

Influence of Livestock Grazing, Floodplain Position, and Time on Soil Nutrient Pools in a Sierra-Nevada Montane Meadow

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Abstract: Limited data exist on quantification of soil nutrient pools in montane meadow ecosystems. Along Big Grizzly Creek in the Plumas National Forest, CA (June 1999–September 2005), soil nutrient pools were quantified by livestock grazing treatment (grazed, ungrazed), floodplain location (stream edge, midfloodplain, forest edge), and season using resin capsules (15-cm depth) and bulk soil samples (0- to 25-cm depths). Resin capsules integrated nutrient availability for three periods: overwinter, plant growth, and senescence. Bulk soil samples were collected immediately after snowmelt (pregrowth), during plant growth, and during plant senescence. During the study period, pulses of N or P did not occur, suggesting strong coupling of mineralization with root/microbial uptake. Soil availability of most nutrients was affected by sampling time and floodplain location; however, differences were small. Soil samples from grazed areas had significantly greater K and Na on clay exchange sites than soil from excluded areas possibly because of supplementation with salt blocks. A seasonal reciprocal relationship occurred for the proportional content of K and Na on clay exchange sites and on resin capsules: Na highest during the cold season, and K highest in the plant senescent period. This relationship may be important in retaining K in soil during snowmelt. Surprisingly, the robust pools of extractable Ca, Mg, K, and Na, and their proportional content on the exchanger differed significantly with time. Overall, the data suggest that the present grazing management plan does not greatly impact nutrient availability.

Key words: Livestock grazing, riparian ecosystems, soil nutrient availability.

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Soil nutrient availability affects primary productivity, plant competition, plant successional processes, and site invasibility by undesirable plants (Tilman, 1985; Huenneke et al., 1990; Goldberg and Barton, 1992; Wilson and Tilman, 1993). In most plant communities, soil nutrient availability varies spatially across the landscape, vertically through the soil profile, and temporally (Burke, 1989; Gross et al., 1995; Jobbágy and Jackson, 2001). Spatial and temporal variability of soil nutrient availability creates nutrient niches. Characteristics and heterogeneity of these niches, such as maximum level of nutrients, nutrient distribution with soil depth, the balance of nutrients, duration of nutrient availability, and seasonality of nutrient availability, constrain plant community composition and affect plant competition (Grime, 1977; Bedford et al., 1999; Davis et al., 2001; Fransen et al., 2001).

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A primary control of soil nutrient availability, especially for N, S, and P, is the rate of soil organic matter mineralization (Stevenson, 1994). Mineralization of organic matter is an extremely complex process with a multitude of interacting biotic and abiotic factors (Sollins et al., 1996). Soil nutrient availability is also influenced through equilibrium reactions with primary mineral dissolution and cation and anion exchange sites (Barber, 1995). When soil nutrient availability is strongly coupled to plant and microbial uptake, levels in the soil remain low and the ecosystem is somewhat resistant to vegetation change; if mineralization and uptake become decoupled, nutrient availability can greatly increase, placing the system at risk for vegetation change, often to weedy species (Burke et al., 1998).

Given its importance, soil nutrient availability has been rarely quantified, spatially and temporally, on montane meadow and riparian habitats in the western United States. Elevated nutrient availability can change plant species composition and decrease species diversity (Bedford et al., 1999); yet, relatively limited research exists on general soil characteristics and soil nutrient availability in response to disturbance (Bohn and Buckhouse, 1985; Wheeler et al., 2002; Kauffman et al., 2004). Moreover, a greater understanding of the dynamics of nutrient availability would increase the chances of successful restoration/rehabilitation (Goodwin et al., 1997). Management decisions can alter soil nutrient availability. For example, livestock grazing, if improperly implemented, can decouple nutrient availability with nutrient uptake and increase risk of vegetation changes (Fleischner, 1994).

The purpose of this article was to report on a 6-year study, during which various pools of soil nutrient availability were quantified in a Sierra-Nevada montane meadow ecosystem. Our working null hypothesis posits that livestock grazing, time (season), and floodplain location will not significantly affect soil nutrient availability.

MATERIALS AND METHODS

The study area is along the upper reach of Big Grizzly Creek, a tributary to Lake Davis and the Feather River (120°37' W; 39°59' N) in the Plumas National Forest, CA. The study area has had considerable research including soil genesis (Blank et al., 1995), ecophysiology of native vegetation (Svejcar and Riegel, 1998), and the effect of stocking rates on nutrition and plant growth (Huber et al., 1995). The associated floodplain ranges from about 150 to 500 m in width. The surrounding uplands are forested with *Pinus contorta* species *murrayana* [Grev. and Balf.] Cricht. (lodgepole pine), *Abies concolor* [Gordon and Glend.] Lindley (white fir), and *Pinus jeffreyi* [Grev. and Balf.] (Jeffrey pine). Floodplain vegetation is dominated by *Poa pratensis* L. (Kentucky bluegrass), *Juncus balticus* Wild. (Baltic rush), *Carex nebrascensis* Dewey (Nebraska sedge), and *Deschampsia caespitosa* [L.] Beauv. (tufted hairgrass). The relative proportion of vegetation differs depending on floodplain location.

TABLE 1. Precipitation Records for the Study Period[†]

Dates Measured	Precipitation	
	Total, cm	% of Average
July, 29, 1998–September 16, 1999	107	114
September 16, 1999–July 25, 2000	76	82
July 25, 2000–June 6, 2001	44	48
June 6, 2001–June 13, 2002	64	69
June 13, 2002–June 24, 2003	84	92
June 24, 2003–June 23, 2004	74	81
June 23, 2004–September 13, 2005	86	94

[†]Data collected at nearby Three Mile Valley (elevation, 1,798 m) maintained by the California Department of Water Resources.

The study area is located at an elevation of 1,777 m. Yearly precipitation averages 89 cm, approximately 85% of which is in the form of snow falling in the months of November through March. Precipitation records for the study period were taken from Three Mile Valley (about 5 km east from the study area) at a similar elevation (Table 1). Soil properties for the three floodplain positions are presented in Table 2. The meadow is often flooded during spring snowmelt. In a previous study conducted on the meadow in 1990–1991, water table depths in the mid-floodplain position ranged from less than 20 cm in April and receded to more than 100 cm by July and through October (Svejcar and Riegel, 1998).

