland DOC averaged 70%–80% higher, and mean DON was 87%–150% higher than streamwater in crystalline and mixed basins, respectively (Table 1). Wetland Mg^{2+} and ANC concentrations were marginally higher than streams in both basin types, but differences were not statistically significant. There were no consistent differences between wetland and stream Ca^{2+}, K^+, SO_4^{2-}, or inorganic N forms.

Dilution during the peakflow season altered solute concentrations in streams, but had little effect on wetlands (Fig. 3). Stream pH, EC, Ca^{2+}, ANC, and Mg^{2+} concentrations all declined significantly during peak flow in both basin types. In general, the seasonal change in streamwater chemistry was more pronounced in the crystalline basins. The only significant seasonal dilution in wetland porewater was for Ca^{2+} in crystalline basins. In contrast to other solutes, stream DOC concentration increased marginally during peak flow (p=0.10); wetland DOC remained constant seasonally in the mixed basins, and was too variable to detect a difference by season in the crystalline basins.

Within individual wetlands, DOC was also the only solute that differed between the point of groundwater emergence and the base of the wetland. The average concentration for porewater DOC near the point of groundwater emergence was 1.76 mg L^{-1} and near the stream confluence was 4.48 mg L^{-1} (i.e., approximately two-fold longitudinal increase; $p<0.01$). Streamwater sampled above

