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Linkages Between Riparian Characteristics, Ungulate Grazing, and Geomorphology and Nutrient Cycling in Montane Grassland Streams

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Abstract

Catchment characteristics and disturbances control the conditions and processes found in stream ecosystems. We examined nutrient cycling linkages between riparian soils and adjacent streams and the impacts of the removal of ungulate grazing on these ecosystems and processes at six grazing exclosure sites in the Valles Caldera National Preserve, NM, USA. The exclusion of native and domestic ungulate grazers for 3 yr significantly increased the riparian aboveground biomass of standing vegetation (273 ± 155 in grazed vs. 400 ± 178 $g \cdot m^{-2}$ in exclosures) and litter (58 ± 75 in grazed vs. 110 ± 76 $g \cdot m^{-2}$ in exclosures) ($P = 0.003$ and 0.006, respectively). Except for an increase in total soil phosphorous (P) at three of the six sites, soil nutrient values were minimally affected by grazing after five growing seasons. Within the six sites studied, no connection was found between 0–15-cm depth soils, which were P-limited based on stoichiometric ratios, and stream nutrient availability or limitation, which were nitrogen limited. Stream geomorphology was not significantly altered by 5 yr of grazing exclusion. The elimination of grazing suppressed instream nutrient processing with significantly longer NH_4 uptake lengths ($P = 0.003$). These results suggest the exclusion of ungulate grazing impacts terrestrial characteristics (increased standing vegetative biomass) that are linked to ecosystem services provided by adjacent aquatic ecosystems (reduced N-uptake). Management plans should carefully balance the positive effect of grazing on stream nutrient processing and retention reported here with the well-documented grazing-related loss of other ecosystem services such as decreased fish and aquatic invertebrate habitat and effects on water-quality parameters such as turbidity and water temperature.

Resumen

Las características del escurrimiento y los disturbios contralan las condiciones y procesos encontrados en ecosistemas de arroyos. Examinamos la relación del ciclo de nutrientes entre suelos ripiaros y arroyos adyacentes y el impacto de la remoción de ungulados pastoreando en esos ecosistemas y procesos en seis sitios excluidos al pastoreo en Valles Caldera National Preserve, NM, USA. La exclusión de ungulados nativos y exóticos pastoreando, por tres años incremento significativamente la biomasa aérea de la vegetación (273 ± 155 en pastoreo vs. 400 ± 178 $g - m^{-2}$ en exclusiones) y mantillo (58 ± 75 en pastoreo vs. 110 ± 76 $g \cdot m^{-2}$ en exclusiones) ($P = 0.003$ and 0.006, respectivamente). A excepción de un incremento total de fósforo (P) en el suelo en tres de los seis sitios, los valores de nutrientes del suelo fueron mínimamente afectados por el pastoreo después de cinco temporadas de pastoreo. Dentro de los seis sitios estudiados, no se encontró conexión entre 0 a 15 cm de profundidad del suelo, las cuales fueron limitadas en P basados en proporciones estequiométricas, y la disponibilidad de nutrientes del arroyo o limitaciones las cuales fueron limitadas en nitrógeno. La geomorfología del arroyo no fue significativamente alterada por los cinco años de exclusión al pastoreo. La eliminación del pastoreo suprimió el proceso de nutrientes dentro del arroyo con significativamente mayor duración en la absorción de NH_4 ($P = 0.003$). Estos resultados sugieren que la exclusión de ungulados pastoreando impacta las características terrestres (incremento en la biomasa de la vegetación de pie) que está relacionada a los servicios que provee el ecosistema por ecosistemas acuáticos adyacentes (reducción de absorción de N). Los planes de manejo deberán equilibrar cuidadosamente el efecto positivo del pastoreo en procesado de nutrientes en los arroyos y la retención reportada aquí con la bien documentada perdida de otros servicios del ecosistema por pastoreo tales como la disminución del hábitat de peces e invertebrados acuáticos y efectos en parámetros de calidad del agua como la turbidez y temperatura del agua.

Key Words: grazing exclusion, nutrient cycling, riparian soil chemistry, riparian vegetation, stream geomorphology, water quality

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INTRODUCTION

Terrestrial characteristics and disturbances are largely responsible for the conditions and processes found in stream ecosystems. This principle was eloquently presented by H. B. N. Hynes who wrote, "In every respect the valley rules the stream" (Hynes 1975), a statement that has since guided a significant body of research and the development of theories connecting terrestrial and stream ecosystems. Streams are four dimensional: longitudinal connections link upstream to downstream segments, lateral exchanges connect terrestrial and aquatic environments, vertical flows link ground and surface water, and the fourth dimension of time encompasses seasonal and long-term geomorphic fluctuations (Wiens 2002). The lateral and vertical connections between streams and catchments operate at a variety of spatial and temporal scales. Climate, topography, and geology place broad-scale constraints on stream hydrology, geomorphology, sediment delivery, and water chemistry (Allan 2004; Allan and Johnson 1997; Wiens 2002). Finer-scale patch characteristics, seasonal cycles, and episodic events are superimposed upon catchment-scale attributes regulating energy and nutrient exchange between terrestrial and aquatic environments (Wiens 2002).

Stream-water chemistry is tightly coupled to catchment parent geology, soil chemistry, and disturbance. This coupling is maintained through lateral inputs of surface water with dissolved and particulate constituents (Edwards and Withers 2008; Elsenbeer et al. 1995), and groundwater inputs comprised of water in equilibrium with upland and riparian soils and underlying parent geology (Mulholland 1992; Smart et al. 2001). Stream-water chemistry sampling and spatially explicit geologic and land-use data sets have been used in combination to determine the relative importance of catchment variables in determining stream chemistry values. Underlying catchment parent geology was an important and seasonally consistent predictor of stream water chemistry in each of these studies (Johnson et al. 1997; Cresser et al. 2000; Dow et al. 2006); however, its relative importance varied between subregions (Dow et al. 2006). Additionally, geology/land-use interactions explained significant portions of water chemistry variability, indicating land use and geology covary (Johnson et al. 1997; Dow et al. 2006).

Catchment and riparian attributes and disturbances not only affect stream-water chemistry but also impact in-stream processing and regulation of the bioavailable components of water chemistry. Restoration of an incised stream channel altered stream geomorphology and hydrology, and increased phosphorus (P) and nitrate (NO_3) uptake by 50% and 2000%, respectively (Bukaveckas 2007). Paired stream reaches with intact and deforested riparian zones showed undisturbed reaches exhibited greater organic material processing and nutrient retention when these parameters were assessed on a per-unit-stream-length basis (Sweeney et al. 2004). Johnson et al. (2009) found significantly higher ammonium (NH_4) demand in urban streams as compared to agricultural and forested systems, likely resulting from increased light availability in urban streams with reduced canopy cover. These results highlight the importance of stream ecosystems for regulating water chemistry and the effects of disturbance on these ecosystem services.