In 1998, two paddocks, 40 m × 40 m, were randomly assigned and built to exclude livestock. The paddocks extended

across Grizzly Creek to the forest/floodplain interface. Grazing management during the study period consisted of a three-pasture 3-month rotation, which means that areas outside the enclosure were grazed about 1 month each year (Scott Lusk, Plumas National Forest, personal communication). Synthesis of field notes and photographic records throughout the study period indicates that livestock-excluded areas contained more litter (visually), greened up later in the spring, and had more soil disturbance from burrowing rodents (R.B., personal observation). Measurements of nutrient availability were first taken in June 1999, and the last measurements were September 2005. Two differing methodologies were chosen to quantify soil nutrient availability. Resin capsule technology (Yang et al., 1991) integrates nutrient availability during the period the capsules are in the soil. Resin capsules were placed at 15 cm in one paddock and in an adjacent unfenced area. When possible, a coring device was used to remove a plug, the capsules were inserted, and the plug was replaced. If soil was extremely wet, a soil spade or hand trowel was used to cut away soil to insert the capsules. Six resin capsules were randomly placed along a line approximately parallel to the stream in each of three floodplain positions (stream edge, midfloodplain, and forest edge) and by treatment (grazed, ungrazed) for a total of 36 capsules per measurement period. Measurement periods were from late fall to spring (overwinter), spring to midsummer (plant growth), and from midsummer to late fall (senescence). The exact period of measurement depended on snowpack and plant phenology. Capsule locations in each floodplain location were shifted for each measurement time. In an adjacent paddock and unfenced area, bulk soil samples were collected usually three times a year to quantify various soil nutrient pools. Four randomly located replicates were collected from a depth of 0 to 25 cm from three

TABLE 2. Soil Characteristics for Stream Edge, Midfloodplain, and Forest Edge Pedons[†]

Horizon	Depth	Munsell Color	Texture	Organic Matter	C:N	pH	CEC
	cm	wet		%			cmol/kg
-----Stream edge-----							
A1	0–5	10YR 3/1	Silty clay loam	15.3	11.1	4.61	nd
A2	5–14	10YR 2/1	Silty clay loam	11.7	9.5	4.69	nd
Bt1	14–24	10YR 3/1	Silty clay	6.1	9.4	4.89	nd
Bt2	24–50	10YR 3/2	Silty clay	1.6	8.5	5.19	nd
BC	50–59	2.5Y 4/2	Silty clay	0.9	9.2	5.41	nd
2C	59–70+	2.5Y 5/4	Silty clay loam	0.5	13.0	5.73	nd
-----Midfloodplain-----							
Oa	0–10	10YR 2/1	Silt loam	26.7	19.1	5.00	60
A	10–20	10YR 2/1	Clay	9.7	12.7	5.29	55
AB	20–28	2.5Y 2/0	Clay	5.2	9.6	5.39	44
Bw	28–46	2.5Y 2/0	Silty clay	3.1	13.9	5.58	42
2C	46–58	10YR 4.5/2	Silty clay loam	1.6	11.2	5.96	28
3Btgb	58–81	2.5Y 2/0	Silty clay	1.9	8.9	5.69	43
-----Forest edge-----							
A	0–10	10YR2.5/1	Sandy clay loam	8.6	16.2	4.83	30
AB	10–23	10YR 3/2	Sandy clay loam	3.4	11.7	4.92	23
Bt1	23–41	10YR 3/1.5	Sandy clay loam	2.9	12.4	4.96	18
Bt2	41–66	10YR 4.5/2	Loam	1.2	15.8	5.25	19
2Btb	66–97	5Y 3.5/1	Clay loam	1.2	11.3	5.87	29

[†]Percent organic matter determined by multiplying % carbon times 1.7.

nd: not determined; CEC, cation exchange capacity by sum of cations, pH 7.0 ammonium acetate extraction.

floodplain positions (stream edge, midfloodplain, and forest edge) and treatment (grazed, ungrazed) for a total of 24 samples per measurement period. Samples were collected during pre-growth (before appreciable plant growth and at which time the soils were saturated), during peak plant growth, and when vegetation had senesced. As per the resin capsule measurements, time depended on snowpack depth and plant phenology.

In the laboratory, resin capsules were washed extensively with deionized water and dried. Nutrients were desorbed by shaking a resin capsule with 40 mL of 1N HCl for 1 h in a 50-mL polypropylene tube (Skogley et al., 1996). Atomic absorption/emission spectroscopy was used to quantify Ca, Mg, K, Na, Fe, and Mn. Desorbed ortho-P was quantified using molybdenum blue chemistry (Olsen and Sommers, 1982). Nitrate was quantified using ion chromatography (Ag filters used to remove Cl^-). Ammonium was quantified using flow injection membrane diffusion methodology. To compare among different collection dates, data were converted to amount sorbed per day by dividing the total amount of a particular nutrient by the number of days the capsules were in the soil. The mole percentage of individual cations sorbed was calculated by dividing the moles of each cation by the summed moles of Ca, Mg, Na, and K and multiplying by 100. Soil samples were returned to the laboratory and air-dried when necessary to facilitate sieving through 2-mm openings. These soils contained few coarse fragments, and the sieving process served to homogenize the soil and break apart large aggregates. We also strove to analyze soils quickly, within 1 week, at least for those attributes potentially affected by storage. The following nutrient pools were determined: (i) KCl-extractable NO_3^- and NH_4^+ (readily available plant N; Bundy and Meisinger, 1994); (ii) 30-day N mineralization potentials with all samples maintained near field capacity (potentially available N; Hart et al., 1994); (iii) ammonium acetate-extractable Ca^{+2} , Mg^{+2} , K^+ , and Na^+ (robust pool dominated by cations sorbed to the soil clay complex; Thomas, 1982); (iv) pH (in 0.01 CaCl_2 matrix; McLean, 1982); and (v) immiscibly displaced Cl^- , Ca^{+2} , Mg^{+2} , Na^+ , and ortho-P (corresponds to nutrients in the soil solution and readily available to plants;

Mubarak and Olson, 1977). We also quantified enzyme activities of urease and amidase (important for N mineralization; Tabatabai, 1994). The mole percentage of each cation extracted by ammonium acetate was calculated by dividing the moles of each cation by the summed moles of Ca, Mg, Na, and K and multiplying by 100. All standards were NIST certified and made up in an appropriate matrix. All data were corrected for moisture content to 105°C weight determined on a separate subsample.

