Regional analysis of inorganic nitrogen yield and retention in high-elevation ecosystems of the Sierra Nevada and Rocky Mountains

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Abstract. Yields and retention of dissolved inorganic nitrogen (DIN: $NO_3^- + NH_4^+$) and nitrate concentrations in surface runoff are summarized for 28 high elevation watersheds in the Sierra Nevada of California and Rocky Mountains of Wyoming and Colorado. Catchments ranged in elevation from 2475 to 3603 m and from 15 to 1908 ha in area. Soil cover varied from 5% to nearly 97% of total catchment area. Runoff from these snow-dominated catchments ranged from 315 to 1265 mm per year. In the Sierra Nevada, annual volume-weighted mean (AVWM) nitrate concentrations ranged from 0.5 to 13 μ M (overall average 5.4 μ M), and peak concentrations measured during snowmelt ranged from 1.0 to 38 μ M. Nitrate levels in the Rocky Mountain watersheds were about twice those in the Sierra Nevada; average AVWM NO_3^- was 9.4 μ M and snowmelt peaks ranged from 15 to 50 μ M. Mean DIN loading to Rocky Mountain watersheds, 3.6 kg ha⁻¹ yr⁻¹, was double the average measured for Sierra Nevada watersheds, 1.8 kg ha⁻¹ yr⁻¹. DIN yield in the Sierra Nevada, 0.69 kg ha⁻¹ yr⁻¹, was about 60% that measured in the Rocky Mountains, 1.1 kg ha⁻¹ yr⁻¹. Net inorganic N retention in Sierra Nevada catchments was 1.2 kg ha⁻¹ yr⁻¹ and represented about 55% of annual DIN loading. DIN retention in the Rocky Mountain catchments was greater in absolute terms, 2.5 kg ha⁻¹ yr⁻¹, and as a percentage of DIN loading, 72%.

A correlation analysis using DIN yield, DIN retention and surface water nitrate concentrations as dependent variables and eight environmental features (catchment elevation, slope, aspect, roughness, area, runoff, soil cover and DIN loading) as independent variables was conducted. For the Sierra Nevada, elevation and soil cover had significant (p < 0.1) Pearson product moment correlations with catchment DIN yield, AVWM and peak snowmelt nitrate concentrations and DIN retention rates. Log-linear regression models using soil cover as the independent variable explained 82% of the variation in catchment DIN retention, 92% of the variability in AVWM nitrate and 85% of snowmelt peak NO_3^- . In the Rocky Mountains, soil cover was significantly (p < 0.05) correlated with DIN yield, AVWM NO_3^- and DIN retention expressed as a percentage of DIN loading (%DIN retention). Catchment mean slope and terrain roughness were positively correlated with steam nitrate concentrations and nega-

tively related to %DIN retention. About 91% of the variation in DIN yield and 79% of the variability in AVWM NO_3^- were explained by log-linear models based on soil cover. A log-linear regression based on soil cover explained 90% of the variation of % DIN retention in the Rocky Mountains.

Introduction

Regional analyses of N budgets have shown that watershed characteristics such as runoff, elevation and atmospheric N deposition are related to watershed N export and provide a means of estimating N yields over broad areas (Howarth et al. 1996; Lewis in press). Lewis et al. (1999) found that yields of all N fractions were strongly related to runoff and runoff explained nearly 85% of the variance in yield of N in undisturbed forested and savanna catchments ranging in area from 0.1 to 5×10^6 km. Six alpine and subalpine watersheds from the Sierra Nevada were included in these analyses, but were found to form a distinctive cluster owing to their exceedingly low rate of N yield (i.e., less than 10% of the mean yield measured for the other study catchments).

In another analysis, using data from undisturbed temperate-zone watersheds of the United States (United States Geological Survey Hydrologic Benchmark Network), Lewis (in press) found an equally strong relationship between runoff and N yield. Based on this study, the rate of dissolved inorganic nitrogen (DIN: NO₃ + NH₄) yield from Sierra Nevada watersheds is less than 40% of the rate found in temperate zone watersheds with similar runoff and atmospheric N deposition. The finding that alpine and subalpine catchments export less N than temperate or tropical watersheds with similar characteristics is surprising since ecosystem retention of N may be constrained in high-elevation regions. Short growing seasons, extensive and deep snowcover and sparse vegetation result in low N retention capacity and a large temporal disconnection between N availability (spring snowmelt) and vegetative N demand (summer). Thus, alpine and subalpine watersheds seem to comprise a distinct population for studying the relationships between catchment characteristics and N yield and for evaluating the impact of increased N deposition.

Episodic declines in acid neutralizing capacity (ANC) have been observed in alpine and subalpine catchments and results largely from ionic dilution following an initial pulse of nitrate and base cations (Melack & Stoddard 1991; Stoddard 1995); episodic acidification (ANC values < 0) may occur when nitrate pulses are sufficiently large (Stoddard 1995; Leydecker et al. 1999). Increasing N deposition to alpine and subalpine ecosystems in the

Colorado Front Range has resulted in increases of DIN in surface waters and current modeling studies suggest that alpine tundra and subalpine forests may experience nitrogen saturation at N deposition greater than 4-6 kg N ha⁻¹ yr⁻¹ (Baron et al. 1994; Williams et al. 1996a; Heuer et al. 1999; Williams & Tonnessen 2000). To date, ecological changes from N deposition appear to be restricted to the Front Range, but as urbanization increases in and near the Rocky Mountains the extent of N-affected ecosystems may increase. In the Sierra Nevada, recent shifts in limitation of algal growth at Lake Tahoe and Emerald Lake have been associated with alterations in both N and P supply (Jassby et al. 1994; Sickman & Melack 1998; Sickman et al. unpublished data). Given the current status of high elevation ecosystems in the western United States and the likelihood that N deposition will increase (Galloway et al. 1994), it would be valuable to predict, on a regional basis, the N retention capacity of these ecosystems. If critical and target loads for nitrogen are to be determined, data from a regionally extensive set of catchments are required (Williams 1997; Williams & Tonnessen 2000). To date, however, there have been few process-level studies on N cycling in alpine and subalpine watersheds (e.g., Brooks et al. 1996, 1998; Meixner et al. 1998, 1999) of sufficient detail to model accurately the impact of increased N loading. Furthermore, it will be difficult to extrapolate results from plot-scale modeling studies to larger regions despite recent improvements in biogeochemical modeling (Baron et al. 1994; Kiefer & Fenn 1997; Magill et al. 1997) given the potentially large temporal and spatial variability of N sources, sinks and transformations at the landscape scale.

In contrast, there is a wealth of catchment-scale data on the input and loss of nitrogen from alpine and subalpine watersheds in the Sierra Nevada and Rocky Mountains. We propose that this information can provide a basis for predicting the N retention capacity of high elevation ecosystems over large areas. Nitrogen budgets for alpine and subalpine watersheds in the western United States have been accumulating since the early 1980s and the dataset is now of a size that allows for a statistical analysis of environmental and catchment features influencing the N retention capacity of high elevation ecosystems. Similar analyses, using variables such as runoff, catchment area and elevation, have been successful in predicting elemental fluxes and chemical concentrations in surface runoff across large regions and over a broad range of conditions (Meybeck 1982; Hedin et al. 1995; Howarth et al. 1996; Lewis et al. 1999).

Using previously published and unpublished data from high elevation watersheds in the western United States, we investigate the relationships between catchment N export and retention and seven watershed variables: elevation, watershed area, runoff, % soil cover, inorganic nitrogen loading,

and catchment aspect, slope and roughness. Our goal is to test the hypothesis that nitrogen yields, retention capacity and surface water chemistry (NO_3^-) can be predicted on the basis of general environmental and terrain variables in high elevation ecosystems. If successful, these variables will provide a basis for assessing the sensitivity of high elevation ecosystems to increased N deposition and may prove useful in regional-scale modeling of N biogeochemistry and setting of critical nitrogen loads.