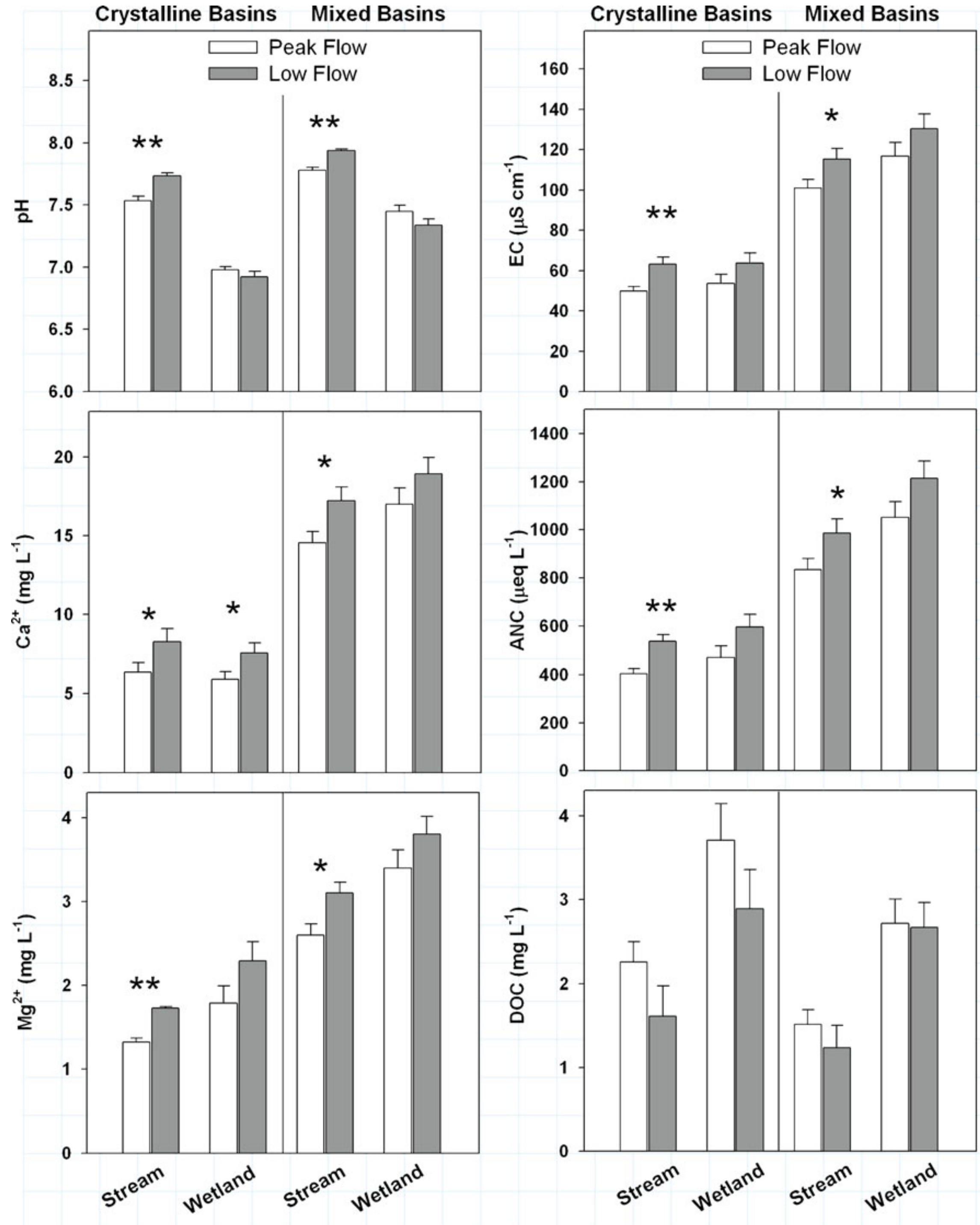

Fig. 3 Seasonal patterns of streamwater and wetland porewater chemistry in basins with crystalline bedrock and mixed crystalline bedrock and sedimentary strata. Bars show mean and standard error and symbols indicate significant seasonal differences for streams or wetlands within the two basin types (* $p<0.05$; ** $p<0.01$)

and below wetland confluences differed little chemically, and the hydrochemical fluxes from the wetlands were insufficient to cause notable changes in stream solute concentrations. In fact, ANC was the only streamwater solute that was statistically higher downstream than upstream of the intersection with the study wetlands. Differences were limited to the low-flow period for the mixed geology basins ($p=0.04$), and probably have little ecological relevance (923 vs. 916 µeq L^{-1} in downstream and upstream samples, respectively).

Discussion

This study shows that the hydrochemistry of both headwater streams and slope wetlands in the study area are sensitive to relatively minor differences in underlying bedrock. Wetland porewater and streamwater pH, Ca^{2+}, Mg^{2+}, ANC, and to a lesser extent K^{+}, were higher in basins comprised of a mixture of sedimentary and crystalline bedrock (Table 1). Precambrian crystalline rock predominates throughout the study area, but weatherable minerals originating from a small band of sedimentary material and a region of complex faulting (Eppinger et al. 1985) were sufficient to alter the chemical composition of streamwater and shallow ground water emerging within slope wetlands. Similarly, in another Colorado basin formed on granitic and metamorphic bedrock, weathering of trace amounts of bedrock calcite was responsible for 51% of the Ca^{2+} exported in streamwater (Clow et al. 1997). It is well known that the chemical composition of streams, springs, and wetlands are influenced by distinct bedrock type (Valett et al. 1996; Soulsby et al. 1999; Chapman et al. 2003). This work contributes to a growing body of evidence that shows significant hydrochemical differences in surface water occurring in basins with only minor differences in geology (Johnson 2000; Chapman et al. 2003).

Differences in underlying bedrock and the related responses in wetland hydrochemistry also influenced plant species cover and composition at the study sites. Wetland porewater ANC, Ca^{2+}, Mg^{2+}, and K^{+} concentrations were 2.2, 2.6, 1.8, and 2.2 times those in the mixed bedrock basins, respectively, and porewater pH was 0.4 units higher (Table 1). Bryophyte cover was higher in those wetlands occurring in crystalline bedrock basins, where porewater was more dilute and acidic (Tables 1 and 2). Grass and sedge cover was higher in the basins with mixed bedrock type, as was the cover of a number of forb species (Table 2). Peatland plant species diversity often increases with greater cation concentrations and lower acidity (Karlin and Bliss 1984; Vitt and Chee 1990; Hall et al. 2001), and we found higher species diversity in mixed-bedrock wetlands. Unlike these southern Rocky Mountain sites, in slope wetlands of southern California's Santa Ana Mountains, a two-fold change in Ca^{2+} concentration and 1.0 unit increase in pH had no effect on plant species diversity or evenness (Stein et al. 2004).

The hydrochemistry of slope wetlands in the two basin types correspond with existing peatland and fen classes. Average porewater pH and Ca^{2+} were 7.0 and 6.6 mg L^{-1} for the crystalline bedrock type wetlands and 7.4 and 17.6 mg L^{-1} for the mixed bedrock wetlands, respectively. Our study wetlands on crystalline bedrock correspond to intermediate and moderate wetland classes. Study sites on mixed crystalline and sedimentary bedrock straddle the division between intermediate and more mineral-rich wetlands. The term "transitional" has been applied to wetlands such as those in the mixed bedrock study sites that share chemical characteristics with intermediate and mineral-rich classes. Distinction of the study sites based on bedrock composition concurs with the Ca^{2+} levels used as a preliminary guide to differentiate "mineral poor" (pH<6.8; Ca^{2+} 2–10 mg L^{-1}) and "mineral rich" (pH<6.0; Ca^{2+} >10 mg L^{-1}) Rocky Mountain slope wetlands (Johnson 2001).