The resin and bulk soil data sets were analyzed separately. The resin data set was analyzed using analysis of variance (ANOVA) (normalization required for some attributes) with categorical variables *season* (overwinter, plant growth, senescence), *floodplain position* (stream edge, midfloodplain, forest edge), and *treatment* (grazed, ungrazed). Resin capsules damaged or brought to the soil surface by animal activity were excluded from analyses. Bulk soil samples were also analyzed using ANOVA (normalization required for some attributes) with categorical variables *time of sampling*, *floodplain position* (stream edge, midfloodplain, forest edge), and *treatment* (grazed, ungrazed). To clarify nutrient availability among sampling times, data during the 6 years were grouped by *season* (pregrowth, growth, senescence) and analyzed by ANOVA. Tukey's honest significant difference test was used to separate means.

RESULTS

Nutrient Pools Measured in Bulk Soil Samples

N availability (KCl-extractable N) in the surface 25 cm of soil was influenced by a significant treatment \times floodplain position \times time interaction (Table 3; Fig. 1). Higher N availability on stream edge ungrazed sites for May 3, 2004, was responsible for the three-way interaction. Overall, soil N availability was greatest during the spring before appreciable vegetation growth had occurred, declined slightly during the summer when vegetation was rapidly growing, and declined further after plant senescence. During pre-growth and plant growth seasons, availability of soil N trended downward from stream edge to forest edge locations. No significant differences occurred in available soil N

TABLE 3. ANOVA Values for Quantified Soil Attributes

Attribute	Trt	Pos	Time	Trt \times Pos	Trt \times Time	Pos \times Time	Trt \times Pos \times Time
KCl-N	0.7949	<0.0001	<0.0001	0.2657	0.0079	0.0002	0.0014
Mole % NH_4^+	0.1559	0.0073	<0.0001	0.9785	<0.0001	0.0221	<0.0001
Net N mineralization	0.3425	<0.0001	<0.0001	0.4433	0.0108	0.0034	0.0078
Amidase activity	0.0006	<0.0001	<0.0001	0.0128	0.0008	0.0001	0.0223
Urease activity	0.1041	0.0001	<0.0001	0.1305	0.0002	0.0168	<0.0001
pH	0.0522	<0.0001	<0.0001	0.0460	0.0043	<0.0001	0.0057
Acetate-Ca	0.0895	<0.0001	<0.0001	0.9237	0.0038	<0.0001	0.0169
Acetate-Mg	0.7612	<0.0001	<0.0001	0.0275	0.0020	<0.0001	0.0021
Acetate-K	0.2164	0.0004	<0.0001	0.0472	0.0319	0.7088	0.8000
Acetate-Na	<0.0001	<0.0001	<0.0001	0.0062	<0.0001	<0.0001	0.0026
Mole % Ca exchanger	<0.0001	0.0035	<0.0001	0.7096	0.0005	<0.0001	<0.0001
Mole % Mg exchanger	0.4678	<0.0001	<0.0001	0.0002	0.0013	<0.0001	<0.0001
Mole % K exchanger	0.1931	<0.0001	<0.0001	0.0362	0.0473	0.6439	0.6740
Mole % Na exchanger	<0.0001	<0.0001	<0.0001	0.0062	<0.0001	<0.0001	0.0026
Solution Ca^{+2}	0.4649	<0.0001	<0.0001	0.0465	0.0407	0.0032	0.5010
Solution Mg^{+2}	0.7464	<0.0001	<0.0001	0.0002	0.0064	0.0062	0.2750
Solution K^+	0.9075	0.0101	0.0040	0.2807	0.0090	0.0008	0.8904
Solution Na^+	<0.0001	<0.0001	<0.0001	0.2744	0.0069	<0.0001	0.8158

Pos: position; Trt: treatment.

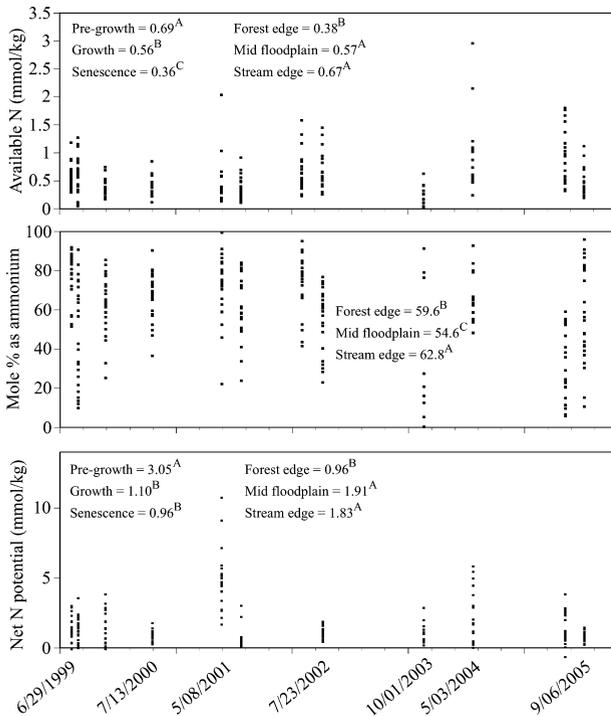


FIG. 1. Graphic summary of available N, molar proportion of available N as ammonium, and net 30-day N mineralization potentials for each measurement time. Data inside each panel show significant ($P \leq 0.05$) main effect differences caused by season and floodplain position.

between the grazed or ungrazed treatments. The molar proportion of available N as ammonium was influenced by a significant treatment \times floodplain position \times time interaction (Table 3; Fig. 1). Surprisingly, the molar proportion as ammonium was statistically similar among seasons, averaging 60.3, 61.0, and 55.5, respectively, for pre-growth, growth, and senescence. The highly significant time \times treatment interaction largely occurred because on October 1, 2003, ungrazed sites averaged 46.4 and grazed averaged 8.0. Overall, the molar proportion as ammonium was significantly greater on stream edge position, followed by forest edge and midfloodplain positions. A significant interaction among treatment, floodplain position, and time affected net 30-day N mineralization potentials (Table 3; Fig. 1). Net N mineralization potential of soil was greatest when collected pre-growth and declined significantly in the plant growth and plant senescence seasons. The stream edge and midfloodplain positions had greater net N mineralization potentials than the forest edge location. On May 8, 2001, the grazed treatment had significantly greater net N mineralization potential (5.7 mmol/kg) than ungrazed sites (4.1 mmol/kg).