Methods

Our statistical analyses are restricted to alpine and subalpine catchments of the Sierra Nevada and Rocky Mountains and to inorganic nitrogen budgets, i.e., inputs and losses of nitrate and ammonium. Little data are available on the fluxes of organic nitrogen in high elevation catchments, although there is growing evidence that organic N is an important component in atmospheric deposition and ecosystem nitrogen losses (Church 1999; Neff et al. in press). Current studies show that forested watersheds at low to middle elevations have high N retention rates and little DIN yield and, for that reason, are not included in our analyses.

Chemical data used were drawn primarily from previously published studies (Tables 1 and 2). For some Sierra Nevada catchments, fluxes were computed based on unpublished records of stream chemistry, stream discharge and loading using methods from Melack et al. (1998) (Table 1). In all cases the raw data were evaluated for completeness and quality. All catchments had comprehensive estimates of annual inorganic N loading in wet deposition and in some instances dry deposition (Table 3). In cases where no dry deposition estimates were available we conservatively assumed that dry N loading was 25% of wet inorganic N deposition; we based this percentage on dry deposition measurements made at Niwot Ridge and Emerald Lake (Sievering et al. 1996; Williams et al. 1995; Sickman et al. in press). Outflow DIN losses were based on at least biweekly chemistry during snowmelt runoff (the period of greatest N yield) and periodic sampling during the remainder of the year; for the majority of the Sierra Nevada catchments, automated samplers were used to collect samples every 1-2 days during snowmelt runoff. Data had to span at least one annual cycle to be included and in most cases several years were available (Table 1). Data from sub-regions (≥ 10 ha) of larger catchments were included in the analysis (e.g., Andrews Creek and Icy Brook) if measurements of N fluxes and surface water chemistry were available.

Table 1. Landscape characteristics of high elevation watersheds in the Sierra Nevada. Soil cover is expressed as a percentage of total catchment area. Mean slope and mode aspect are in degrees. Mean roughness is dimensionless

Catchment	Elevation	Area ha	Runoff mm yr ⁻¹	Soil Cover	Mean Slope	Mode Aspect	Mean Roughness	Years of Record	Sources 1
Crystal	2951	135	424	53%	21	105	42	1990–93	A
Emerald	2800	120	1120	22%	29	278	38	1985–98	A
Lost	2475	25	1210	36%	41	214	34	1990–93	A
Marble Fork-Kaweah	2621	1908	1245	40%	18	278	34	1993–94	A
Pear	2904	136	703	22%	24	281	37	1990–93	A
Ruby	3390	44	507	18%	27	108	42	1990–94	Ą
Spuller	3131	76	789	33%	22	09	37	1990–94	Ą
Topaz	3218	178	969	41%	10	108	32	1990–98	Ą
High	3603	15	811	2%	17	93	45	1993–94	В
Low	3444	225	976	8%	26	103	42	1993–94	В
M1	3078	106	1265	20%	18	318	36	1993–94	В
M2	3188	06	995	18%	11	315	39	1993–94	В
M3	3249	29	986	10%	11	360	39	1993–94	В
Mills	3554	177	912	%9	26	82	43	1993–94	В
Treasure	3420	175	989	10%	29	101	42	1993–94	В
Sierran Mean =	3135	260	882	23%	20	187	36		

¹Sources: A: Melack et al. 1998; B: Stoddard 1995, Sickman and Stoddard unpublished data

Independent variables

Watershed features used as independent variables in the statistical analyses, i.e., elevation, area, runoff and soil cover, were chosen because they were obtainable and are surrogates for complex environmental processes that are known to control N cycling in catchments. These processes include both the size of and fluxes between the major watershed nitrogen pools, the transit time and pathways for water movement and the degree of soil and groundwater flushing. Elevation (at catchment outlet) captures several catchment features including, vegetation biomass and type, length of growing season and vegetative N demand (Fisk et al. 1998). Area is a proxy for time and distance of N transport in a watershed (Lovett et al. 2000) and may provide a surrogate for hydrologic flowpaths and variable source-area dynamics; all of which exert control on nitrogen cycling in watersheds (Creed & Band 1998). Runoff reflects the amount of flushing experienced by catchment soil, the amount of water available to vegetation and soil moisture properties that may affect N processes such as denitrification; runoff is also highly correlated with precipitation. The rationale behind including soil cover in the analysis is based on several recent studies suggesting that soil microbial processes control N cycling in high elevation ecosystems (Brooks et al. 1999; Brooks & Williams 1999; Heuer et al. 1999). Soil cover was computed as a percentage of total catchment area. Soil depths and development are most likely positively related to soil area, thus soil area may approximate soil volume, soil N content and the magnitude of soil microbial N processes. Inorganic nitrogen loading (expressed in units of kg ha⁻¹ vr⁻¹) was included, because it provides a basis for testing whether current N loads are affecting surface water chemistry and N yields, and sets the baseline against which potential future increases in N loading may be gauged.

Three additional terrain indices, mean slope, mode aspect and mean roughness, were computed from the U.S. Geological Survey National Elevation Dataset (NED), and used as independent variables in the correlation analysis. The NED is a seamless, 30 m-resolution, gridded elevation dataset that has been filtered to minimize artifacts. Slope was calculated by fitting a plane to the elevation values of a 3 \times 3 neighborhood of cells around each NED cell; the direction the fitted plan faces is the aspect for the cell. Terrain roughness (Andrew et al. 1999) reflects variation in slope and aspect at each cell of the NED and was computed as follows:

$$R_{ij} = ((V_s/V_m)^*100) + ((A_n/8)^*100)$$

Where R_{ij} is the roughness at cell row i, column j; V_s is the standard deviation of slope in a 3 \times 3 cell neighborhood around cell ij; V_m is the maximum

standard deviation in slope for any 3×3 cell neighborhood for all of the 28 study watersheds; and A_n is the number of different aspect classes (binned into eight, 45 degree sectors) found within each 3×3 cell neighborhood. Any NED cell with a high variation in slope and many different aspect classes within the 3×3 cell neighborhood would have a high roughness value. The mean roughness value for each of the 28 watersheds was used in the correlation analysis.

Slope was included in the correlation analyses as a measure of the steepness of the catchment, which may influence hydrologic residence time or flow-routing in mountainous terrain (Clow & Sueker 2000). Aspect controls the input and distribution of solar radiation in a catchment (Dozier & Frew 1990) and may capture variations in the relative timing of snowmelt (Cline et al. 1998) and patterns of soil moisture which could effect N cycling (Sickman et al. in press). Mean roughness is a measure of the relative terrain complexity among the study sites and may provide an index for time and distance of N transport in a watershed, hydrologic flowpaths and residence time, and variable source-area dynamics.

Dependent variables

Five dependent variables were used in the statistical analyses: dissolved inorganic nitrogen yield (DIN: $NO_3^- + NH_4^+$), annual volume-weighted mean (AVWM) nitrate concentration, peak snowmelt nitrate concentration, and DIN retention (both net and % change). In cases where there was more than one year of data, we averaged the annual estimates to obtained a single value for each variable. Averaging was necessary in order to balance the influence of catchments with many years of data (i.e., Emerald and Loch Vale) with catchments with few years of data.