Overgrazing by native and domestic ungulates is a specific watershed disturbance that alters catchment soil characteristics (Kauffman et al. 2004; Piñeiro et al. 2010) and has negatively impacted up to 80% of the streams in the arid western United States through degraded riparian and in-stream vegetation, water quality, stream channel morphology, and hydrology (Kauffman and Krueger 1984; Belsky et al. 1999; Sarr 2002). Grazing is reported to have a range of effects on soils that vary with soil and vegetation type, grazing intensity and duration, and sampling period (Piñeiro et al. 2010). Piñeiro et al. (2010) reported in a review that ecosystems with annual precipitation between 400 and 850 mm showed similar patterns, with grazing lowering soil root content, increasing soil organic matter (SOM) carbon:nitrogen (C:N ratios), suggesting potential N limitation for SOM decomposition, and either increasing or not changing soil bulk density. Thus, although grazing impacts soil characteristics, and catchment and riparian attributes influence stream water chemistry in a variety of systems, it is unclear how grazing-related impacts may interact with soil and hydrobiogeochemical processes to alter stream chemistry.

Grazing also affects streamside vegetation, with significant decreases in the total aboveground biomass of riparian vegetation observed in as little as 2 yr of moderate grazing pressure (Clary and Kinney 2002). Long-term grazing exclosure (30 yr) resulted in a near doubling of litter cover, a fourfold reduction of bare ground, a fivefold increase in shrub cover, and a 30% increase in graminoid cover (Schulz and Leininger 1990). Changes in riparian vegetation in turn affect stream geomorphology in grasslands where vegetation encroachment on the active channel and sediment trapping ultimately narrow and deepen stream channels (Magilligan and McDowell 1997; Nagle and Clifton 2003). Grazing impacts can alter stream geomorphology in as little as 2 yr of heavy grazing (Clary and Kinney 2002; Ranganath et al. 2009); however, 2–4 yr of exclosure were insufficient to produce significant recovery results in other systems (George et al. 2002; Lucas et al. 2009). This narrowing of stream channels may decrease instream nutrient retention as narrow channels and associated higher velocities inhibit nutrient uptake (Sweeney et al. 2004; Bukaveckas 2007).

Grazing has been shown to impact terrestrial, aquatic, and riparian areas; however, few studies have attempted to connect these impacts and link them to instream ecosystem processes such as nutrient cycling and retention. This study was designed to test three hypotheses related to terrestrial/aquatic linkages and ungulate grazing:

(H1) Instream water chemistry would reflect riparian soil chemistry, with the same nutrient being limiting in both systems.

(H2) Ungulate grazing removal (exclosure) would affect riparian soil characteristics and vegetation biomass with increased riparian vegetation, and decreased SOM C:N ratios and soil bulk density

(H3) The effects of ungulate grazing removal would decrease instream nutrient cycling through altered riparian vegetation and stream geomorphology.

METHODS

Site Description

The Valles Caldera National Preserve (VCNP) is composed of ~36 000 ha located in northern New Mexico (lat 35°50′–36°00′N, long 106°24′–106°37′W) encompassing a volcanic caldera formed ~1.2 million yr BP (Fig. 1). The VCNP ranges in elevation from ~2 500 m in the valley floors to 3 430 m at Redondo Peak, a resurgent volcanic dome (Heiken et al. 1990). Approximately 10 000 ha of montane grassland, 700 ha of wetlands, and 100 km of stream length are found in the valley floors of the VCNP (Muldavin and Tonne 2003). The soils of the VCNP are either forest or grassland soils, with rocky, loamy textured, forest soils classified as Andisols, Alfisols, and Inceptisols derived from volcanic rocks on the hill slopes, and deep, organic rich grassland Mollisols found in the valley bottoms (Muldavin and Tonne 2003). Streams in the VCNP are low-gradient, high-sinuosity systems, with no woody riparian vegetation present in meadow areas. Typical precipitation patterns in the VCNP include snow during winter months, dry spring and early summer conditions, and significant rainfall inputs during mid- to late summer from North American monsoon events (Fig. 2). Precipitation during this study ranged from 500 to 700 mm $\cdot$ yr^{-1} (Fig. 2).

Domestic grazing in the VCNP is limited to summer months because of low winter temperatures and substantial snow accumulation. Livestock grazing in the Valles Caldera (VC) began in the mid-1800s, initially supporting small sheep herds (Anschuetz and Merlan 2007; Martin 2003). By the early 1900s, an estimated 100 000 sheep were grazed annually in VC (Martin 2003; Anschuetz and Merlan 2007). A decline in wool prices in the 1940s led to the replacement of sheep with cattle, resulting in the annual grazing of ~12 000 cattle by the late 1950s (Martin 2003; Anschuetz and Merlan 2007). From 1960 to 2000, ~3 000–7 000 cattle were grazed in the VC during summer months. Since the designation of the VCNP in 2000, cattle grazing levels have been dramatically reduced with ~300 cattle grazed in 2004 and 2005, 100 in 2006, ~500 in 2007 and 2009, and ~2 000 in 2008 (unpublished data). Animal unit months $\cdot$ $hectare^{-1}$ ranged from 0 to 0.7 for the sites in this study (Tim Haarmann, VCNP Ranch Manager, personal communication, Table 1). Grazing by native ungulates including elk and deer was largely eliminated by the early 1900s by hunting (Martin 2003). The New Mexico Department of Game and Fish reintroduced elk to the Jemez Mountains in 1947. Elk populations in 2004–2009 were estimated at 3 000 ± 500 animals (Anderson 2009). Combined cattle and elk grazing pressure in riparian habitats varied annually during the study; forage utilization measurements by VCNP staff at 10 riparian sites from 2002 to 2009 averaged 30.4% ± 9.5% (mean ± SD), with a range from 17.4% in 2009 to 45.3% in 2004 (R. R. Parmenter, unpublished monitoring data, VCNP).

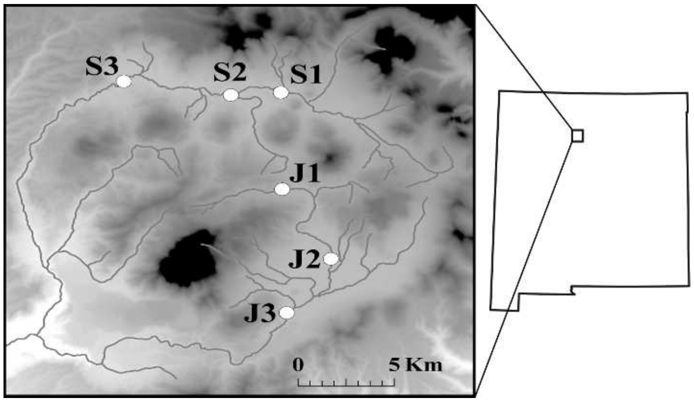

Figure 1. Map of study sites in the VCNP. Exclosures are designated by white circles, streams are gray lines, and topography grades from white at low elevations to black at high elevations.

