

Landscape Controls on Organic and Inorganic Nitrogen Leaching across an Alpine/Subalpine Ecotone, Green Lakes Valley, Colorado Front Range

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ABSTRACT

Here we report measurements of organic and inorganic nitrogen (N) fluxes from the high-elevation Green Lakes Valley catchment in the Colorado Front Range for two snowmelt seasons (1998 and 1999). Surface water and soil samples were collected along an elevational gradient extending from the lightly vegetated alpine to the forested subalpine to assess how changes in land cover and basin area affect yields and concentrations of ammonium-N ($\text{NH}_4\text{-N}$), nitrate-N ($\text{NO}_3\text{-N}$), dissolved organic N (DON), and particulate organic N (PON). Streamwater yields of $\text{NO}_3\text{-N}$ decreased downstream from 4.3 kg ha^{-1} in the alpine to 0.75 kg ha^{-1} at treeline, while yields of DON were much less variable ($0.40\text{--}0.34 \text{ kg ha}^{-1}$). Yields of $\text{NH}_4\text{-N}$ and PON were low and showed little variation with basin area. $\text{NO}_3\text{-N}$ accounted for 40%–90% of total N along the sample transect and was the dominant form of N at all but the lowest elevation site. Concentrations of DON ranged from approximately 10% of total N in the alpine to 45% in the subalpine. For all sites, volume-weighted mean concentrations of total dissolved nitrogen (TDN) were significantly related to the DIN:DON ratio ($R^2 = 0.81$, $P < 0.001$). Concentrations of $\text{NO}_3\text{-N}$ were signifi-

cantly higher at forested sites that received streamflow from the lightly vegetated alpine reaches of the catchment than in a control catchment that was entirely subalpine forest, suggesting that the alpine may subsidize downstream forested systems with inorganic N. KCl-extractable inorganic N and microbial biomass N showed no relationship to changes in soil properties and vegetative cover moving downstream in catchment. In contrast, soil carbon–nitrogen (C:N) ratios increased with increasing vegetative cover in catchment and were significantly higher in the subalpine compared to the alpine ($P < 0.0001$). Soil C:N ratios along the sample transect explained 78% of the variation in dissolved organic carbon (DOC) concentrations and 70% of the variation in DON concentrations. These findings suggest that DON is an important vector for N loss in high-elevation ecosystems and that streamwater losses of DON are at least partially dependent on catchment soil organic matter stoichiometry.

Key words: nitrogen; DON; DOC; surface water chemistry; snow; biogeochemistry; Colorado Front Range.

INTRODUCTION

Research in forested ecosystems has shown that dissolved organic nitrogen (DON) is often the dom-

inant form by which N is exported in surface waters and is therefore a crucial component of the total N budget (for example, see Campbell 2000a; Kortelainen and others 1997; Sollins and McCorison 1981). At Como Creek, a forested watershed in the Colorado Front Range of the Rocky Mountains, Lewis and Grant (1979) found that DON concentrations were approximately an order of magnitude

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higher than dissolved inorganic nitrogen (DIN) concentrations over two runoff seasons. Furthermore, DON accounted for an average of 80% and as much as 97% of total N loss from primary forests at 100 sites in temperate South America with extremely low rates of N deposition (Perakis and Hedin 2002; Hedin and others 1995). These results have led to the suggestion that DON losses at the watershed scale are decoupled from ecosystem demands for N and therefore may contribute to the persistence of N limitation in terrestrial ecosystems; this is known as the "leaky faucet" hypothesis (Hedin and others 1995; Vitousek and others 1998).

In headwater catchments, organic forms of N have received little attention in N cycling studies (Chapman and Edwards 2001; Campbell and others 2000b; Creed and Band 1998). High-elevation watersheds in the Colorado Front Range are subject to high rates of inorganic N deposition in wetfall as compared to other mountain regions in Colorado and the western United States (Williams and others 1996a; Sickman and others 2001). Moreover, alpine ecosystems are highly sensitive to changes in precipitation chemistry because of their poorly developed soils, sparse vegetation, and short growing seasons. Present rates of N deposition in the Colorado Front Range appear to be altering the structure and function of both aquatic (Baron and others 1994; Caine 1995; Williams and Tonnessen 2000) and terrestrial (Fisk and Schmidt 1996; Bowman and Steltzer 1998; Baron and others 2000) ecosystems. In turn, export of inorganic N in surface waters of these high-elevation catchments has increased relative to high-elevation catchments in other areas of the western United States (Coats and Goldman 2001; Sickman and others 2001). The role of organic N as a vector for N export from these montane catchments is not well understood.