Links Between Slope Wetlands and Headwater Streams

Slope wetlands are a conduit for delivery of carbon to headwater streams. The saturated conditions of these wetlands create an environment where incomplete oxidation of organic matter leads to carbon accumulation and release to streams (Chimner et al. 2002; Hood et al. 2003; Kaushal and Lewis 2003; Andersson and Nyberg 2008). In these subalpine watersheds, maximum stream DOC concentrations coincided with peak stream discharge, in spite of solute dilution by snowmelt (Fig. 3). This seasonal DOC pattern is commonly attributed to percolating snowmelt flushing the carbon produced by later summer and wintertime microbial processes from the surface soil horizons of upland and wetland environments to streams (Hongve 1999; Andersson and Nyberg 2008) and is consistent with seasonal DOC patterns of soil leachate in forested uplands (Stottlemyer et al. 1997). In contrast, wetland porewater DON concentrations remained constant throughout the growing season. Wetland DOC concentrations remained constant in the mixed basins and were too variable to detect a seasonal difference in concentration in the crystalline basins (Fig. 3), and suggest that carbon turnover is more continuous than in upland areas where soil moisture limits microbial activity (Hough and Cole 2009). Where streams and wetlands are linked, the spring pulse of DOC into streams demonstrates a seasonal increase in hydrologic flow-through between them.

During the low-flow portion of the hydrograph, discharge of shallow ground water from springs and wetlands contributes a greater proportion of stream flow (Chapman et al. 2003). We observed increased concentrations for a number of stream solutes during low flow (Fig. 3); wetland solute concentrations were more stable seasonally. There was a small but statistically significant indication that inputs from individual wetlands altered low-flow stream solute concentrations (i.e., 1% increase in ANC); but, due to low discharge relative to stream flow or the seasonal change in hydrologic connectivity between wetlands and streams, direct wetland influences on stream chemistry were undetectable for other solutes. Static nutrient concentrations may also indicate that in-stream uptake processes influence fluxes even over short distances in these headwater streams (Brookshire et al. 2009).

Wetland density is known to be high in portions of Colorado's subalpine forests, but owing to the small size of openings in the forest canopy, relatively few are mapped by either cover type or soil type (Retzer 1962; Alstatt and Miles 1983). In the Fool Creek watershed, a 290-ha, north-facing tributary to St. Louis Creek on the Fraser Experimental Forest, wetland openings are associated with many of the 157 mapped springs. Recent surveys suggest, however, that the density of both springs and slope wetlands are lower in other tributaries. The distribution of these small landscape features complicates efforts to distinguish the individual and cumulative influence of slope wetlands at the larger watershed and regional scales. Research indicates, however, that such wetlands may serve as the primary source of catchment DOC generation and export (Creed et al. 2003) and decrease overall surface water nitrate inputs (Spoelstra et al. 2010).

Headwater slope wetlands are the point of intersection between surface and ground water in many high-elevation headwater catchments, but they are also part of an extensive hydrologic network that regulates the quality and quantity of water delivery for downstream uses and ecosystems (Cirmo and McDonnell 1997; Soulsby et al. 1999; Winter 2001; Meyer et al. 2003; Lowe and Likens 2005). The study wetlands, located along streams that deliver water via transbasin diversion to Colorado's densely populated Front Range urban corridor, exemplify the complex relationship between high-elevation source areas and downstream users throughout the southern Rocky Mountains. Increased water demand and growing uncertainty about future water supply will intensify concern about how to define, utilize, and conserve the hydrologic links between wetlands and headwater stream systems (Leibowitz et al. 2008). Future decisions regarding conservation and water management in headwater basins will require a more thorough understanding of how watershed characteristics such as bedrock geology influence wetland and stream chemistry.

Acknowledgments We gratefully acknowledge K. Nelson, C. Foy, C. Geisting, and J. Shirley for field help and N. Quiet for conducting laboratory analyses. D. Cooper, R. Chimner, R. Kolka, K. Carsey, and D. Rhoades provided guidance on sampling and helped us classify study wetlands and site geology. K. Elder and M. Dixon provided stream discharge and precipitation data from the Fraser Experimental Forest. Comments from B. Johnson, D. Binkley, S. Miller and an anonymous reviewer greatly improved the text and our interpretations of the findings. L. Porth, and R. King provided advice on statistical analyses. The Department of Forest, Rangeland, and Watershed Stewardship at Colorado State University and the USDA Forest Service, Rocky Mountain Research Station provided funding for the project.

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