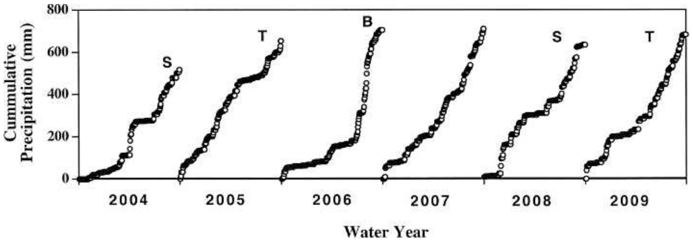

Figure 2. Cumulative precipitation (mm) for the indicated water years (1 October 1 to 30 September) measured at the VCNP headquarters (near site J3). Symbols indicate collection periods for soils (S), vegetation biomass (B), and stream injection studies (T).

Streams in the VCNP span a range of stream sizes from first to third order, with the largest streams having a base-flow discharge of approximately 100 L $\cdot$ s^{-1}. Background concentrations of NH_4–N and P (as PO_4) in this study were less than 50 μg $\cdot$ L^{-1} at all sites (Table 2). Numerous exceedances for water-quality standards were reported throughout the VCNP watersheds in 2001 (Joseph and Henderson 2006). All streams within the VCNP had exceedances for temperature and turbidity, whereas the J2, J3, and S1–S3 reaches (see Fig. 1) also had exceedances for dissolved oxygen and pH. Elk and cattle were cited as possible contributors to these exceedances, particularly to turbidity, but their exact effect was unknown (Joseph and Henderson 2006).

General Study Design

Six sets of grazing exclosure sites were established on 1 June 2004 in the VCNP (Fig. 1). All of the exclosures were located in valley bottom grasslands and consisted of ~2.5 ha open control (C) and fenced exclosure (E) plots (160 by 160 m) with 2.5-m-high fence. Plots contained ~300 m of stream length. Three sets of exclosures were constructed in each of the two largest watersheds draining the VCNP, the East Fork of the Jemez River (EFJ) and Rio San Antonio watersheds (Fig. 1). Sites in the EFJ watershed were designated as J1, J2, and J3 in the upstream to downstream direction. Two of the sites in the EFJ (J1 and J2) were on Jaramillo Creek, the major tributary to the EFJ. All three sites in the Rio San Antonio watershed were on the main stem of the Rio San Antonio and are designated as the S1 (upstream), S2 (midstream), and S3 (downstream) sites. Base flow discharge at the study sites ranged from ~ 15 L $\cdot$ s^{-1} at J1 to ~100 L $\cdot$ s^{-1} at the J3 and S3 sites. At the S2 site, a location upstream of the exclosure was used as the control area for the soil and vegetation collections, whereas a downstream location was used to measure stream geomorphology and uptake parameters. The downstream control location for the stream measurements was chosen after the study began because

Table 1. Livestock stocking rate units (animal unit months · ha^{-1}) at Valles Caldera National Preserve stream sites.

	Site					
Year	S1	S2	S3	J1	J2	J3
2002	0.14	0.14	0.14	0	0.29	0.29
2003	0.26	0.26	0.26	0	0.55	0.55
2004	0.23	0.23	0.23	0	0.54	0.54
2005	0.23	0.23	0.23	0	0.48	0.48
2006	0	0	0	0	0.16	0.16
2007	0.04	0.04	0.04	0.21	0.09	0.09
2008	0.72	0.52	0.52	0.11	0.26	0.26
2009	0	0.47	0	0	0	0

Table 2. Background concentrations (± SD) at stream sites: 2005 and 2009.

Site	Year	Ammonium (g · L^{-1})	Phosphate (g · L^{-1})
J2	2005	12 ± 0.06	33 ± 0.03
S2	2005	10 ± 0.04	17 ± 0.03
S3	2005	10 ± 0.05	13 ± 0.03
J1	2009	9 ± 0.84	46 ± 7.02
J2	2009	14 ± 0.07	42 ± 1.25
J3	2009	7 ± 0.02	20 ± 0.03
S1	2009	7 ± 0.28	13 ± 2.90
S2	2009	7 ± 0.10	14 ± 2.51
S3	2009	3 ± 1.20	19 ± 0.37

it was more geomorphically similar to the E plot than the upstream location. C plots were located downstream of E plots at the J1, J2, and S1 sites and upstream of E plots at the J3 and S3 sites. Because of budgetary and personnel constraints, soil, stream, and vegetation biomass measurements were performed in 2004 and 2008, 2005 and 2009, and 2006, respectively.

Soil Physical and Chemical Measurements

Soil collections were concentrated within the riparian zone, operationally defined as within 10 m of the stream bank. At each plot, five samples were taken at approximately 25-m intervals beginning at least 25 m from the fencing on each side of the stream, resulting in 10 sample locations per plot (120 total sample locations). At each sample location, separate samples were taken for determination of bulk density and for chemical analyses. Samples were collected before the summer growing season in 2004 (shortly after exclosure gates were closed) and in the fall of 2008 (five growing seasons later).

Bulk density was determined by making a vertical cut into the soil and extracting an intact 5.08-cm-diameter by 5.08-cm-depth core from the face of the cut at a depth of 10 cm. The cores were placed in soil cans, oven dried to constant weight in the lab, and weighed for determination of bulk density (g · cc^{-1}). Samples for chemical analyses included the 0–15-cm depth of the mineral soil (organic horizons, if present, were removed). The reasons for taking cores to this depth are (1) this depth corresponds to the depth of expected impact by ungulate hooves and should be more closely correlated with potential changes in bulk density; and (2) past sampling indicated that this depth includes the A horizon yet minimizes the portion of lower soil horizons within the sample. Soil cores (5.08 by 15–cm length) were extracted, placed in sterile bags, and returned to the lab where they were sieved to pass 2 mm (> 2-mm portion weighed and recorded). Field moisture of the samples collected in 2004 was very low, representing air-dried conditions, and thus the sieved portion was not subjected to additional drying procedures prior to chemical analyses. The samples collected in 2008 were air dried for storage until chemical analyses were performed. All subsequent chemical analyses were corrected to oven-dry mass to account for the moisture retained by each sample.