Despite the importance of DON in the N cycle of a wide variety of ecosystems, little is known about the process-level controls on fluxes of DON from catchment soils to surface waters (Michalzik and others 2001). Soil carbon–nitrogen (C:N) ratios may be an important control on DON export. Soil C:N ratios have been shown to be effective predictors of basin-scale dissolved organic carbon (DOC) (Aitkenhead and McDowell 2000) and $\text{NO}_3\text{-N}$ (Gunderson and others 1998) export from various biomes. These findings suggest that dissolved organic matter and nitrification/ $\text{NO}_3\text{-N}$ loss may be derived from different but related sources in soil organic matter (for example Goodale and others 2000). However, recent research on a chronosequence of soils in Hawaii suggests that organic and inorganic components of the N flux from soils are regulated

by different factors and that DON fluxes are influenced by soil sorption capacity. Moreover, unlike $\text{NO}_3\text{-N}$, DON fluxes are somewhat decoupled from immediate microbial demand for N (Neff and others 2001). Taken together, these findings suggest that evaluating the relationship between soil C and N stoichiometry and streamwater concentrations of inorganic and organic N species in headwater catchments may provide insight into the controls on surface water N concentrations.

Here we evaluate dissolved inorganic N ($\text{DIN} = \text{NO}_3\text{-N} + \text{NH}_4\text{-N}$) and organic N (DON and particulate organic nitrogen [PON]) concentrations and yields along an elevational transect extending from an alpine ecosystem to a forested ecosystem on North Boulder Creek in the Front Range of the Colorado Rocky Mountains. Samples were collected during the snowmelt runoff season in 1998 and 1999. We hypothesized that organic N would be a substantial portion of total streamwater N in both the alpine and the subalpine reaches of the catchment, and further that the balance of organic versus inorganic N in surface waters would change across the alpine/subalpine ecotone. In particular, we expected that in the subalpine greater soils coverage and abundant vegetation would lead to an increase in the relative importance of organic N in streamwater. In the North Boulder Creek catchment, there are substantial changes in soil properties and stream chemistry across the alpine/subalpine ecotone. To better understand the catchment characteristics governing N leaching, we evaluated how downstream changes in land cover influenced observed patterns of N loss. Additionally, we assessed the extent to which soil C and N and the major solutes in streamwater were related to streamwater N concentrations at different elevations along the sampling transect. The longitudinal sampling along the stream course allowed us to substitute space for time to begin to understand how controls on N export may change with changes in ecosystem N status in the Rocky Mountains.

STUDY SITE

Green Lakes Valley is an east-facing headwater catchment, 2720 ha in area, extending from Silver Lake at 2963 m to the crest of the Continental Divide at 4000 m in the Colorado Front Range (Figure 1). The Green Lakes Valley is characterized by a continental climate with a mean annual temperature of -3.8°C and an average of 1000 mm of precipitation annually (Williams and others 1996b), 80% of which is in the form of snow (Caine 1996). Stream pH increases down valley with slightly