Enzyme activities of amidase and urease and pH were all significantly influenced by a significant interaction among treatment, floodplain position, and time (Table 3; Fig. 2). Overall, amidase activity was greater in ungrazed than grazed treatments; the greatest differences occurred in midfloodplain positions (ungrazed, 16.9 $\mu\text{mol/g/h}$; grazed, 13.6 $\mu\text{mol/g/h}$). Differences among season, treatment, or floodplain position were small; however, amidase activity was significantly greater during the pre-growth season and in midfloodplain positions. Controlling the significant three-way interaction for both amidase and urease was that on May 3, 2004, ungrazed midfloodplain positions had

greater enzyme activities than grazed stream edge positions. Overall, urease activity was least during the growing season and greatest in midfloodplain positions. Soil pH trended downward with time and was greatest during the plant growth season and in midfloodplain positions.

Acetate-extractable nutrient pools of Ca and Mg varied considerably by time and floodplain position (Table 3; Fig. 3). The three-way interactions for Ca and Mg are complex, but the most important aspect is that during the measurement period of 6 years, extractable Ca and Mg (also K and Na) differed significantly among sampling dates. Extractable Ca and Mg were least in forest edge positions and were statistically similar among seasons. The significant date by treatment interaction for Ca is controlled by the dates July 13, 2000 (grazed, 74.6 mmol/kg; ungrazed, 85.9 mmol/kg) and June 8, 2005 (grazed, 65.0 mmol/kg; ungrazed, 73.2 mmol/kg). The significant date \times treatment interaction for Mg is controlled by the dates July 13, 2000 (grazed, 19.4 mmol/kg; ungrazed, 23.3 mmol/kg) and August 7, 2001 (grazed, 18.2 mmol/kg; ungrazed, 20.9 mmol/kg). Acetate-extractable K was affected by time (Table 3; Fig. 3). When these data are grouped by growth season, acetate-extractable K was significantly greater during plant senescence. Like Ca and Mg, extractable K was least in forest edge floodplain positions. The grazed treatment had significantly greater acetate-extractable Na than did the ungrazed sites (Table 3; Fig. 3). Extractable Na was greatest in the spring and summer season and declined significantly in the fall season.

Acetate-extractable data, presented on a mole percentage basis, were highly affected by treatment, time, and floodplain position (Table 3; Fig. 4). The interactions are complex but can be summarized as follows. First, the mole percentages of all cations vary markedly during the 6 years of the study; but most

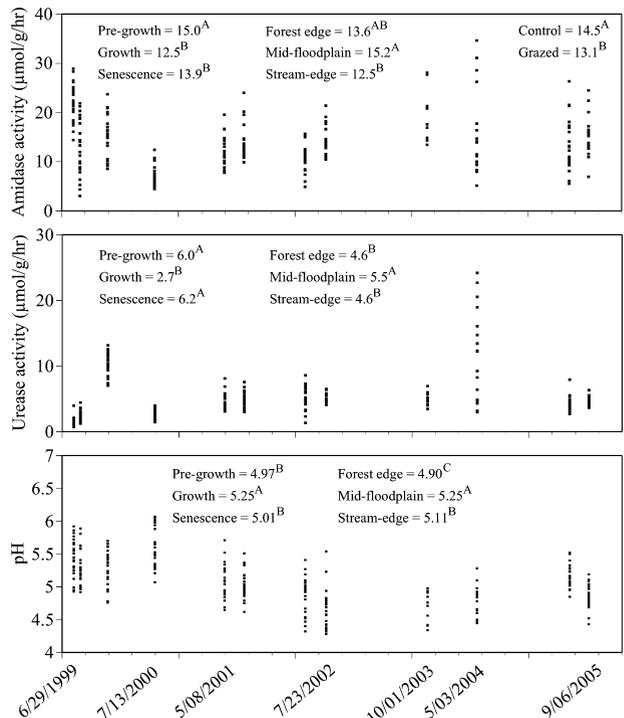


FIG. 2. Graphic summary of enzyme activities of amidase and urease and soil pH for each measurement time. Data inside each panel show significant ($P \leq 0.05$) main effect differences caused by season, floodplain position, and treatment.

interestingly, mole percentages of K and Na change reciprocally by season. During plant senescence, the mole proportion of K on the exchanger was greatest, relative to other seasons, whereas Na was the least. Second, the mole percentage of Na on the exchanger phase was significantly greater for the grazed treatment than the ungrazed treatment. Third, the mole percentages of K and Na reciprocally change with floodplain location: from stream edge to forest edge, mole percentages of K significantly increased, whereas Na significantly decreased.

Cations in the soil solution were affected by treatment, season, and floodplain position (Table 3; Fig. 5). Soil solution Ca^{+2} and Mg^{+2} were greatest during pre-growth and growth seasons then significantly declined during plant senescence. The forest edge floodplain position had the least solution Ca^{+2} relative to the other positions. Solution Mg^{+2} was greatest in midfloodplain positions, and in those positions, was significantly greater on the grazed treatment (0.14 mmol/L) than on controls (0.11 mmol/L). On August 7, 2001, the grazed treatment had significantly more K^+ (0.082 mmol/L) than the controls (0.033 mmol/L). The significant time by floodplain position interaction for K^+ was manifested as such: on August 7, 2001, the midfloodplain position had significantly greater K^+ (0.105 mmol/L) versus the forest edge position (0.044 mmol/L) or