Extractable inorganic N was determined by extraction of a measured amount of soil with 100 ml of 2 M KCl. The soil solution was shaken thoroughly and allowed to settle for 14–18 h. The clarified solution was decanted and analyzed with the use of a Technicon AutoAnalyzer II for NH_4–N with an alkaline phenol method and for NO_3–N+NO_2–N with a cadmium reduction method (reported as mg N · kg^{-1} soil). Total N and C were determined with the use of a ThermoQuest CE Instruments NC2100 Elemental Analyzer (ThermoQuest Italia S.P.A., Rodano, Italy) by high-temperature combustion and the resulting gases eluted on a gas chromatography column and detected by thermal conductivity. Total N and C were expressed as mg · g^{-1} of soil sample. Modification of the method of Stelzer and Lamberti (2001) was used to determine total P. The weighed portion of soil was combusted at 500°C for 1 h, followed by addition of 1 M HCl and incubation at 80°C for 30 min to dissolve the P. After dilution and settling, the clarified solution was analyzed for PO_4–P with the use of a molybdate method on a Technicon AutoAnalyzer II and was expressed as mg · g^{-1} of soil sample. All total C, N, and P values were converted to mmol · kg^{-1} for stoichiometric comparisons and for expression of all elemental ratios (C:N, N:P, C:P, and C:N:P).

Aboveground Biomass Measurements

The aboveground biomass of upland and riparian vegetation was measured once during 11–19 October 2006. Five randomized linear stream distances were chosen at each C and E plot with the use of a 10-m buffer from all fences to eliminate edge effects. At each linear distance, a riparian (within 5 m of the stream) and upland (greater than 20 m from the stream) location were randomly selected. Standing vegetation was clipped to 1 cm of the ground and litter was raked and collected separately in one quadrat (1 m^2) per location. Samples were oven dried at 50°C to constant weight and weighed to determine standing aboveground biomass and litter (g · m^{-2}).

Stream Solute Injections

Stream flow characteristics and uptake parameters for NH_4 and PO_4 were measured with the use of solute injections in both the C and E plot reaches during the summer at three sites in 2005 and at six sites in 2009. Solute injections were performed using the Stream Solute Workshop (1990) protocols. One injection was performed per day, as the time necessary to complete an injection is ~ 6–8 h. Injections for paired C and E plots were conducted over a 2-d period to facilitate comparisons. Injections were performed at the downstream plot first to avoid contamination. Prior to the start of injections, samples were collected at six stations downstream of the injection point to determine background concentrations of Br, NH_4, and PO_4. Immediately following background sampling, Br (conservative solute) and NH_4 and PO_4 (nonconservative solutes) were injected simultaneously for 100–140 min at a constant rate calculated to elevate background concentrations by 800–1 000 $\mu g \cdot L^{-1}$ for Br and 50 $\mu g \cdot L^{-1}$ for NH_4 and PO_4. Following the start of the injection, three samples were collected at each station during the solute plateau as determined visually by the clearing of Rhodamine-WT tracer dye added to the stream at the beginning of the injection. Samples were filtered immediately in the field with the use of 0.7-µm pore-sized Whatman Glass Fiber Filters and were stored at 4°C until they were frozen (within 10 h of collection).

Uptake lengths (S_W) for NH_4 and PO_4 were estimated from the change in concentration between the background and plateau samples at each of the six sampling stations downstream of the injection point ($\Delta C[x,t] = C[x,t] - C[x,t_0]$, where t=time, x=station distance in meters, and $C(x,t)$ and $C(x,t_0)$ are the concentrations of the solute measured at the plateau and before the injection began, respectively). The ratio of nonconservative to conservative solutes ($r_c = \Delta C/\Delta Br$) was used to correct for changes in solute concentrations due to dilution of solutes rather than biological uptake. The longitudinal loss rate k_l of the nonconservative solutes was estimated by nonlinear regression from the relationship $r_c(x) = r_0 \exp(-k_l x)$, where r_0 is the nonconservative to conservative solute ratio at $x = 0$. Longitudinal loss rates were converted to uptake lengths with the use of $S_W = -1/k_l$ (Newbold et al. 1982). Because S_W is influenced by stream scale, uptake lengths were converted to a mass transfer coefficient or uptake velocity (V_f, $mm \cdot min^{-1}$) and areal uptake rates (U, $\mu g \cdot m^{-2} \cdot min^{-1}$) to compare uptake between streams of different sizes. V_f and U are calculated as $V_f = k_l u d$ (where u=water velocity [$m \cdot s^{-1}$] and d=water depth [m]) and $U = V_f C$ (where C=background nutrient concentration [$\mu g \cdot L^{-1}$]).

Analysis of the conservative solute data (Br) was conducted with the use of a one-dimensional advection-dispersion model that includes a transient storage component (OTIS, Runkel 1998) to estimate discharge (Q) and cross-sectional area (A). With the use of Q (width×depth×velocity) and A (width×depth in meters), average water velocity (v_w, $m\,s^{-1}$) was calculated as $v_w = Q/A$. Average water depth was calculated as d=A/width with the use of the mean reach widths from 20 evenly spaced cross-sectional geomorphology transects.

Ammonium samples were analyzed by the phenylhypochlorite method and a 10-cm flow path modified from Hansen and Koroleff (1983). Phosphate was measured with the use of the stannous chloride method (Standard Method 4500-P D; Clesceri et al. 1998). Bromide was analyzed by ion chromatography (Dionex, Standard Method EPA 300.1).

Statistical Methods

Analysis of variance (ANOVA) was used to determine the significance of treatment, between and within sites, and between year effects on soil properties. When necessary, data were log transformed to meet criteria for ANOVA. When significant differences were determined with ANOVA, differences between the individual factors were determined with Scheffe F test. All figures of soil properties show mean and standard deviation. Level of significance is $P < 0.05$, unless otherwise indicated. ANOVA with blocks (sites) was used to determine the significance of exclosure effects on aboveground biomass and litter. A mixed-model ANOVA was used to determine the effects of exclosure on nutrient spiraling metrics and stream physical characteristics. This model included site as a random effect, treatment as a within-site variable, and year as a fixed effect to assess cumulative effects at the three sites where parameters were measured in more than 1 yr. Linear regression was used to examine relationships between nutrient uptake and stream physical characteristics.

RESULTS

Soil Physical and Chemical Measurements

Soils of the riparian areas in the VCNP show a range in chemical properties (Figs. 3 and 4) with significant differences between sample sites for most of the soil properties in both sampling periods. However, the differences between sampling periods often exceeded the differences between sites within a sampling period. There was an increase in soil total P, C, and N at four of the six sites in the 2008 samples relative to the 2004 samples (Figs. 4a–4c), along with a general decline in the C:P and N:P ratios between these samplings (C:P from a mean of 257 [± 63] to 242 [± 40; P=0.033] and N:P from 20.0 [± 5.5] to 18.3 [± 3.7; P=0.006], Figs. 4e and 4f). There were no significant differences between the C and E plots within all sites for all soil properties for samples collected in 2004, which was shortly after closure of the exclosure plots. The differences between sample periods can be attributed to the effects of grazing exclusion for only one soil property in 2008. The only effect of grazing exclusion on soil properties occurred for total P with the E plots significantly lower than the C plots at three of the six sites in 2008 (J1, J2, and S2; Fig. 4c).