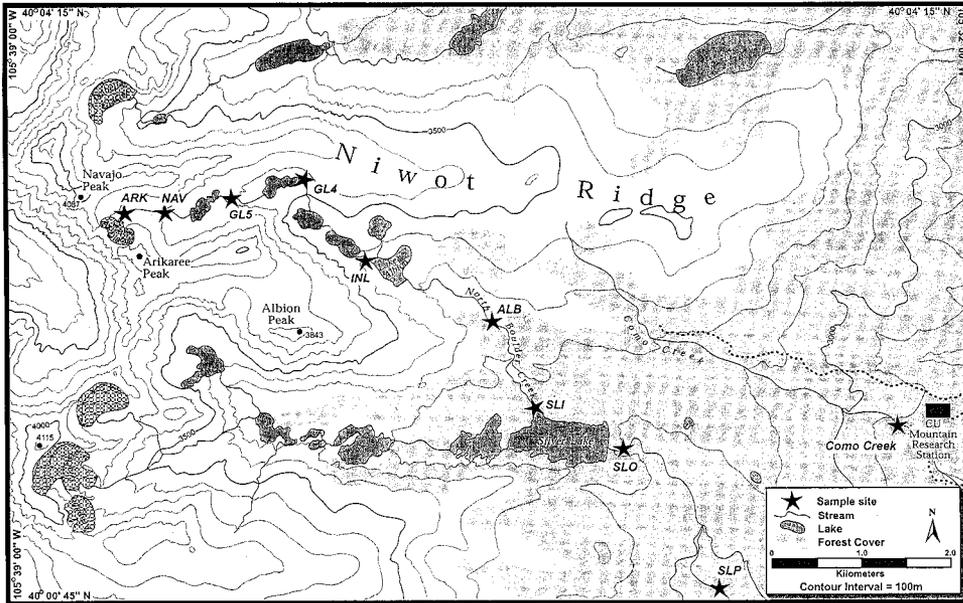


Figure 1. Topographic map of the North Boulder Creek catchment in the Green Lakes Valley. North Boulder Creek originates from the Arikaree glacier, just east of the Continental Divide (3900 m a.s.l.). Como Creek drains a predominantly forested catchment on the southeast flank of Niwot Ridge before joining North Boulder Creek. Stream and soil sampling sites for the 1998 and 1999 field seasons are denoted by stars.

acidic values (pH 5–6) at the highest sites to neutral values (pH 6.5–7.5) at the lower, forested sites (Caine 1995). Inorganic N deposition in wetfall is approximately $4 \text{ kg ha}^{-1} \text{ y}^{-1}$ (Williams and Tonnessen 2000), with additional contributions from dry deposition equal to approximately half those for wetfall (Sievering and others 1996). The valley is located within the City of Boulder Watershed, and public access has been restricted since the 1930s. As a result, the hydrologic and biogeochemical systems are protected from recreational and commercial perturbations.

The 5 km^2 of the catchment above Lake Albion is unforested and alpine in nature (Figure 1). Steep rock walls and talus slopes are the dominant landforms, and vegetation is sparse. In the upper valley, soils are limited in extent, depth, and development as a result of late Pleistocene glaciation (Madole 1982). Catchment soils are a mixture of Cryic Inceptisols and Entisols, with Histosols in wetter areas on the valley floor (Burns 1980). Below Lake Albion, the catchment is dominated by a mixed conifer forest composed primarily of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) with some limber pine (*Pinus flexilis*) at treeline and regrowth lodgepole pine (*Pinus contorta*) lower in the basin. This portion of the catchment is typified by extensive vegetative cover and developed soils on glacial till and moraine deposits. Watershed soils overlie granitic and metamorphic parent material. Soils are Inceptisols and intermixed Alfisols, with Histosols in wet meadow areas. Soil depths range from 30 to 100 cm, with the deeper soils

located on well-drained glacial moraines. Soil pH values range from 4.5 to 6.0.

Above Silver Lake, the Green Lakes Valley consists of a linear cascade of five lakes. Preliminary stream sampling was done at 10 sites along the main stem of North Boulder Creek (NBC) in 1998. A more thorough sampling scheme was repeated for nine of these sites in 1999 (Figure 1). The highest site was the outflow from the Arikaree Glacier at 3785 m; the lowest site was 3 km downstream from the outflow of Silver Lake Reservoir at 2963 m (Table 1). There were five alpine sample sites (ARK, NAV, GL5, GL4, and INL) that ranged in elevation from 3345 to 3785 m and in catchment area from 9 to 355 ha. There were four forested sample sites (ALB, SLI, SLO, and SLP) ranging in elevation from 2963 to 3250 m and in basin area from 709 to 2720 ha. The ALB site is at treeline and represents the transition from an alpine ecosystem to a forested subalpine ecosystem (Figure 1).