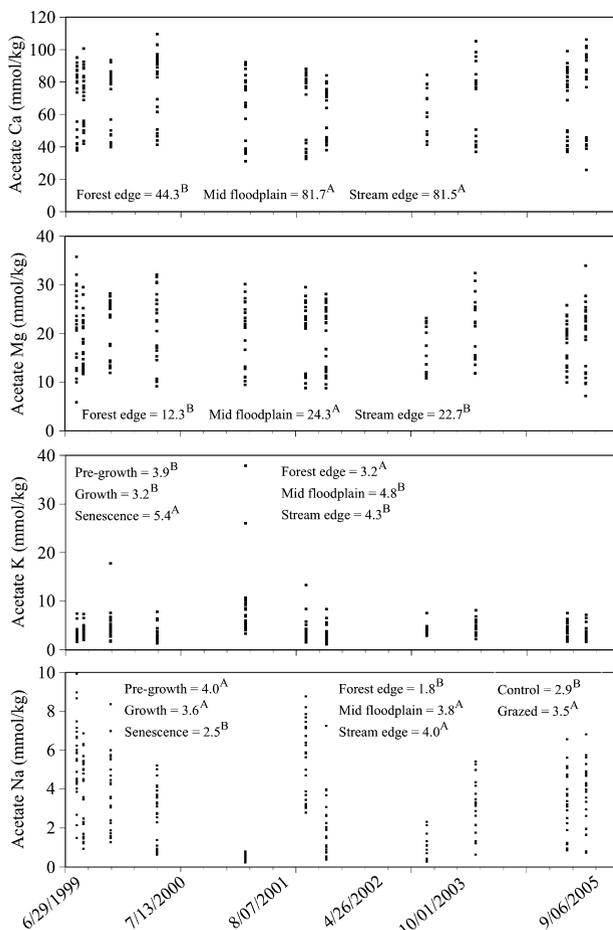


FIG. 3. Graphic summary of acetate-extractable pools of Ca, Mg, K, and Na for each measurement time. Data inside each panel show significant ($P \leq 0.05$) main effect differences caused by season, floodplain position, and treatment.

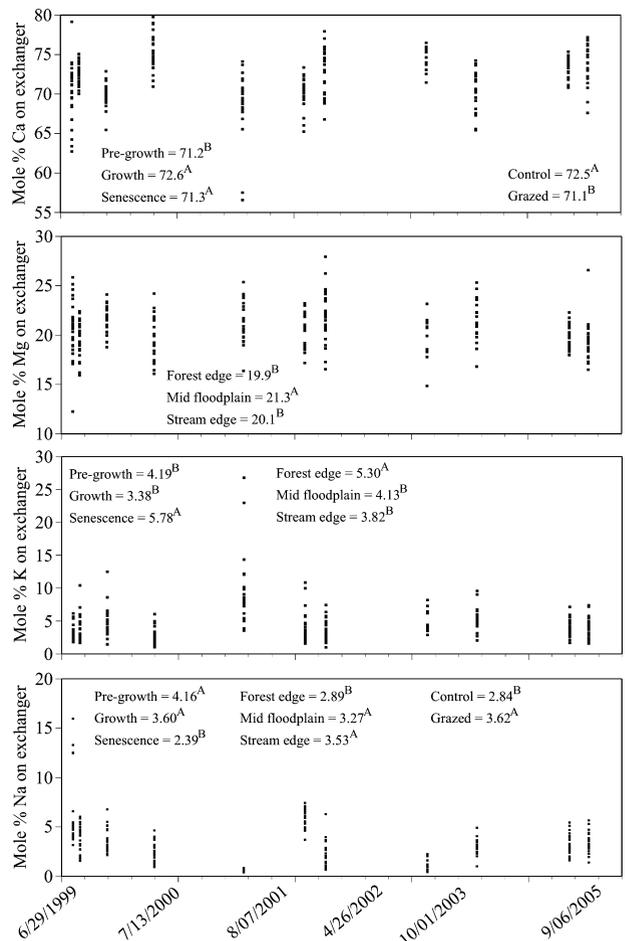


FIG. 4. Graphic summary of molar proportion of Ca, Mg, K, and Na in the acetate-extractable pool for each measurement time. Data inside each panel show significant ($P \leq 0.05$) main effect differences caused by season, floodplain position, and treatment.

the stream edge position (0.023 mmol/L); on April 26, 2002, the forest edge position had significantly greater K^+ (0.070 mmol/L) versus the midfloodplain position (0.043 mmol/L) or the stream edge position (0.036 mmol/L). A significant time \times floodplain position interaction and a time \times treatment interaction affected soil solution Na^+ . On May 3, 2001, and July 23, 2002, the grazed treatment had significantly more Na^+ (0.38 mmol/L and 0.35 mmol/L) than the corresponding ungrazed treatment (0.27 mmol/L and 0.25 mmol/L). Overall, solution Na^+ was greatest during the pre-growth season and declined during the plant growth and senescence seasons.

Nutrient Availability Measured by Resin Capsules

Unlike bulk soil samples, which are a one-time measurement of nutrient availability, resin capsules integrate nutrient availability during the period they are inserted into the soil. Of all the nutrients quantified by resin capsules, only N was affected by grazing (Table 4; Fig. 6A). In an interaction with floodplain location, resin-extractable N was significantly lower on grazed midfloodplain positions (3.3 $\mu\text{mol/d}$) relative to the corresponding ungrazed sites (7.0 $\mu\text{mol/d}$). The molar proportions of Mg, K, Na, and Ca and total K on resin capsules were affected by a main

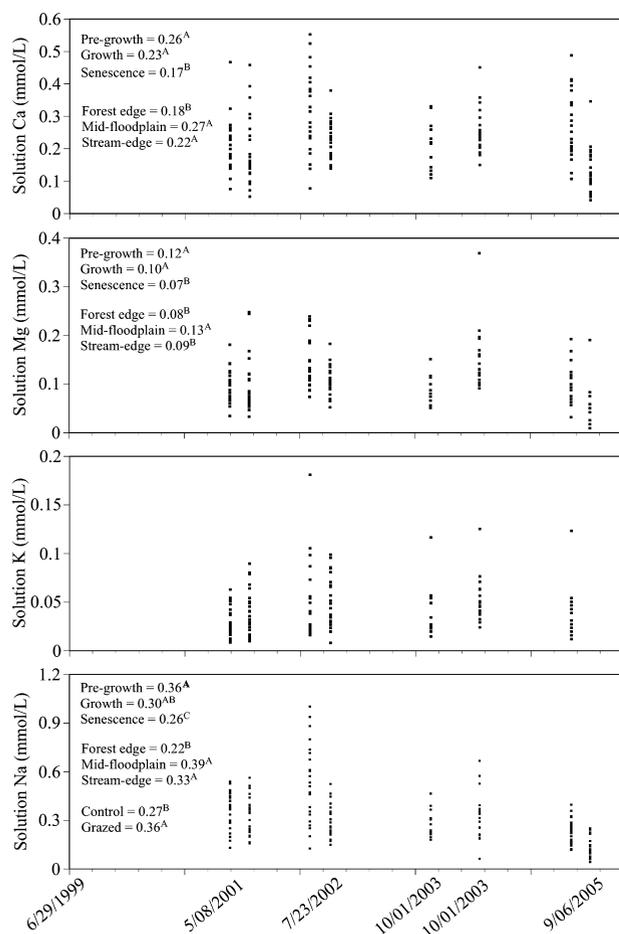


FIG. 5. Graphic summary of the soil-solution pools of Ca, Mg, K, and Na, for each measurement time. Data inside each panel show significant ($P \leq 0.05$) main effect differences caused by season, floodplain position, and treatment.