DIN yield is the amount of dissolved inorganic nitrogen exported via catchment outflow and was expressed in kg N ha⁻¹ yr⁻¹ (i.e., nitrogen fluxes are expressed in terms of the mass of elemental N and not compound mass). With the exception of Green Lakes #4, DIN yield was computed by the authors of the original study. DIN yield at Green Lakes #4 was computed from raw data (discharge and chemical concentrations) obtained from the Niwot Ridge LTER database. DIN yield estimates from the Hourglass catchments include only nitrate losses and were included because ammonium concentrations in high elevation watersheds are typically at or near the detection limit (Landers et al. 1987). Annual volume-weighted mean nitrate concentrations are discharge-weighted averages of outflow nitrate concentrations. In the case of Snake River and Deer Creek, AVWM nitrate was computed from nitrate yields and catchment runoff. For Green Lakes #4 we computed AVWM nitrate from raw data (discharge and chemical concentrations) obtained from

the Niwot Ridge LTER database. Peak nitrate concentrations were determined from time-series data during snowmelt runoff when available; the average of all available years was used for each catchment. The intensity of chemical sampling allowed us to make accurate estimates of peak concentrations at all catchments since peak concentrations occurred only slightly before peak runoff (i.e., 1 to 3 weeks). Nitrate concentrations were included in the analyses because they provide a means for judging the N saturation status of catchments and the degree of strong acid-anion acidification during snowmelt.

Inorganic nitrogen retention was computed by subtracting DIN yield from DIN loading. For the analyses we expressed retention both in absolute terms (net DIN retention: kg N ha $^{-1}$ yr $^{-1}$) and as a fraction of loading (% DIN retention: % of DIN loading). Expressing retention as a fraction of loading allowed us to compare the N retention efficiency of catchments with different N loading.

Correlation and regression procedures

Pearson product moment correlations were used to measure the strength of association between the dependent and independent variables within the Sierra Nevada and Rocky Mountain datasets. The Pearson correlations were tested with Bonferroni's method to evaluate the statistical significance of the associations. Due to the conservative nature of the test we assigned a threshold of p < 0.1 to determine whether variables were significantly correlated. Once significant correlations were identified, linear and log-linear models were developed between the dependent and independent variables using standard regression and multiple regression procedures. In the multiple regression analysis, multi-colinearity between independent variables was assessed by computing a variance inflation factor (VIF) to ensure that independent variables were not significantly correlated to one another.

We also performed a regression tree analysis (least squares fitting method: Systat version 7.01) on the pooled dataset (Rocky Mountain plus Sierra Nevada, n=26 to 28 depending on dependant variable; see Table 3) to determine whether the watershed and terrain variables could explain differences in dependant variables at larger spatial scales. Owing to our relatively small sample size, tree growth was severely constrained. Regression trees were limited to 5 end-nodes with a minimum of 4 catchments per node. The minimum proportional reduction in error allowed at any branch in the tree was 0.1.

The catchments used in the analysis are located in the alpine and subalpine zones of the Sierra Nevada of California and Rocky Mountains of Colorado and Wyoming. They capture a wide range of the geographic, geologic and hydrochemical variation among high elevation watersheds in the western United states (Tables 1 and 2). For the Sierra Nevada watersheds, elevations ranged from 2,475 m to 3,603 m and the mean elevation was 3,135 m (Table 1). The Rocky Mountain catchments were of similar elevation with an overall average outlet elevation of 3,186 m (Table 2). Soil coverage in the Sierra Nevada watersheds tended to be lower than in the Rocky Mountains; in all of the Sierra catchments, including those with higher soil coverage such as Crystal, most of the watershed was above treeline. The overall average soil percentage in Sierra Nevada catchments was 23% and ranged from 5 to 53% (Table 1). In the Rocky Mountains, average soil cover was 59% with a range from 5 to 97% (Table 2). In catchments with low soil coverage, talus and bedrock comprise the majority of the watershed area. Mean slope of the study catchments ranged from 10° to 29° in the Sierra Nevada and from 6° to 35° in the Rocky Mountains; the overall mean slope in each data set was 20° (Tables 1 and 2). Catchments in both mountain ranges had a wide variety of aspects (Tables 1 and 2). On average the Sierra Nevada catchments had higher terrain roughness (mean = 39) than the Rocky Mountain watersheds (mean = 34), although the most topographically complex watershed, Andrews Creek (R = 47), is located in the Rocky Mountains (Tables 1 and 2).

At all sites, precipitation fell predominately as snow during the winter and the accumulated snowpack underwent little melt or evaporative losses until spring snowmelt (Williams & Melack 1991; Leydecker & Melack 1999; Baron 1992). Rainfall was sparse, comprising on average about 10-25% of annual precipitation. The snowmelt period accounted for nearly all stream discharge and solute export; winter snowmelt in the Sierra Nevada accounted for less than 5% of annual runoff (Melack et al. 1998); we assume a similar relationship is true for the Rocky Mountains owing to comparable environmental conditions. Average catchment runoff was slightly higher in the Sierra Nevada (mean 882 mm) than in the Rocky Mountains (755 mm). The Emerald, Pear, Topaz and M-site watersheds are all located along the western slope of the southern Sierra Nevada within the Tokopah Valley of Sequoia National Park. This valley comprises the headwaters of the Marble Fork of the Kaweah River. Crystal and Spuller watersheds lie along the eastern slope of the central Sierra. Lost watershed is situated near the crest of the Sierra Nevada near Lake Tahoe. The remainder of the Sierra Nevada watersheds are located along the eastern slope within Rock Creek canyon. Mills and Low are nested subcatchments within the Ruby watershed.

Table 2. Landscape characteristics of high elevation watersheds in the Rocky Mountains. Soil cover is expressed as a percentage of total catchment area. ND = no data available. Mean slope and mode aspect are in degrees. Mean roughness is dimensionless

Catchment	Elevation m	Area ha	Runoff $mm ext{ yr}^{-1}$	Soil Cover	Years of Record	Mean Slope	Mode Aspect	Mean Roughness	Sources ¹
Loch Vale	3050	099	750	18%	1984–93	33	5	44	C
Icy Brook	3225	290	815	15%	1992	34	311	4	C, D
Andrews Creek	3300	160	1082	5%	1992	35	310	47	C, D
East Glacier	3282	29	029	81%	1988–90	10	171	35	ш
West Glacier	3276	19	1591	39%	1988–90	17	120	38	Щ
Rabbit Ears Pass	2910	200	609	95%	1991–92	9	198	32	Щ
Hourglass-Alpine	3192	66	1150	ND	1986–87	14	6	26	Ü
Hourglass-Subalpine	2871	924	720	ND	1986–87	16	6	24	Ü
Green Lakes #4	3550	200	857	20%	1985–93	27	341	39	H, I
East St. Louis	2878	803	315	95%	1987–88	18	310	29	'n
Fool Creek Alpine	3180	29	400	%16	1987–88	13	27	25	J
Snake River	3350	1040	430	%59	1996	22	279	30	×
Deer Creek	3350	1170	420	85%	1996	18	327	30	×
Rocky Mt. Mean =	3186	439	755	26%		20	186	34	

¹Sources: C: Baron & Campbell 1997; D: Campbell et al. 1995; E: Reuss et al. 1995; F: Peters & Leavesley 1995, N.E. Peters personal communication; G: Stednick 1989; H: Williams et al. 1996a; I: Niwot Ridge Long-term Ecological Database (BIR 9115097); J: Stottlemyer & Troendle 1992, R. Stottlemyer personal communication; K: Heuer et al. 1999.

Loch Vale watershed and its two subcatchments, Icy Brook and Andrew Creek, are located in Colorado Front Range of Rocky Mountain National Park. East and West Glacier watersheds are in the Glacier Lakes Ecosystem Experiment Site (GLEES) area of southeastern Wyoming. Rabbit Ears Pass watershed is situated in the North Fork Walton Creek basin southeast of Steamboat Springs, Colorado. The two Hourglass catchments are tributaries of the Cache la Poudre River and lie outside the northern boundary of Rocky Mountain National Park. Green Lake #4 is one of a series of lakes located near Niwot Ridge in the Colorado Front Range near Denver, Colorado. East St. Louis and Fool Creek are study areas in the Fraser Experimental Forest (FEF), 137 km west of Denver. The Snake and Deer Creek catchments are located west of the continental divide near FEF.