Additional samples were collected on Como Creek, a subsidiary stream draining the forested southeast flank of Niwot Ridge (Figure 1). Como Creek provides a forested control watershed that allows us to test whether alpine basins subsidize the N balance of downstream forested catchments. The upper reach of the Como Creek watershed extends slightly above treeline to 3560 m in elevation and contains no talus or exposed bedrock. More than 80% of the watershed is forested with conifers and some aspen. Dominant trees and shrubs include *Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta*, *Pinus flexilis*, *Populus tremuloides*, and *Salix*. Stream

Table 1. Stream Sampling Sites Along an Elevational Transect of North Boulder Creek for the 1999 Snowmelt Runoff Season

Site	Abbreviation	Elevation (m)	Catchment Area (ha)	Landscape Type
Arikaree Glacier	ARK	3785	9	Alpine
Navajo Bench	NAV	3720	42	Alpine
Green Lake 5	GL5	3620	135	Alpine
Green Lake 4*	GL4	3550	221	Alpine
Albion Inlet*	INL	3345	355	Alpine
Albion Townsite*	ALB	3250	710	Forested
Silver Lake Inlet*	SLI	3122	810	Forested
Silver Lake Outlet*	SLO	3122	2230	Forested
Below Silver Lake*	SLP	2963	2720	Forested

Samples at all nine sites were analyzed for inorganic N ($\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$) and organic N (DON and PON). Samples from a subset of sites (with asterisks) were also analyzed for DOC.

samples were collected at the University of Colorado Mountain Research Station at an elevation of 2900 m. The watershed area above the sampling site is 664 ha.

METHODS

Discharge Measurements

Water level is measured with a pressure transducer at the following three sites: NAV, GL4, and ALB. During the seasons considered here, water levels were recorded at hourly (ALB) and 10-min (NAV and GL4) intervals and calibrated by field measurements every 2–5 days. The resulting water-level records are converted to volumetric discharges by empirical ratings that are validated by gauging at different flow levels for each season. These rating curves have remained consistent throughout the period of study. We focus on the time period from April to October because flows are low with little variation during the winter season.

Stream Chemistry

Stream samples were collected as grab samples following the protocol of Williams and others (1996c). Samples were collected weekly on North Boulder Creek and Como Creek through peak snowmelt runoff and biweekly to monthly during baseflow in the late summer and fall in 1998 and 1999. Polyethylene bottles were soaked with deionized water overnight and then rinsed copiously; bottles were further rinsed three times with sample water at the time of collection. Samples were transported within a few hours of collection to our wet chemistry laboratory, where subsamples were immediately fil-

tered through glass fiber filters with a nominal pore size of 1.0 μm and stored in the dark at 4°C for subsequent analysis. Samples for DOC analysis were collected in precombusted amber glass bottles at six sites (Table 1). At the time of collection, DOC samples were filtered through precombusted Gelman A/F glass fiber filters with an approximate pore size of 1.0 μm .

All water samples were analyzed for pH, acid neutralizing capacity (ANC), conductance, and major ions at the Kiowa Environmental Chemistry Laboratory, which is located approximately 6 km from North Boulder Creek. Nitrate was determined using a Dionex DX 500 ion chromatograph with an IonPac AS4A-SC Analytical Column. The detection limit was 0.03 $\mu\text{moles L}^{-1}$; precision was 1.1%. Ammonium was determined on a Lachat QuikChem 4000 Flow Injection Analyzer using a method based on the Berthelot reaction. The detection limit was 0.33 $\mu\text{moles L}^{-1}$; precision was 0.91%. Total nitrogen (TN) in both filtered and unfiltered samples was determined by a potassium persulfate digestion to oxidize all dissolved forms of N into $\text{NO}_3\text{-N}$, which was then measured on a Lachat QuikChem 4000 Flow Injection Analyzer. Detection limits for TN were 0.17 $\mu\text{moles L}^{-1}$; precision was 1.62%. DON was calculated by subtracting measured inorganic N ($\text{NO}_3\text{-N} + \text{NH}_4\text{-N}$) from the TN value of the filtered sample. PON was calculated by subtracting the TN of a filtered subsample from the TN of the original unfiltered sample.