effect caused by season (Table 4; Fig. 6B). The molar proportion of Mg was least overwinter (9.7%) and increased significantly during plant growth (15.0%) and senescence (16.3%). Potassium and Na molar proportions behaved reciprocally with season. From

overwinter to plant senescence, K increased from 5.9% to 13.0% to 27.0%, whereas Na declined from 49.9% to 31.0% to 26.0%. Molar proportion of Ca was greatest during plant growth (40.1%) and significantly less overwinter (34.5%) and senescence (30.7%). The amount of K sorbed per day mimicked K on a molar proportion basis; least overwinter (0.14 $\mu\text{mol/d}$) and significantly increased during plant growth (0.39 $\mu\text{mol/d}$) and senescence (0.63 $\mu\text{mol/d}$). Most nutrients, measured by resin capsules, were affected by significant floodplain location by season interactions (Table 4; Fig. 6C). Resin-available Ca and Mg behaved similarly; overall least in stream edge and greatest in midfloodplain (wettest) positions. The controlling interaction of Ca and Mg was that in the plant growth season, resin availability was greatest in mid-floodplain positions. Overall, resin-available soil N significantly increased from overwinter and plant growth seasons to plant senescence, at which time, N was much higher in midfloodplain positions. Availability of P mimicked the pattern for N. Overall, resin-available Fe was least during senescence (0.007 $\mu\text{mol/d}$), somewhat greater overwinter (0.029 $\mu\text{mol/d}$), and far greater during plant growth (0.163 $\mu\text{mol/d}$). The interaction was controlled during the plant growth season, where the stream edge position had far less available Fe (0.009 $\mu\text{mol/d}$) than the midfloodplain (0.159 $\mu\text{mol/d}$) or forest-edge positions (0.194 $\mu\text{mol/d}$). Overall, greatest Mn availability occurred during plant growth (0.0047 $\mu\text{mol/d}$), and unlike Fe, was only slightly less during overwinter (0.0030 $\mu\text{mol/d}$) and senescence (0.0033 $\mu\text{mol/d}$). Like Fe, the interaction term was controlled during the plant growth season, where the stream edge site had significantly less Mn (0.0014 $\mu\text{mol/d}$) than the midfloodplain (0.0076 $\mu\text{mol/d}$) or forest edge (0.0058 $\mu\text{mol/d}$) positions.

DISCUSSION

General Considerations

This study was conducted on the upper reaches of Big Grizzly Creek, a stringer montane meadow system. Lack of replication in other meadow systems limits the scope of geographic interpretation; however, the studied meadow is typical of those forming in andesitic provinces in the northern Sierra Nevada and Modoc Plateau of northern California (Graham and O'Geen, 2010). These meadow systems are biogeochemically open and flooding after snowmelt can both remove, add, and relocate plant litter, organic detritus, and soil (Xiong and Nilsson, 1997). Moreover, considerable nutrients, especially N and P, can be added through snowfall (Sickman et al., 2003). Except for the

TABLE 4. ANOVA Analyses of Resin Capsule Data

Attribute	Trt	Pos	Sea	Trt × Pos	Trt × Sea	Pos × Sea	Trt × Pos × Sea
Mole % Mg	0.1699	0.0586	0.0001	0.2625	0.8122	0.9379	0.5644
Ca	0.3708	0.0184	0.0784	0.1705	0.0901	0.0108	0.2851
Mole % K	0.6081	0.1884	<0.0001	0.1337	0.0653	0.6332	0.6730
Total-N	0.0193	0.0380	<0.0001	0.0259	0.7685	0.0144	0.6533
Mole % Na	0.3884	0.0883	<0.0001	0.3158	0.0311	0.8160	0.2651
P	0.3393	<0.0001	<0.0001	0.2855	0.3430	0.0238	0.6846
Mole % Ca	0.5175	0.3771	<0.0001	0.1976	0.9405	0.0824	0.9304
Mg	0.9843	<0.0001	<0.0001	0.8468	0.2794	<0.0001	0.0901
K	0.7393	0.1960	0.0020	0.1295	0.8137	0.2106	0.2748
Fe	0.3165	<0.0001	<0.0001	0.6410	0.1942	<0.0001	0.5119
Mn	0.0258	<0.0001	<0.0001	0.1291	0.6063	<0.0001	0.0377

Pos: position; Sea: season; Trt: treatment.