Results

Nitrate chemistry, DIN yields and DIN retention

On the whole both AVWM and peak nitrate concentrations were higher in the Rocky Mountains than in the Sierra Nevada. Average AVWM nitrate for the Sierra Nevada watersheds was 5.4 μ M and for the Rocky Mountain catchments it was 9.4 μ M (Table 3). Peak snowmelt concentrations averaged 14 μ M in the Sierra and 27 μ M in the Rocky Mountains. There was, however, a large overlap in these concentrations. Several of the highest elevation sites in the Sierra Nevada, High Lake, Low Lake and the M-sites, had nitrate concentrations greater than Rocky Mountain catchments located in Wyoming and west of the continental divide i.e., the GLEES watersheds, the Snake River and Dear Creek watershed. For the entire dataset, Loch Vale watershed and its subcatchments had the highest AVWM nitrate levels. Peak concentrations were greatest at Rabbit Ears Pass in the Rocky Mountains, 50 μ M, and at High Lake watershed in the Sierra Nevada, 38 μ M.

Atmospheric deposition of nitrogen in the Rocky Mountain dataset, 3.6 kg ha⁻¹ yr⁻¹, was double the rate measured for the Sierra Nevada catchments, 1.8 kg ha⁻¹ yr⁻¹ (Table 3). Atmospheric N deposition to catchments along the Front Range of the Rocky Mountains has increased over the past decade, and at Niwot Ridge, N loading as high as 7 kg ha⁻¹ yr⁻¹ has been measured in recent years (Fenn et al. 1998).

DIN export from the Rocky Mountain catchments, 1.1 kg ha⁻¹ yr⁻¹, was greater than the rate of 0.69 kg ha⁻¹ yr⁻¹ measured for the Sierra Nevada watersheds. The Loch Vale watersheds and subcatchments stand out with yields in the range of 1.7 to 3.1 kg ha⁻¹ yr⁻¹. In the Sierra Nevada, relatively high DIN yields, 1.2 to 1.5 kg ha⁻¹ yr⁻¹, were measured at High Lake, Low

Table 3. Nitrogen chemistry and fluxes in high elevation watersheds in the Sierra Nevada and Rocky Mountains. Units for nitrate concentration are μ M. Units for inorganic N (DIN) and dissolved inorganic N (DIN) are kg N ha⁻¹ yr⁻¹. Data for outflow mean nitrate are annual volume-weighted means. Outflow peak nitrate is the highest nitrate concentration measured during the annual snowmelt nitrate pulse. ND = no data available

Catchment	Outflow Mean NO ₃	Outflow Peak NO ₃	DIN Load	DIN Yield	Net DIN Retention	% DIN Retention
Sierra Nevada:						
Crystal	0.5	1.0	2.0	0.03	2.0	98%
Emerald	4.9	7.0	2.6	0.80	1.8	69%
Lost	0.6	1.8	2.1	0.13	2.0	94%
Marble Fork-Kaweah	2.4	6.0	2.0	0.43	1.5	78%
Pear	4.0	9.0	2.5	0.40	2.1	84%
Ruby	4.1	11	1.5	0.32	1.2	79%
Spuller	4.1	13	1.8	0.44	1.4	76%
Topaz	1.8	1.5	2.4	0.18	2.3	93%
High	13	38	1.2	1.5	-0.3	-24%
Low	9.6	24	1.2	1.3	-0.1	-7%
M1	4.6	17	2.1	0.98	1.1	53%
M2	6.5	16	1.9	0.83	1.1	57%
M3	7.1	22	1.9	0.95	1.0	51%
Mills	9.3	22	1.2	1.2	0.0	0%
Treasure	8.9	17	1.1	0.82	0.3	27%
Sierran Mean =	5.4	14	1.8	0.69	1.2	55%
Rocky Mountains:						
Loch Vale	16	27	c 3.9	1.7	2.2	56%
Icy Brook	22	32	c 3.9	2.2	1.7	43%
Andrews Creek	24	38	c 3.9	3.1	0.8	21%
East Glacier	0.6	15	^{ab} 2.6	0.08	2.5	97%
West Glacier	4.9	30	^{ab} 4.9	1.25	3.6	74%
Rabbit Ears Pass	9.9	50	^{ab} 2.8	0.69	2.1	75%
Hourglass-Alpine	11	ND	ND	1.8	ND	ND
Hourglass-Subalpine	5.2	ND	ND	0.55	ND	ND
Green Lakes #4	13	30	^{ab} 5.9	1.6	4.3	73%
East St. Louis	2.1	ND	a 3.2	0.14	3.1	96%
Fool Creek Alpine	1.0	ND	a 3.9	0.14	3.7	96%
Snake River	5.7	5.7	b 2.3	0.54	1.8	77%
Deer Creek	7.1	16	^b 1.9	0.39	1.5	79%
Rocky Mt. Mean =	9.6	27	3.6	1.1	2.5	72%

^aDry deposition was not measured directly but assumed to equal 25% of wet deposition.

^bDIN loading was estimated by a combination of snow surveys and NADP data.

^cDIN loading was estimated from NADP data.

Lake and Mills; these catchments are adjacent to one another and located along the eastern slope of the Sierra Nevada in the Rock Creek drainage. Other Rock Creek catchments such as Ruby and Treasure, had yields similar to watersheds along the western slope of the Sierra: < 1.0 kg ha⁻¹ yr⁻¹.

Despite higher rates of N loading, the Rocky Mountain catchments were more efficient at retaining DIN than the Sierra Nevada watersheds. Overall net DIN retention for the Rocky Mountain dataset was 2.5 kg ha⁻¹ yr⁻¹, which represents 72% of loading. In the Sierra Nevada, overall DIN retention was 1.2 kg ha⁻¹ yr⁻¹ or 55% of DIN loading. At several locations, including the GLEES watersheds, catchments in the Fraser Experimental Forest (East St. Louis and Fool Creek), and the Crystal, Lost and Topaz watersheds, DIN retention was greater than 90%. At the other extreme, three Sierra Nevada watersheds, High, Low and Mills, had no retention or had a net export of DIN, i.e., losses of DIN exceeded inputs. The negative retentions at Low Lake watershed are within the expected errors for the N budgets; however, the net DIN export at High Lake is well outside these errors (errors for fluxes were estimated by combining error in analytical chemistry, waters fluxes and sampling frequency using standard error propagation techniques, see Sickman et al. in press and Melack et al. 1998). For the Rocky Mountain sites, the Loch Vale catchments retained the lowest percentage of DIN loading, i.e., 21 to 56%.

Correlations and regression analysis

Prior to using the independent variables in the correlation and regression analyses, we tested for significant correlations among these variables (Tables 4 & 5). For the Sierra Nevada, elevation was found to be negatively correlated with DIN loading (Pearson r = -0.755, Bonferroni p = 0.032) and positively correlated with catchment roughness (Pearson r = 0.71, Bonferroni p = 0.079). The relationship between elevation and roughness is intuitive and demonstrates that topographic complexity generally increases with elevation in the Sierra Nevada. The negative correlation between elevation and DIN loading probably results because of the cluster of watersheds in the Rock Creek basin (i.e., Ruby, Low, Mills, Treasure, High) which are at high elevation but receive lower rates of DIN loading. The correlation between elevation and soil cover in the Sierra Nevada (Pearson r = -0.693, p = 0.118) was nearly significant and suggests that soil cover generally decreases with elevation.