Aboveground Biomass

Aboveground biomass of vegetation in the VCNP had a mixed response to grazing exclusion by the end of three growing seasons. Upland standing vegetation and litter values from the six sites both increased in E plots; however, these values were not significantly different from C plots ($P > 0.05$). In contrast, standing aboveground biomass and litter biomass in the riparian zone from the six sites were significantly greater in E plots than in the C plots (P=0.005 and 0.006, respectively). Riparian standing aboveground biomass averaged 273 (SD=155) and 400 (178) $g \cdot m^{-2}$ for the C and E plots, respectively, whereas riparian litter values were 58 (75) and 110 (76) $g \cdot m^{-2}$ for the C and E plots, respectively.

Stream Physical Characteristics

Width, depth, area, and average velocity were measured in VCNP streams during 2005 and 2009. The most variable parameters were width 0.71 (J1-C, 2009) to 5.05 m (J3-E, 2009), discharge 17 (J2-C, 2009) to 123 $L \cdot s^{-1}$ (S3-C, 2009), and width:depth ratios 3 (J1-E, 2009) to 44 (S3-E, 2009) (Table 3). Depth and velocity were more consistent between sites with

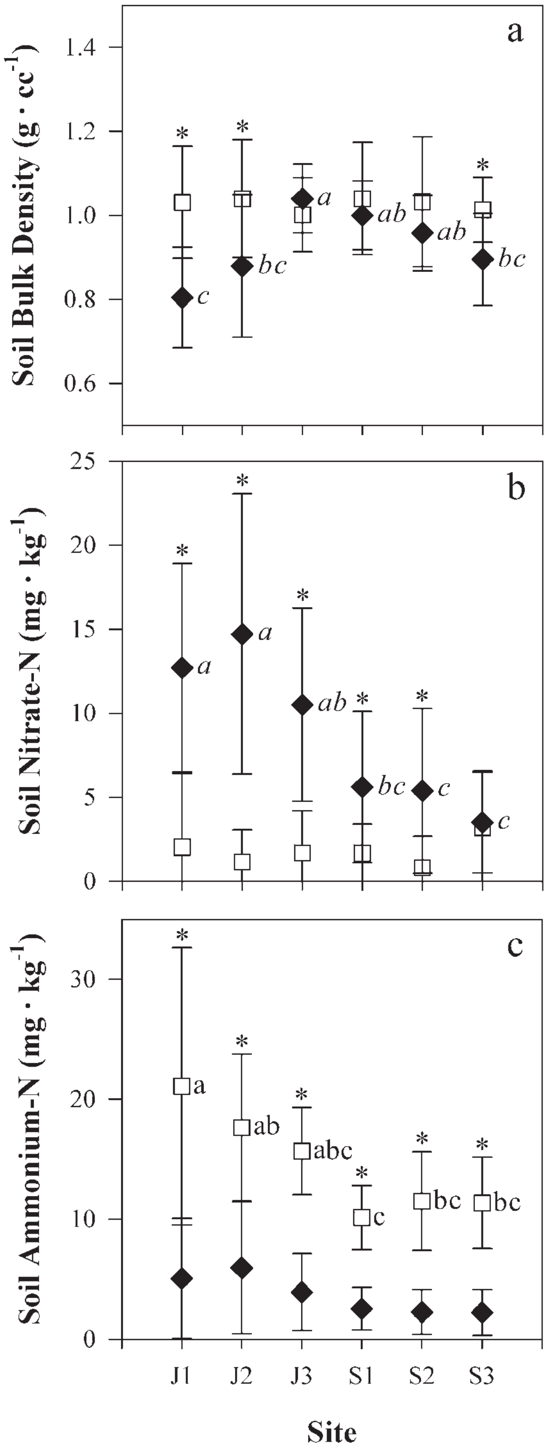

Figure 3. Soil bulk density (**a**), nitrate-N (**b**), and ammonium-N (**c**) in riparian grassland soils from three sites within the East Fork of the Jemez River watershed (J1, J2, J3) and the Rio San Antonio watershed (S1, S2, S3) in the VCNP. Samples were collected in 2004 before the summer growing season (open squares) and in the fall of 2008 (solid diamonds; diamonds sometimes cover squares). Within a collection, sites that are significantly different have different letters (regular font for 2004, italic for 2008). Within a site, significant differences between years ($P < 0.05$) are indicated by asterisks.

a range of 0.10 (J2-E, 2009) to 0.27 m (J1-E, 2009) for depth, and 0.07 (J2-C, 2009) to 0.22 m s^{-1} (S1-E, 2009) for velocity (Table 3). Exclosure minimally impacted stream physical characteristics. None of the physical variables, width, depth, area, or average velocity, were significantly different in the E versus C reaches ($P > 0.05$); however, at marginally significant levels width was lower ($P = 0.06$) and velocity higher ($P = 0.07$) in exclosure plots. When velocity and depth were considered as a combined variable (velocity × depth) the mean C and E values (0.024 ± 0.008, 0.027 ± 0.008) were significantly different with higher values in the E plots ($P = 0.02$).

Stream Nutrient Cycling Parameters

The uptake of N and P in VCNP streams varied between nutrients, sites, treatments, and years. Injections of NH_4 revealed strong N sequestration during each of the 18 experiments. Ammonium S_W ranged from 52 (J2-C, 2005) to 559 m (S1-E, 2009), V_f ranged from 3.8 (S1-E, 2009) to 20.5 mm · min^{-1} (S3-C, 2005), and U ranged from 28 (S1-E, 2009) to 224 μg · m^{-2} · min^{-1} (J2-C, 2005) (Fig. 5). Injections of PO_4 revealed sequestration during 13 of the experiments and PO_4 release during 5 experiments. In general, when PO_4 uptake occurred, it was an order of magnitude lower than NH_4 uptake. For experiments with positive uptake values for PO_4 S_W ranged from 350 (J2-C, 2005) to 5 800 m (J3-C, 2009), V_f ranged from 0.19 (J2-C, 2009) to 4.84 mm · min^{-1} (S1-E, 2009), and U ranged from 4 (J3-C, 2009) to 61 μg · m^{-2} · min^{-1} (S1-E, 2009). The extremely low uptake of PO_4 in VCNP streams hindered accurate determination of PO_4 spiraling parameters in these systems, as minimal longitudinal declines in PO_4 were difficult to measure accurately.

Ammonium S_W values were greater in the E reaches for eight out of the nine comparisons (Fig. 5), resulting in significant E/C differences ($P = 0.008$). Ammonium V_f and U values were greater in C reaches for seven out of the nine comparisons, with the exception of J1 and J3 in 2009 (Fig. 5); however, V_f and U values from the C and E plots were only marginally significantly different ($P = 0.095$ and 0.090, respectively). Year was included as a fixed effect in the model, but was not found to be a significant predictor for any of the nutrient uptake parameters.