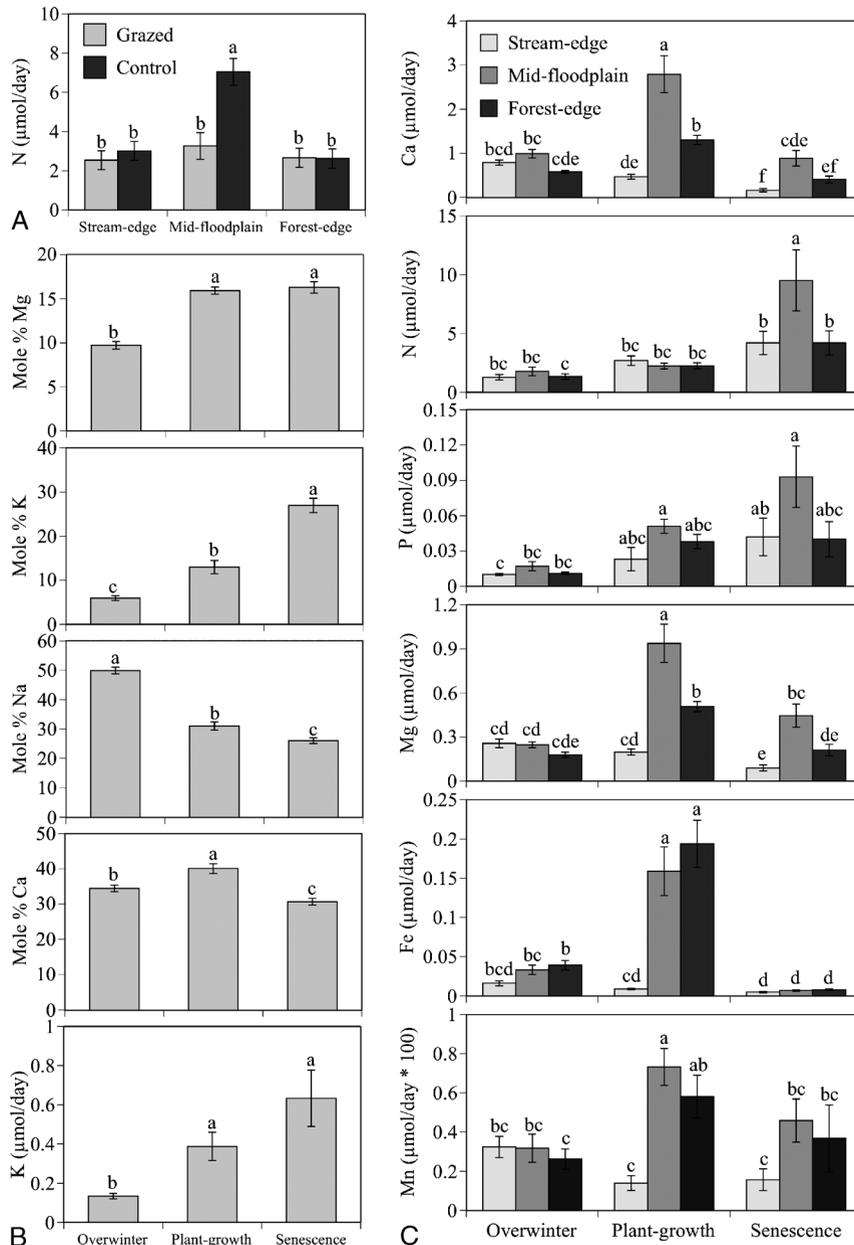


FIG. 6. Graphic summary of resin capsule data showing statistically significant main effects and interactions. For each panel, letters denote significant ($P \leq 0.05$) differences.

first year, this study was conducted in less-than-average precipitation (Table 1), which may have affected the measured values of some nutrients. Nonetheless, 6 years of data should provide strong statistical validity to the influence of grazing, season, and floodplain position on soil nutrient availability.

Grazing and Soil Nutrient Availability

If nutrient cycling becomes decoupled—mineralization exceeds uptake from roots or microbes—availability of nutrients such as N, S, and P can become elevated and place the system at risk to invasion by weedy species, altered successional trajectories, and decreases in species richness (Hobbs and Huenneke, 1992; Fleischner, 1994; Bedford et al., 1999). Livestock grazing, through physical disturbance such as trampling and vegetation

removal can enhance organic matter mineralization and the cycling of soil nutrients (Floate, 1981; Risser and Parton, 1982; Ladd et al., 1993; Holland et al., 1996). In addition, urine and feces from livestock can increase soil nutrient availability (Güsewell et al., 2005). In this study, on a wet montane meadow, the present grazing management plan—grazed about 1 month each year to use approximately 50% of the forage—minimally affected soil nutrient availability, no matter the seasonality of measurement, of N, P, Ca, or Mg relative to livestock-excluded areas. Moreover, we found no evidence that livestock grazing of the meadow reduced N mineralization potentials as had been reported (Kauffman et al., 2004). Furthermore, in our study, grazing did not increase net N mineralization potential of soil, as has been reported (Frank and Groffman, 1998). Low levels of

available soil N in this study indicate tight coupling of mineralization with root and microbial uptake and suggest that the present grazing management plan does not appreciably increase the risk of weedy plant invasion caused by excess available N. Biondini et al. (1998) reported that grazing pressure to remove less than 50% of net annual productivity sustains rangeland productivity and range condition.

Levels of extractable Na^+ (at senescence) and the proportion of Na^+ on clay exchange sites were significantly greater on grazed areas relative to ungrazed sites. In an earlier study on this meadow, higher levels of Na^+ were found in lysimeter water from grazed areas compared with ungrazed areas. We speculated that because livestock had access to salt blocks containing 97% to 98% NaCl, livestock urine and feces enriched the soil in Na^+ (Blank et al., 2006). Long-term manure application has been shown to increase soil salinity (Na^+) (Hao and Chang, 2003).

Season and Soil Nutrient Availability

As a general construct, mineralization of nutrients associated with the soil organic fraction increases as soil temperatures and water contents become optimal with the beginning of the growing season (Paul and Clark, 1989) but can be clouded by interactions with the soil microbial community and plant uptake (Schmidt et al., 1999). Given this relationship, intuitively, one would expect considerable differences in soil nutrient availability among seasons, at least for those controlled through organic matter mineralization such as N and P. In the pregrowth phase, cold soil temperatures limit mineralization. Indeed, resin-available N and P were least during the overwinter period. Bulk soil samples, however, had greatest N availability and net N mineralization potential during the pregrowth season. Moreover, in the plant growth season, when optimal moisture and soil temperatures should increase the kinetics of N and P mineralization, resin-available N only very slightly increased and resin-available P increased, but not significantly. For bulk samples taken during the plant growth season, available N significantly declined and availability of P differed depending on the pool measured; the extractable P pool declined and the soil solution pool increased. During plant senescence, resin-available N and P exhibited their greatest values, but only for midfloodplain positions. During the same season, bulk soil availability of N declined, soil solution P declined, and extractable P increased. An explanation of these complex and conflicting results should consider seasonal change in the proportion of N and P in microbial and plant biomass (Bardgett et al., 2002). In the former study, microbial biomass sequestered most N in the spring, but later in the growing season as soil mineralization rates increased, the proportion of soil N in roots surpassed that in microbial biomass. As plants senesced, microbes again increased their proportion of ecosystem N. Our resin capsule data generally support this model: low N and P in overwinter and pregrowth (low mineralization and sequestration by microbial biomass) and increasing N and P during plant growth (elevated mineralization and release from microbial biomass). The large increase in resin-available N and P during plant senescence on midfloodplain soil may be caused by retranslocation from aboveground tissue combined with root turnover (Chapin et al., 1975; Bernard et al., 1988).