In the Rocky Mountains soil cover was negatively correlated with both mean slope (Pearson r = -0.885, Bonferroni p = 0.008) and mean roughness (Pearson r = -0.933, Bonferroni p = 0.001), suggesting that steeper, more topographically complex watersheds contain less soil (Table 5). Mean

Table 4. Summary of Pearson Product Moment correlations and Bonferroni probabilities among catchment landscape features for his helevation watersheds of the Sierra Nevada Sionificant correlations (n < 0.1) are underlined

			ı				
	Elevation	Area	Runoff	Soil Cover	DIN Loading	Mean Slope	Mode Aspect
Pearson Correlation:							
Area	-0.348						
Runoff	-0.448	0.272					
Soil Cover	-0.693	0.299	-0.103				
DIN Loading	-0.755	-0.015	0.138	0.654			
Mean Slope	0.185	-0.004	-0.306	-0.262	-0.208		
Mode Aspect	0.132	-0.032	0.250	-0.283	0.010	-0.238	
Mean Roughness	0.713	-0.293	-0.457	-0.598	-0.716	0.482	-0.035
Bonferroni Probability:							
Area	1.000						
Runoff	1.000	1.000					
Soil Cover	0.118	1.000	1.000				
DIN Loading	0.032	1.000	1.000	0.227			
Mean Slope	1.000	1.000	1.000	1.000	1.000		
Mode Aspect	1.000	1.000	1.000	1.000	1.000	1.000	
Mean Roughness	0.079	1.000	1.000	0.520	0.075	1.000	1.000

slope was also positively correlated with mean roughness (Pearson r = 0.778, Bonferroni p = 0.048).

The correlation analysis showed that soil cover was strongly related to stream nitrate concentrations, DIN yield and DIN retention for watersheds in both the Sierra Nevada and Rocky Mountains (Tables 6 and 7). In addition, elevation showed strong correlations with nitrate concentrations and DIN retention for Sierra Nevada catchments. No significant relationships were found between elevation and any dependent variables in the Rocky Mountains. As was the case with the correlation between DIN loading and elevation, the cluster of sites in the Rock Creek basin is probably responsible for the negative correlation between DIN loading and nitrate concentrations observed within the Sierra dataset (Table 6).

In the Rocky Mountains, mean slope was positively correlated with the DIN yield and AVWM nitrate, and mean roughness was positively related to AVWM nitrate; both of these topographic indices were negatively correlated with % DIN retention (Table 7). In contrast, there were no statistically significant correlations between the topographic indices and dependant variables in the Sierra Nevada (Table 6).

DIN yield was positively related to elevation in the Sierra Nevada, although the linear model did not explain a majority of the variation in DIN yield (Figure 1(a)). Soil cover was negatively correlated with DIN yield. Loglinear models using soil cover were good predictors of DIN yield for both the Sierra Nevada and Rocky Mountain watersheds; 82-91% of the variation in yield was explained by these log-linear equations (Figure 1(b)). The slopes of the regression equations between soil cover and DIN yield were significantly different (p < 0.05) and show that DIN yield in the Rocky Mountains increased more rapidly as soil cover declined than it did in the Sierra Nevada Net DIN retention was inversely related to elevation and positively related to soil cover in the Sierra dataset (Figures 2(a) & (b)). No significant relationship was found between net DIN retention and catchment features in the Rocky Mountains. For the Sierra Nevada catchments, asymptotes of DIN retention $(\sim 2.0 \text{ kg ha}^{-1} \text{ yr}^{-1})$ occurred in catchments below ca. 3000 m elevation and > 25% soil cover. Zero or negative retentions were found in high elevation catchments with sparse soils.

In the Sierra Nevada, %DIN retention generally decreased with elevation (Figure 3(a)). The effect of soil cover on DIN retention was similar in the Sierra Nevada and Rocky Mountains when DIN retention was expressed as a percentage of DIN loading (Figure 3(b)). Percent DIN retention declined with decreasing soil cover in a logarithmic fashion with a high degree of overlap between the two mountain ranges. Natural logarithmic models using soil cover explained about 87% and 90% of the variation in %DIN reten-

Table 5. Summary of Pearson Product Moment correlations and Bonferroni probabilities among catchment landscape features

	Elevation	Area	Runoff	Soil Cover	DIN Loading	Mean Slope	Mode Aspect
Pearson Correlation:							
Area	-0.202						
Runoff	0.257	-0.552					
Soil Cover	-0.303	0.179	-0.655				
DIN Loading	0.313	-0.566	0.619	-0.480			
Mean Slope	0.391	0.019	0.221	-0.885	0.433		
Mode Aspect	900.0	0.398	-0.140	-0.295	0.263	0.504	
Mean Roughness	0.427	-0.389	0.428	-0.933	0.518	0.778	-0.065
Bonferroni Probability:							
Area	1.000						
Runoff	1.000	1.000					
Soil Cover	1.000	1.000	0.800				
DIN Loading	1.000	1.000	1.000	1.000			
Mean Slope	1.000	1.000	1.000	0.008	1.000		
Mode Aspect	1.000	1.000	1.000	1.000	1.000	1.000	
Mean Roughness	1.000	1.000	1.000	0.001	1.000	0.048	1.000

Table 6. Summary of Pearson Product Moment correlations and Bonferroni probabilities between N fluxes, N retention and nitrate concentrations and catchment landscape features for high elevation watersheds of the Sierra Nevada. Significant correlations (p < 0.1) are underlined. No correlations are shown between DIN loading and DIN retention because loading is used in the computation of retention

	DIN Yield	AVWM NO ₃	Peak NO ₃	Net DIN Retention	% DIN Retention
Pearson Correlation:					
Elevation	0.644	0.787	0.750	-0.769	-0.740
Area	-0.193	-0.242	-0.240	0.104	0.175
Runoff	0.284	-0.008	0.061	-0.084	-0.088
Soil Cover	-0.867	-0.901	-0.848	0.836	0.829
DIN Loading	-0.665	-0.781	-0.747	_	_
Mean Slope	0.134	0.223	0.051	-0.189	-0.201
Mode Aspect	0.027	0.231	0.319	-0.175	-0.097
Mean Roughness	0.570	0.716	0.671	-0.700	-0.686
Bonferroni Probability:					
Elevation	0.385	0.020	0.052	0.032	0.065
Area	1.000	1.000	1.000	1.000	1.000
Runoff	1.000	1.000	1.000	1.000	1.000
Soil Cover	0.001	0.000	0.003	0.004	0.005
DIN Loading	0.273	0.024	0.056	_	_
Mean Slope	1.000	1.000	1.000	1.000	1.000
Mode Aspect	1.000	1.000	1.000	1.000	1.000
Mean Roughness	1.000	0.107	0.248	0.147	0.189

tion for the Sierra Nevada and Rocky Mountains, respectively. The slopes of the equations were significantly different (p < 0.05) and show that retention increased more rapidly in the Sierra Nevada with expanded soil cover than in the Rocky Mountains. Based on the log-linear models, 80% retention was reached in the Sierra Nevada with catchment soil cover of 30%, whereas this threshold was reached in the Rocky Mountains when soils covered 60% of catchment area.