Linear regression was used to investigate relationships between stream physical characteristics and nutrient cycling metrics. Velocity was a significant positive predictor of NH_4 S_W ($P = 0.02$) and was negatively related to U ($P = 0.03$), while NH_4 V_f was positively related to stream width ($P = 0.02$) and cross-sectional area ($P = 0.008$) (Fig. 6).

DISCUSSION

Soil to Stream Connections

The VCNP riparian grassland soils have C:P and N:P ratios higher than the average reported for grasslands worldwide (C:P of 200 to 300 and N:P of 14 to 24 for VCNP compared to 166 and 12.3, respectively (Cleveland and Liptzin 2007). VCNP soil nutrient ratios indicate that the riparian soils are low in P relative to the other elements and indicate that P could be

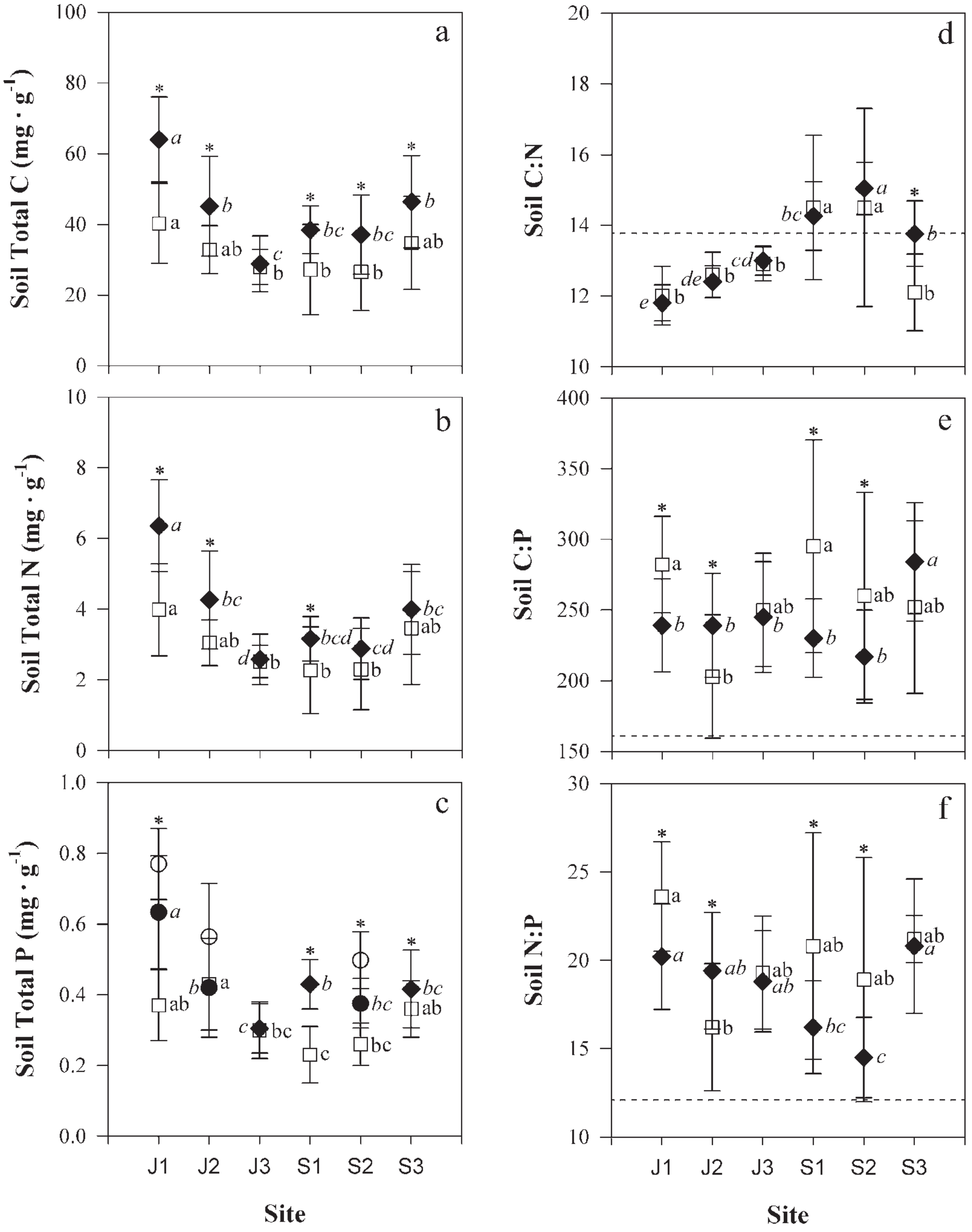

Figure 4. Soil characteristics of riparian grassland soils in the VCNP (see Fig. 3 legend for descriptions). Dashed lines (**d, e,** and **f**) indicate grassland averages (Piñeiro et al. 2010). Significant effects of exclosures ($P < 0.05$) occurred at three sites for total P in 2008 (**c**; sites J1, J2, and S2; E plots, filled circles; C plots, open circles).

limiting soil microbial (Sinsabaugh et al. 2009) and/or plant production (Cleveland and Liptzin 2007).

The uptake of NH_4 in VCNP streams is within the range of uptake values reported for other first- to third-order streams; however, the PO_4 uptake is lower than that from other stream ecosystems (Ensign and Doyle 2006). Additionally, PO_4 S_W were on average approximately 10 times longer than NH_4 S_W, resulting in $S_{W\text{-}N}$:$S_{W\text{-}P}$ ratios of ~ 0.1. Spiraling theory predicts that ratios of less than one indicate N limitation (Cross et al. 2005), providing strong evidence that during stable summer base flow N is the limiting nutrient in VCNP streams. This finding is consistent with a study of nutrient limitation in 157 streams in Arizona that found N limitation at 72% of all of the sites studied and at 89% of the sites sampled at base flow (Grimm and Fisher 1986). Similar results were also found at sites in western New Mexico (Coleman and Dahm 1990), suggesting N limitation may be a widespread characteristic of streams in the southwestern United States.

The P limitation in VCNP riparian soils compared to the N limitation in streams indicates a lack of connection between 0–15-cm depth soil chemistry and instream nutrient cycling. This apparent decoupling of terrestrial and aquatic processes is likely a result of a hydrologic disconnect between soils at 15-cm depth and stream recharge during mid to late summer when the

Table 3. Valles Caldera National Preserve stream physical characteristics: 2005 and 2009.