A strong seasonal variation in availability of Fe and Mn occurred, but only for the midfloodplain and forest edge positions. Resin-available Fe was greatest during the growing season and far less during the overwinter and plant senescent seasons. Likewise, resin-available Mn was greatest during the plant growth season, but only slightly less in the other seasons. Solubility of Fe and Mn is strongly correlated to soil redox potential and pH

(Lindsay, 1979). Earlier research on the meadow indicated that the soil redox potential early in the growing season (late May to early June) approached -100 mV (Blank et al., 2006), which, combined with surface soil pH of near 5.0, suggests high solubility of Fe and Mn. In addition, plants may exude siderophores from roots and further increase the availability of Fe and Mn (Dakora and Phillips, 2002). The lack of season effect on the availability of Mn and Fe for the stream edge soil may be its relative dryness (caused by being a slightly elevated levee position) and lack of extended periods of reduced soil conditions, which would increase the solubility of Fe and Mn (Lindsay, 1979) compared with the other floodplain locations.

The content of extractable cations and their molar proportion on the exchange complex significantly varied by time of collection. In these acid soils, the extractable pool is likely dominated by cations on exchange sites (McBride, 1994). Given the relatively high cation exchange capacity of these soils (Table 2), it is somewhat surprising to note the significant variations in both content and molar proportion of cations during the 6 years of the study. We hypothesize that the extremely large root length densities, typical of *Carex/Juncus* meadows (Manning et al., 1989), may be a factor. In this scenario, year changes in the content and cation proportion in roots are sizable enough to affect the extractable pools.

Season strongly affected, in a reciprocal fashion, the molar proportion of K^+ and Na^+ on resin capsules as well as resin-available K. Relationships displayed for resin capsules were supported by bulk soil data, but not as pronounced. During overwinter, the proportion of resin K of the total cation pool was very low—averaged about 5%—and increased markedly as the soil warmed to average nearly 28% of the cation pool. The proportion of resin-available Na displayed an opposite relationship. We conducted laboratory experiments to clarify this temperature-related phenomenon and found that as soil temperature approaches 1°C , new sorption sites are created and the competitive sorptive behavior of Na^+ and K^+ differs with temperature (Blank, 2010). We conducted an extensive literature search and could find no information on this potentially important phenomenon. Basically, our field data and laboratory data suggest that K^+ is retained in the soil relative to Na^+ (and Mg^{+2}) when the soil is near freezing. This process is certainly fortuitous in these soils because it may retain the important macronutrient K^+ in the rooting zone during the snowmelt period.

Floodplain Position and Soil Nutrient Availability

Vegetation and hydrology change from stream edge to forest edge; thus, one would expect nutrient availability to change likewise. The stream edge position is a very slight levee, and vegetation is dominated by *Juncus balticus* and *Poa pratensis*, with lesser amounts of *Deschampsia caespitosa*. It is somewhat drier early in the growing season than the other positions and rarely has standing water during snowmelt. The midfloodplain position is dominated by *Carex nebrascensis* with lesser amounts of *Poa pratensis* and *Deschampsia caespitosa*. It is the wettest position and has periods of standing water for several weeks after snowmelt. Organic matter content in the surface soil horizons is the highest of all positions. In most years, the midfloodplain position has greater biomass production than the other positions. The forest edge position has the least organic matter content and is coarser textured than the other floodplain locations. Vegetation is dominated by *Juncus balticus*, but this position also has more forbs than the other positions. Snowmelt, from adjacent uplands, floods and saturates soil for periods of days to weeks during snowmelt, but this site also dries quicker during the growing season than the other positions.

High soil organic matter content and finer textured soils are a potential explanation of the generally greater nutrient availability, as quantified by bulk soil samples, of the stream edge and midfloodplain positions relative to the forest edge position. All things being equal, greater organic matter content offers the possibility of greater mineralization and availability of nutrients such as N and P (Schimel et al., 1985). Finer textured soils would generally have greater per weight basis of Ca^{+2} , Mg^{+2} , and K^{+} on exchange sites, which are a pool available to plant roots and microbes (Barber, 1995).

Resin Availability and Bulk Soil Availability—Are They the Same?

In this study, bulk soil samples and resin capsules were used to quantify nutrient availability. Bulk soil sampling describes nutrient availability only at the time of sampling and thus limits extrapolation beyond a few days before or after the sampling was done. Resin capsules integrate nutrient availability during the period they remain in the soil and somewhat mimic plant roots (Yang et al., 1991). Assuming they perform as an infinite sink, capsules will capture and sequester available soil nutrients in a sphere around whose diameter is influenced by individual diffusion coefficients and soil water content (Yang et al., 1991). In essence, resin capsules compete with roots and soil microflora for nutrients in the soil; thus, when roots, bacteria, and fungi are actively uptaking nutrients, resin capsules will underestimate true nutrient availability. Resin capsules have great use in this environment because they can integrate nutrient availability during the winter when heavy snowpacks make it difficult to sample the soil. This ability to quantify soil nutrient availability during overwinter periods is important because beneath a heavy snowpack, the soil seldom freezes and microbial processes can occur albeit at a reduced rate (Brooks et al., 1996).

The major reason resin capsules and extractions of bulk soil samples dissimilarly quantify nutrient availability may be caused by lysis of soil microbes. The osmotic strength of the KCl extractant is quite high; the authors typically use 1.5 M KCl. The authors were unable to find direct citations that report that such extracts can lyse microbial cells. The literature reports, however, that osmoticum of much lower strength can lyse *Staphylococcus aureus* (Yabu and Kaneda, 1995), and that commercial cell lysing products, such as New England BioLabs Cell lysis buffer no. 9803, contain only 150 mmol/L NaCl as an active osmotic agent. In summary, availability quantified by high osmotic strength extractants of bulk soil samples likely includes cell lysis components not integrated by resin capsules.

CONCLUSIONS

During a 6-year period, nutrient availability in a high-elevation montane meadow of the Sierra Nevada, CA, quantified using bulk soil samples and resin capsules, was dynamic and significantly varied by season of sampling and floodplain position. Relative to livestock-excluded paddocks, the present grazing management plan had a minimal impact on most pools of nutrient availability and did not cause elevated N availability at any measurement period. Surprisingly, the robust acetate-extractable cation pools considerably varied during the 6 years of the study, which may be controlled by the very high root length densities characteristic of montane meadows. Higher levels of extractable sodium in the grazed treatment may be tied to salt block supplementation. Nutrient pools in these meadow systems are dynamic and, in part, affected by nutrient additions *via* the snowpack and additions and deletions *via* litter and soil during spring flooding.

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