Annual VWM nitrate concentrations were predictable on the basis of elevation and soil cover in the Sierra Nevada and on the basis of soil cover in the Rocky Mountains (Figures 4(a) and (b)). In the Sierra Nevada, AVWM nitrate increased with elevation ($R^2 = 0.62$). In both mountain ranges, AVWM nitrate decreased in a logarithmic fashion as soil cover increased; these models

Table 7. Summary of Pearson Product Moment correlations and Bonferroni probabilities between N fluxes, N retention and nitrate concentrations and catchment landscape features for high elevation watersheds of the Rocky Mountains. Significant correlations (p < 0.1) are underlined. No correlations are shown between DIN loading and DIN retention because loading is used in the computation of retention

	DIN Yield	AVWM NO ₃	Peak NO ₃	DIN Retention	% DIN Retention
Pearson Correlation:					
Elevation	0.292	0.124	-0.514	0.104	-0.172
Area	-0.341	-0.096	-0.598	-0.367	0.110
Runoff	0.624	0.361	0.391	0.166	-0.481
Soil Cover	-0.924	-0.840	-0.213	0.326	0.881
DIN Loading	0.510	0.294	0.396	_	
Mean Slope	0.765	0.823	0.036	-0.301	-0.811
Mode Aspect	0.294	0.360	-0.130	-0.000	-0.280
Mean Roughness	0.741	0.842	0.419	-0.279	-0.847
Bonferroni Probability:					
Elevation	1.000	1.000	1.000	1.000	1.000
Area	1.000	1.000	1.000	1.000	1.000
Runoff	0.911	1.000	1.000	1.000	1.000
Soil Cover	0.002	0.049	1.000	1.000	0.014
DIN Loading	1.000	1.000	1.000		_
Mean Slope	0.092	0.074	1.000	1.000	0.098
Mode Aspect	1.000	1.000	1.000	1.000	1.000
Mean Roughness	0.149	0.046	1.000	1.000	0.040

explained about 80–90% of the variation in AVWM. The increase in AVWM nitrate with declining soil cover was more rapid in the Rocky Mountains relative to the Sierra Nevada. The inverse relationship observed between DIN loading and AVWM nitrate concentrations is counter-intuitive and is likely an artifact of the cluster of watersheds in the Rock Creek basin which exhibit high nitrate concentrations while receiving lower rates of DIN deposition.

The regression-tree results are summarized in Table 8. In the case of DIN yield, peak nitrate and %DIN retention, DIN loading and soil cover were first and second branching-variables, respectively, in tree growth; these models explained from 72 to 87% of the variation in the dependant variables. A five node tree using DIN loading, elevation and soil cover explained 92% of the variation in DIN retention. For AVWM nitrate, mean roughness was the primary branch-variable in the regression tree.

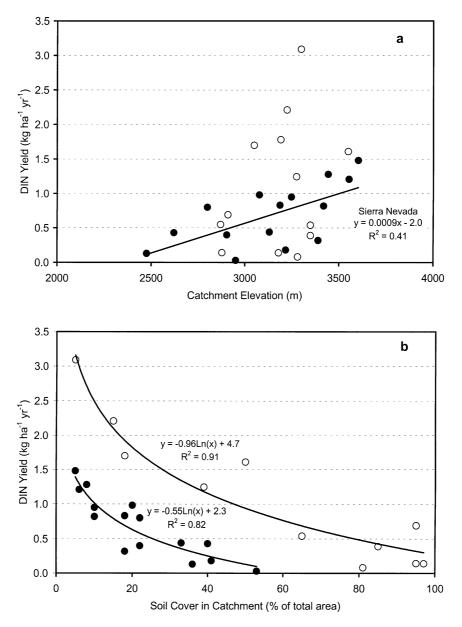


Figure 1. Relationship between catchment DIN yield and elevation and soil cover for high elevation watersheds of the Sierra Nevada (\bullet) and Rocky Mountains (\circ).

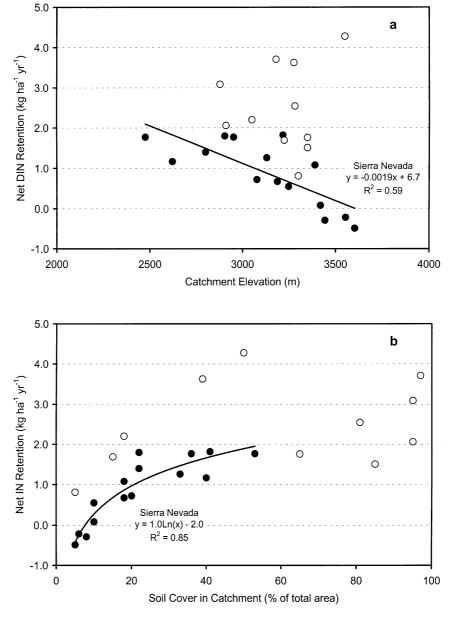


Figure 2. Relationship between net catchment IN retention (i.e., IN loading – DIN yield) and elevation and soil cover for high elevation watersheds of the Sierra Nevada (\bullet) and Rocky Mountains (\circ).

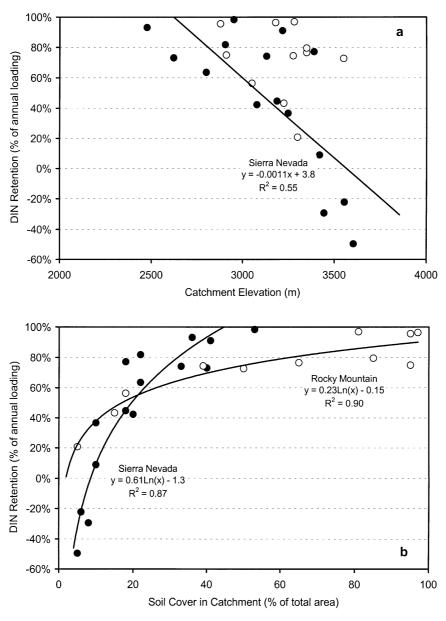


Figure 3. Relationship between percent catchment IN retention (i.e., net I N retention \div IN loading) and elevation and soil cover for high elevation watersheds of the Sierra Nevada (\bullet) and Rocky Mountains (\circ).

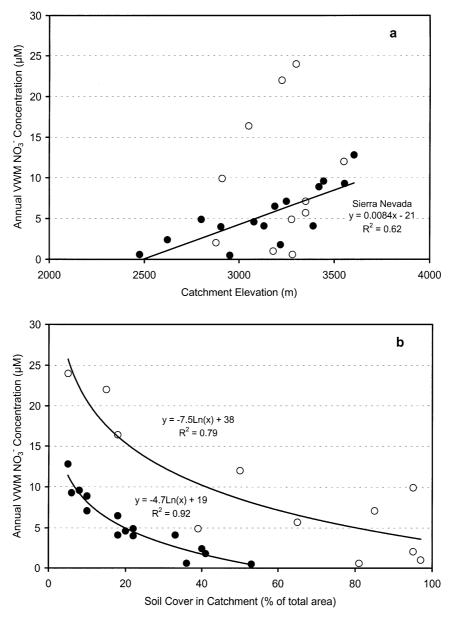


Figure 4. Relationship between the annual volume-weighted mean nitrate concentration in catchment outflow and elevation and soil cover for high elevation watersheds of the Sierra Nevada (\bullet) and Rocky Mountains (\circ) .

Table 8. Summary of regression-tree analysis of pooled Rocky Mountain and Sierra Nevada data sets (n = 26 to 28). Independent variables used in the analysis were: DIN loading (L), elevation (E), %soil cover (S), terrain roughness (R), area, slope, and runoff. Branching variables are shown in order. Tree growth was limited to 5 end-nodes and a minimum of 4 catchments per end-node. The minimum proportional reduction in error allowed at any tree-branch was 0.1

Dependant Variable	Branching Variables	# of End Nodes	Model Fit
DIN Yield	L-S	3	0.73
AVWM NO_3^-	R-E	3	0.79
Peak NO ₃	L-S	3	0.72
DIN Retention	L-E-S-L	5	0.92
% DIN Retention	L-S	3	0.87

Discussion

Landscape controls on N cycling in alpine and subalpine ecosystems

At the catchment scale, soil cover and elevation had substantial predictive value for stream chemistry and N fluxes in alpine and subalpine ecosystems of the Rocky Mountains and Sierra Nevada. High nitrate concentrations and low inorganic nitrogen retention rates were measured in watersheds with little soil and at high altitudes. Neither catchment runoff or area, which were hypothesized to act as surrogates for hydrologic controls on N cycling, had statistically significant relationships to the watershed-scale N parameters used in our analysis. More sophisticated indices of catchment topography (i.e., slope, aspect and roughness) were only useful in predicting nitrate concentration and DIN retention in the Rocky Mountains; however, multiple regression analysis showed that most of these relationships were due to covariance of slope and topographic roughness with soil cover (see Table 5).