Site	Treatment	Year	Wetted width (m)	Depth (m)	Cross-sectional area (m^2)	Velocity ($m \cdot s^{-1}$)	Discharge ($L \cdot s^{-1}$)
J1	C	2009	0.71	0.22	0.15	0.12	18
J1	E	2009	0.73	0.27	0.20	0.12	24
J2	C	2005	2.25	0.16	0.36	0.10	36
J2	E	2005	1.82	0.12	0.23	0.14	32
J2	C	2009	1.69	0.15	0.26	0.07	17
J2	E	2009	1.46	0.10	0.14	0.15	21
J3	C	2009	5.05	0.15	0.77	0.12	95
J3	E	2009	3.85	0.20	0.78	0.12	96
S1	C	2009	2.93	0.16	0.47	0.19	89
S1	E	2009	2.31	0.16	0.37	0.22	82
S2	C	2005	3.04	0.18	0.56	0.17	97
S2	E	2005	2.87	0.20	0.59	0.17	101
S2	C	2009	2.97	0.20	0.61	0.18	108
S2	E	2009	2.96	0.23	0.67	0.16	108
S3	C	2005	4.89	0.20	0.96	0.12	116
S3	E	2005	4.98	0.18	0.88	0.14	118
S3	C	2009	4.81	0.16	0.75	0.16	123
S3	E	2009	5.01	0.11	0.57	0.21	120

stream nutrient uptake parameters were measured. An investigation of stream flow pathways in the VCNP found near-surface runoff that flushes nutrients from upper organic-rich soil horizons was important during spring snow melt, but was not a significant contribution during the summer or fall except during extreme monsoon events (Liu et al. 2008). Summer and fall stream inputs were dominated by deeper subsurface flow and groundwater discharge (Liu et al. 2008). The chemistry of these deeper inputs appears to be influenced by subsoil/parent geology rather than near surface soil chemistry.

These findings are consistent with the result of Cresser et al. (2000), who found near-stream parent geology was a better predictor of instream water chemistry than near-stream soil type. Phosphorus is likely abundant in VCNP subsoils and parent geology, as these materials are relatively young geologically and volcanic ash is a significant source of P (Felitsyn and Kirianov 2002). Additionally, when soil N becomes incorporated into aboveground production, it remains sequestered in decomposing grassland litter for an average of 10 yr before returning to the soil pool (Parton et al. 2007). This tight retention of N in grassland soils may also help explain the apparent disconnect between N-rich soils and N-limited streams.

Grazing Exclusion Impacts on Soil, Vegetation, and Stream Geomorphology and Nutrient Cycling

Grazing intensity in the VCNP results from both livestock and elk grazing and has varied over the past 100 yr. The designation of the VCNP in 2000 led to dramatically reduced cattle grazing and low stocking rates, likely reducing grazing effects in riparian areas. However, annual combined livestock and elk forage utilization measurements in VCNP riparian areas show utilization of an average of 30% of the available forage, indicating continued moderate grazing pressure. The present study was not designed to quantify grazing intensity, or to relate intensity levels to the magnitude of grazing-related responses, but was designed to assess the effects of the total removal of the moderate combined grazing observed in the VCNP on riparian and instream characteristics. Grazing exclusion-related variables had mixed responses to 6 yr (2004–2009, inclusive) of total grazing exclusion, ranging from significant changes and trends to no response. The minimal response for some variables is likely related to the reduced livestock grazing beginning in 2000.

Riparian standing aboveground biomass and litter were the variables expected to respond most rapidly to grazing exclusion. These variables responded within three growing seasons (2004–2006), with significant increases in both variables within E plots. Similar results were documented in both short (Clary and Kinney 2002) and long-term (Schulz and Leininger 1990) riparian grazing exclosure experiments.

At the six exclosure study sites, the greatest differences in most soil parameters occurred between the 2004 and 2008 collections. These changes are attributed to sediment deposition between collections, presumably from out-of-bank flooding events from either snow-melt or summer thunderstorms (personal observation of fresh sediment deposition). The only significant effect of grazing exclusion on soil nutrients was an increase in total soil P at three (J1, J2, and S2) of the 6 C plots with P-rich sediment deposition the logical explanation for the increase. Similar increases in total C and N also occurred, indicating concurrent deposition of organic detritus and/or organic-rich sediment; however, a general decline in the C:P and N:P ratios from 2004 to 2008 indicates that P was in greater relative abundance than C or N in the newly deposited sediment than in the existing soil. Greater overbanking in areas with trampled and degraded stream banks, along with decreased overbanking in exclosures with greater riparian vegetation that acts to constrain high flows laterally are potential mechanisms to explain increased total P in soils of the three C plots. Expected effects of grazing exclusion on soil nutrients are likely masked by sediment contributions at some

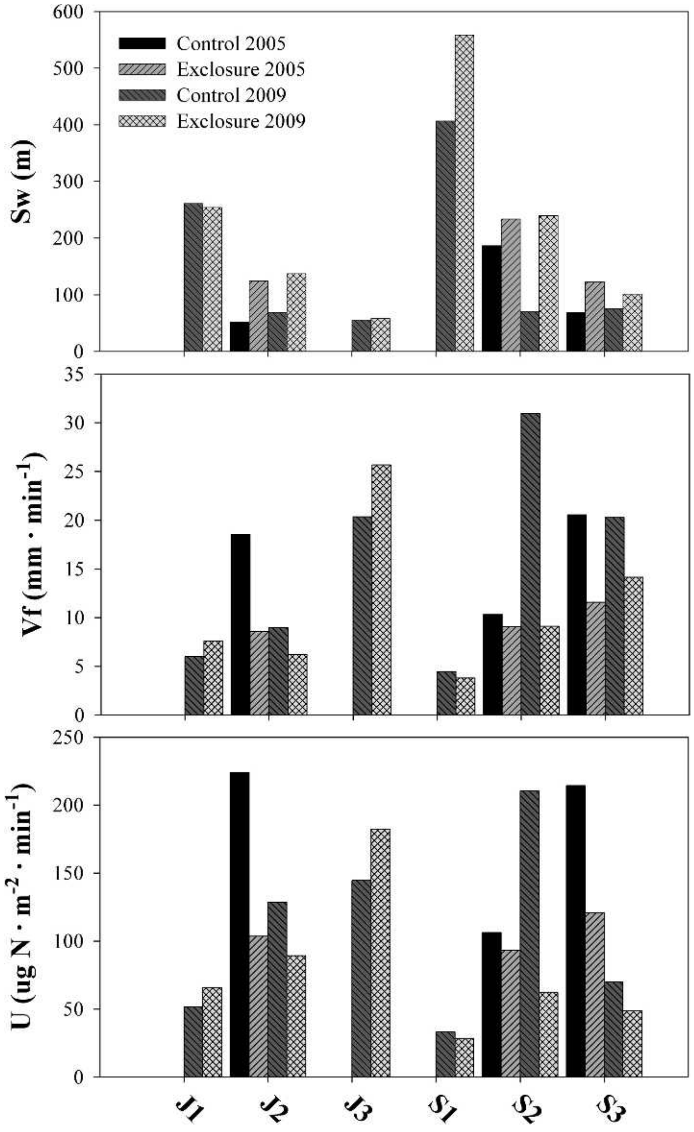

Figure 5. Uptake length (S_W), velocity (V_f) and rate (U) metrics for NH_4 in VCNP stream E and C plots in 2005 and 2009.

sites. The site with the least variation between years and no evidence of significant sediment deposition is J3 (total C, N, P and their ratios were nearly identical in 2004 and 2008, Fig. 4), the lowest site on the East Fork of the Jemez. This site showed no significant effects of grazing exclusion on any soil characteristics.