Our findings are consistent with general ecological theories of environmental controls on biological sequestration and release of nitrogen in alpine soils (Stanton et al. 1994; Fisk et al. 1998; Bieber et al. 1998; Brooks & Williams 1999). Elevation influences the extent and timing of snowcover (snow regime) in high elevation systems. Snow regime in turn, through its effect on moisture and temperature patterns in soils, exerts control on plot-to-catchment scale rates of microbial N transformations in soils and N sequestration by plants (Schimel et al. 1996; Brooks et al. 1999; Sickman et al. in press). Lack of soil-cover constrains N uptake in both higher plants and soil microbial populations by limiting the absolute size of these N pools in the Rocky Mountains and Sierra Nevada. In the Sierra Nevada, increasing

elevation results in shorter growing seasons for plants through longer snow-lie and colder and perhaps drier soil conditions, thereby reducing plant N uptake. Short-term N storage (in labile N pools) is enhanced during years with high snowfall, because N mineralization and nitrification in snow-covered soils continue later into the spring as a result of delayed snowmelt. The combination of lower N uptake by plants and greater labile N in soil results in higher stream nitrate concentrations and lower DIN retention during years with deep, late-melting snowpacks (Sickman et al. in press). For the Sierra Nevada watersheds, we hypothesize that low soil cover and high altitude worked synergistically in curtailing DIN retention by reducing the size of catchment N reservoirs and by decreasing the total flux between these reservoirs and atmospheric N deposition.

Soil cover exerted a quantitatively similar effect on net DIN retention and AVWM nitrate concentrations in both the Sierra Nevada and Rocky Mountains (Figures 1(b) and 4(b)). The similarity of these relationships in Sierra Nevada and Rocky Mountains indicates a consistent effect of soil N processes across the alpine and subalpine regions of the western United States and over a 5 to 6 fold variation in DIN loading rates. The intercepts of the Rocky Mountain equations were about double the Sierra Nevada intercepts, which may reflect the overall 2x higher rate of DIN loading to alpine systems in the Rocky Mountains.

Current DIN yields and AVWM nitrate levels in the Rocky Mountain watersheds may be a forecast of conditions in the Sierra Nevada if atmospheric DIN loading were to double. No simple relationship likely exists between DIN deposition and stream water nitrate at a single catchment or on a year-to-year basis because there are so many factors governing the susceptibility of alpine watersheds to N saturation. However, our regional analysis suggests there may be a relationship between loading and N dynamics at a large spatio-temporal scale and that site specific changes in concentration are lost when examining regional variations. A similar argument is made by Williams & Tonnessen (in press) to justify their estimates of critical N loads in the Rocky Mountains. Annual variation in nitrate concentrations is driven by hydrological and biological factors at the catchment-scale (e.g., Creed & Band 1998, and the present study), but the influence of deposition may emerge when looking at N dynamics at the regional or continental scale over a number of years.

Recent studies of functionally-similar catchments have demonstrated that inter-site differences in nitrate export behavior can exist without variations in DIN loading rates (Creed & Band 1998; Lovett et al. 2000; Clow & Sueker 2000). The regions examined in these analyses ranged in area from 10 to 2000 km². Similarly, in our analysis, DIN loading was not positively corre-

lated with nitrate concentrations of DIN yield in either the Sierra Nevada or Rocky Mountains; regions on the order of 50,000 km² in area. However, when we examined these relationships at a larger spatial scale with the regressiontree analysis (> 1,000,000 km²), small-scale variability was eliminated and a large-scale pattern emerged. DIN loading explained more of the differences in N dynamics for the combined data sets than any of the other terrain or topographic variables we considered. In an analysis of undisturbed watersheds in North America, Lewis (in press) found a positive relationship between catchment DIN loading and DIN yield; this study examined watersheds in a region > 5,000,000 km². These findings suggest that the concept of representative elementary area (REA), proposed by Wood et al. (1988) may apply when examining the regional variability of N dynamics. The REA can be considered the scale at which a statistical treatment of spatial variability can replace a deterministic description. For empirical modeling of the relationship between DIN loading and yield or stream nitrate concentrations, we suggest that studies should examine regions greater than 100,000 km² to form valid conclusions.

Topographic and terrain modeling of N biogeochemistry

Current concerns over the impact of nitrogen deposition on natural ecosystems has led to the need for evaluating global N biogeochemical cycles and for predicting the sensitivity of ecosystems over large regions (e.g., Fenn et al. 1998; Williams & Tonnessen 2000). In particular, there has been considerable effort to: 1) relate simple catchment features such as area, elevation and runoff to N yield from river basins in the context of global biogeochemical cycles (Meybeck 1982; Howarth et al. 1996; Lewis et al. 1999; Lewis in press) and (2) use more complex terrain parameters (e.g., slope, aspect, bedrock geology, vegetation, soil area, DIN deposition and variable source-area dynamics) to predict N yield, retention and surface water nitrate concentrations in smaller watersheds (e.g., Creed & Band 1998; Clow & Sueker 2000). The goal of both types of analyses is to develop empirical models to describe complex biogeochemical processes that can currently only be modeled at small scales.

Empirical models based on catchment features have had mixed success in predicting stream nitrogen concentration in small catchments. Clow & Sueker (2000) were able to explain 97% of the variation in nitrate chemistry of nine subalpine catchment in Rocky Mountain National Park on the basis of regression equations based on catchment slope and surficial geology (i.e., extent of talus). However, when these equations were tested with existing synoptic stream-survey data from the Rocky Mountains the model could only explain 19% of the variation in nitrate concentrations. The authors attribute the model's poor performance to the fact that the synoptic-survey data contain

a high proportion of small, high-elevation catchments with limited areas of subalpine soils compared to the calibration data.

Catchment land-cover was used by Cooper et al. (2000) in modeling long-term stream chemistry in the Tywi catchment of South Wales, United Kingdom. In this study, the authors developed empirical relationships between stream chemistry and landscape types (i.e., based on catchment soil and vegetation) and used these relationships along with the spatial distribution of landscape types and a stream-mixing algorithm to model stream chemistry over a 2000 km² region. The coefficient of determination in a regression between measured and modeled nitrate concentrations was 0.65.

Artificial neural networks (ANN) were used by Lek et al. (1999) to predict stream DIN and TN concentration at 927 sites throughout the United States that were impacted by non-point source pollution. Independent variables used as inputs to the ANNs included catchment area, precipitation, runoff, livestock density and various landscape descriptors (forest, wetland, urban, agricultural). The ANNs were validated using data not used in the training procedure and were shown to explain about 70% of the variation in stream N concentrations.

Lovett et al. (2000) found that variations in stream nitrate concentrations among 39 streams in the Catskill Mountains of New York could not be explained by differences in catchment DIN loading, watershed topography or groundwater inputs. Instead, differences in forest composition which were induced by past land-use practices were believed to have produced the observed variation in nitrate concentrations. However, the variety of topography and DIN loading in these watersheds was much lower than in our analyses and in the previously mentioned modeling studies; the region examined may be below the REA for modeling stream nitrate concentrations from DIN loading or topography. Thus, care must be taken in scaling the findings of Lovett et al. (2000) to larger montane regions of the United States (cf. Stoddard et al. 1998, 1999).

Current N saturation status in Rocky Mountains and Sierra Nevada

Overall, catchment DIN retention is higher in the Rocky Mountain watersheds than in the Sierra Nevada. We suggest that this difference is due primarily to greater soil cover in the Rocky Mountains and not due to greater rates of DIN retention per unit soil area. We base this conclusion on the relationship between DIN retention and soil cover which demonstrates that Sierra Nevada catchments with 20 to 40% soil cover are retaining equal amounts and percentages of DIN to catchments in the Rocky Mountains with > 60% soil cover (Figures 2(b) and 3(b)).

While it is possible that variations in climate and soil properties explain these differences, the data may imply that soils in the Rocky Mountains are less N limited because of higher rates of DIN loading. Alternatively, environmental conditions in the Rocky Mountains may be more severe than in the Sierra Nevada (e.g., greater extent of frozen soils), therefore terrestrial ecosystems in the Rocky Mountains may be less able to prevent N losses. Current ecological theory suggests that terrestrial communities are N limited because of N losses that are not under control of biota [Vitousek & Field 1999]; these losses include leaching of dissolved organic N and denitrification [Vitousek et al. 1998]. The persistence of N limitation in high elevation ecosystems and the inability of biotic communities to prevent episodic nitrate losses may be related to microbial and hydrologic processes which conspire to induce temporal and spatial disconnections between inorganic N availability and demand.

Stoddard (1994) provided a framework to assess the degree to which ecosystems are affected by N deposition that is based on seasonal patterns in surface water nitrate concentrations. Our analyses suggest that rates of catchment-scale DIN retention are also indicative of N-saturation status and correspond well with this framework. Four stages were used in Stoddard's framework to describe the N saturation status of watersheds. At Stage 0, maximum spring episode concentrations are less than precipitation concentrations and growing season concentrations are near the detection limit. Watersheds that meet this criteria include the Crystal, Topaz, Lost, and Marble Fork basins in the Sierra Nevada and East Glacier, Dear Creek, East St. Louis and Fool Creek Alpine basins in the Rocky Mountains. Inorganic nitrogen retention for these stage 0 catchments ranged from 80–100%.

At the next step in the sequence towards N-saturation, Stage 1, nitrate concentrations in spring episodes exceed concentrations in precipitation and there is a delay in the decline of nitrate levels to later in the growing season. In the Sierra Nevada, catchments at Stage 1 of N-saturation would include Spuller, Ruby, Pear, and Emerald. Examples in the Rocky Mountains would include West Glacier. These catchments have DIN retention rates in the range of ca. 70–80%.

Stage 2 of N-saturation includes higher episodic concentrations and elevated nitrate concentrations well into and through the growing season. In the Sierra Nevada, the M-sites and Treasure watersheds can be classified at this stage. These catchments retained from ca. 20 to 60% of DIN loading. Stage 2 watersheds in the Rocky Mountains include Green Lakes #4, Rabbit Ears Pass, Snake River and the Loch Vale watersheds. These Rocky Mountain basins had variable rates of %DIN retention; the overall range was from ca. 20–75%.

Stage 3 of N-saturation differs from stage 2 in that the watershed becomes a net source of N rather than a sink. Two watersheds in the Sierra meet this criteria, High and Low, and one catchment, Mills, is on the verge of stage 3. In all three of these catchments DIN export equals or exceeds DIN inputs from atmospheric deposition. In the case of Low, negative DIN retention is within the expected errors of the N budgets, hence it is possible that the catchment is also still on the verge of stage 3. In the case of High the amount of net DIN export from the basin, is beyond expected errors in flux estimates. Some of the net export can explained by organic nitrogen in precipitation, but this input is more than balanced by organic and particulate nitrogen losses from the basin (Sickman et al. in press).

The conceptual model of Stoddard (1994) is based on data from forested temperate watersheds, primarily in the Northeastern U.S. and Europe. At first exposure, it may seem dubious to apply Stoddard's N saturation stages to alpine watersheds, where the basins are above timberline, soils are thin (when present at all) and the annual hydrologic cycle is dominated by snow accumulation and rapid melt. Yet much of the recent data from alpine watersheds suggests strongly that the same processes that Stoddard used to explain the progression from Stage 0 to Stage 3 in forested watersheds are controlling N export from the alpine zone. In forested watersheds, N is largely immobilized by biotic uptake in soils (Tietema et al. 1998; Nadelhoffer et al. 1995), especially the organic layer of soils (Gundersen et al. 1998). In alpine watersheds, organic soils seem to play a role similar to the one they play in forested watersheds (as partially indicated by the relationships between N retention and soil cover reported in this paper and by earlier studies; Williams et al. 1996b), as do talus fields (Williams et al. 1997; Williams et al. 1995), although they are largely unrecognizable to most scientists as soils. Studies indicate that the NO₃ leaching from watersheds during snowmelt has an isotopic signature largely attributable to soil transformation (e.g., dominated by nitrification, rather than by atmospheric isotope ratios), in both forested and alpine watersheds (Kendall et al. 1995). It seems likely that similarities in N behavior between forested and alpine watersheds outweigh the dissimilarities. The types of pools and processes governing N retention and N leaching are nearly identical; it is only the size of the pools that differ. Smaller N pools in the limited soils of alpine watersheds create the potential for nitrogen saturation to occur at deposition rates that seem trivial when compared to those in the eastern U.S. and Europe.

Nitrogen deposition along the eastern slope of the Sierra Nevada is less than 1.5 kg ha⁻¹ yr⁻¹. This rate of N loading is low compared to current inputs to other North American catchments experiencing adverse effects of N deposition (Fenn et al. 1998). At the High watershed, episodic acidification

occurred during snowmelt (ANC < 0) and net export of ANC was exceeded by hydrogen ion export (Stoddard 1995, Sickman and Stoddard unpublished data). The Ruby watershed is adjacent to the High catchment and receives similar levels of N deposition, yet it did not experience acidic episodes and was a sink for N loading (Sickman & Melack 1998; Melack et al. 1998).

Differences in N cycling between the High and Ruby catchments are probably explained by greater soil cover in the Ruby watershed and a proportionally higher percentage of talus and boulders in the High watershed. Substantial pools of DIN nitrogen have been measured in talus deposits in the Rocky Mountains (Williams et al. 1997; Bieber et al. 1998). In addition, leaching from these pools may represent a large component of the nitrate exported from alpine watersheds such as Andrews Creek and Icy Brook (Campbell et al. 1995; Kendall et al. 1995). The fact that High watershed is exporting DIN in excess of atmospheric loading might be explained by release of N that has been held in long-term storage within the talus. Nitrogen inputs from dry deposition and organic N substrates supplied by small mammals (i.e., waste products and nesting materials) have the potential to build up and persist within talus since there is little or no N utilization by plants and denitrification is unlikely. However, more research, possibly employing detailed analyses of stable isotopes of C and N, will be needed to more fully understand N dynamics within talus fields.

Summary

The correlation analysis confirms that watershed features such as elevation and soil cover are good surrogates for complex N processes controlling catchment-scale N retention. Soil cover was an especially good predictor for catchment DIN yield, stream nitrate concentrations and DIN retention in alpine and subalpine ecosystems in both the Sierra Nevada and Rocky Mountains. The regression models provide a basis for predicting the status of high elevation ecosystems over large regions and under varying inputs of atmospheric N loading. Because the equations quantify the effect of DIN loading on surface water chemistry and nitrogen retention, they may also be useful for evaluating critical N loads in the western United States.

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