The geomorphology of grassland stream ecosystems often responds predictably to grazing pressure, with exclusion resulting in decreased width, increased depth, and decreased width:depth ratios (Magilligan and McDowell 1997; Belsky et al. 1999; Nagle and Clifton 2003; Ranganath et al. 2009). However, the rate at which these changes occur varies between systems with some responding to grazing pressure in as little as 2 (Ranganath et al. 2009) to 5 yr (Clary 1999), whereas others show little response in 4–14 yr (Ranganath et al. 2009). Streams in the VCNP fall into the latter category with only marginally significant changes to width and velocity and no significant changes in cross-sectional area or width:depth ratios detected in the 6 yr (2004–2009, inclusive) following exclosure. When depth and velocity, important parameters for instream nutrient retention, were combined into a single variable (velocity × depth), values were significantly greater in exclosure reaches.

This study was the first to examine the effects of ungulate grazing exclusion on nutrient cycling in adjacent stream ecosystems. Grazing exclusion significantly increased NH_4 uptake lengths. This change occurred rapidly (increased uptake lengths were observed after one and a half growing seasons) and is likely due to increased riparian and emergent vegetation that constrain and shade the channel and by initial geomorphic changes reflected in the combined velocity × depth variable. Shading decreases nutrient uptake in streams by reducing primary production, which is an important mechanism for nutrient retention (Mosisch et al. 2001). Increased depth and stream velocities both decrease interactions between the water column and benthos where most nutrient retention occurs. This effect can be produced by either geomorphic changes in which the shape of the channel is changed (Bukaveckas 2007) or by increased instream vegetation, which can narrow and latterly constrain channels in relatively short time periods (Wilcock et al. 2002).

The relative importance of shading versus geomorphic changes can be assessed by comparing the effects of grazing on uptake lengths (S_W) versus uptake rates (U). Uptake lengths vary in response to both physical changes that alter stream velocity, and changes that alter biological uptake. In contrast, U and uptake velocity (V_f) are normalized for different velocities and thus are designed to measure changes in biological uptake only. Significant increases in S_W and the nonsignificant trends of decreasing V_f and U in exclosure reaches suggest grazing exclusion impacts nutrient uptake through altering both physical and biological parameters in VCNP streams.

IMPLICATIONS

Ungulate grazing exclusion in montane grasslands in the VCNP increased riparian standing aboveground biomass and litter within 3 yr, minimally impacted soil nutrient levels and ratios after 5 yrs, and produced both statistically significant and nonsignificant trends of decreased nutrient retention in adjacent stream ecosystems after 6 yr. These results highlight the long-term nature of ecosystem responses to the elimination of grazing and the need for detailed ongoing long-term monitoring to differentiate interannual variability from true long-term trends.

Ungulate grazing has been implicated in the degradation of many stream characteristics; however, this study provides evidence that grazing exclusion may decrease nutrient retention in some streams, a process that is commonly considered a valuable ecosystem service. In the case of the VCNP streams, grazing-enhanced nutrient retention comes at the expense of large width:depth ratios and unshaded solar loading, resulting in temperature and turbidity impairments. Nonetheless, managers must consider the balance between the value of instream nutrient retention with grazing-related losses of other ecosystem services and products, such as decreased fish and aquatic

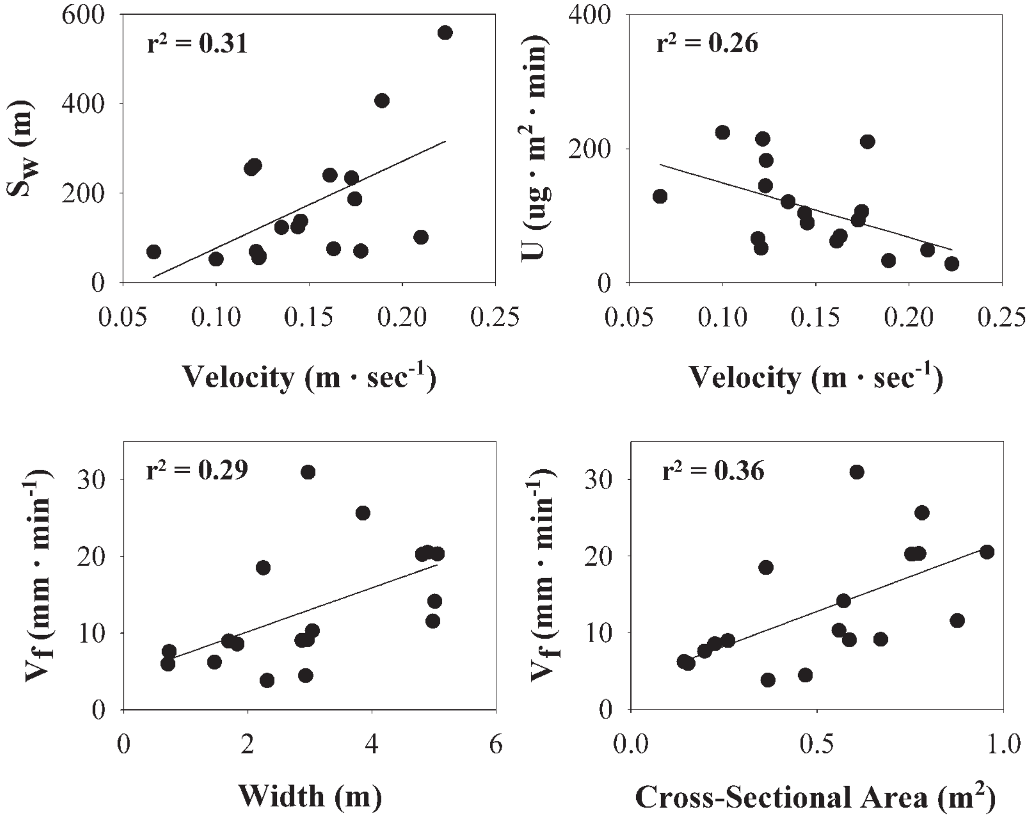

Figure 6. Regression analysis of stream geomorphology and nutrient uptake parameters. All regression relationships shown are significant ($P < 0.05$).

invertebrate habitat and effects on water-quality parameters such as turbidity, temperature, and dissolved oxygen.

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