DOC was analyzed at the Institute of Arctic and Alpine Research in Boulder using a Dohrmann high temperature combustion instrument. Three repli-

cate DOC analyses were done for each sample. The standard deviation for these analyses was typically 0.05 mg C L^{-1} , with a range of 0.01 to 0.12 mg C L^{-1} .

Soil Samples

Soil samples were collected during the growing season in July at the same elevation as stream samples and within 20 m of the stream. Sampling sites were chosen to represent terrestrial areas that would contribute soil water to discharge following the variable source area dynamics of Creed and Band (1998). Soil samples in 1998 were collected as one set of five replicates at each location. Soil samples in 1999 were collected as five sets of three replicates for each location. Each set consisted of three soil cores composited in a new polyethylene bag collected using a 20-cm soil corer. Soils were processed within 12 hs of collection for KCl-extractable NH_4^+ and NO_3^- , microbial biomass N, and total C and N following the protocol of Fisk and Schmidt (1995). Fresh soils were homogenized and passed through a 2 mm sieve. Subsamples of the less than 2 mm fraction were extracted with 2N KCl by shaking at 250 rpm for 60 mins and then allowed to sit at room temperature for 18 h. Extracts were then filtered through prerinsed (300 ml deionized water) Whatman no. 1 filter paper and frozen for later lab analysis. KCl-extractable NH_4^+ and NO_3^- were analyzed by the procedures used for stream samples. Total C and total N were measured on a CHN analyzer (Carlo Erba, Milan, Italy). Microbial biomass N was determined using a chloroform fumigation-direct extraction procedure (Brookes and others 1985). The difference in extractable N content ($0.5 \text{ M K}_2\text{SO}_4$) of the fumigated and unfumigated soils represented the chloroform-labile fraction of the soils, and a correction factor of 0.54 (Brookes and others 1985) was applied to estimate microbial N.

Yields and Volume-Weighted Mean Concentrations of N Species

The yields of the four N species were estimated as the product of measured concentrations and the accumulated water discharge for weekly intervals centered on the day of sampling. Yields of N species are weighted by drainage basin area above the sampling site and expressed as kg N ha^{-1} . Yield calculations are subject to several sources of error, including errors in discharge measurement, analytical error, and low-frequency stream sampling. We estimate errors in discharge measurement to be on the order of 5%–10% (Caine 1996). Errors resulting from weekly stream sampling are estimated to

be on the order of 2%–3% based on time-intensive sampling from smaller subcatchments within Green Lakes Valley (Caine 1989a). Analytical errors for the calculation of the four N species are on the order of 1%. We have no reason to believe that any of these errors are systematic and introduce bias into the data. We estimate overall error involved with calculating yields to be $\pm 15\%$.

Seasonal volume-weighted mean (VWM) concentrations for all four N species, calculated as seasonal mass flux divided by seasonal discharge, were estimated at the three gauged sites (NAV, GL4, and ALB) in both 1998 and 1999. Because not all of the sites were gauged, it was not possible to determine VWM concentrations for each site. However, VWM concentrations at the gauged sites were highly correlated to mean arithmetic concentrations at the same sites ($R^2 = 0.97$, $y = 0.96x + 0.85$, $n = 24$). We therefore assume that mean arithmetic concentrations are representative of discharge-weighted export of N species at the nine sites sampled and refer to these results as seasonal VWM concentrations.

RESULTS

Hydrology

Snowfall in 1998 and 1999 was within 15% of the long-term average. Maximum snow water equivalent (SWE) at the Niwot SNOTEL site 1 km north-east of the Green Lakes Valley was 40.5 cm in 1998 and 36.2 cm in 1999, as compared to a 15-year average of 35.8 cm. Similarly, runoff in the catchment above the ALB site in both years was within 10% of the 15-year average of 688 mm. Our results for the 2 years appear to be typical of general conditions at our research area.

The 1999 seasonal hydrographs for GL4 and ALB exemplify the markedly seasonal flow typical of snowmelt-dominated catchments (Figure 2). Runoff begins to increase in mid-May with the start of spring snowmelt and peaks in late June before declining toward baseflow in the late summer. Down valley, total discharge increased from $2,250,000 \text{ m}^3$ at GL4 to $4,120,000 \text{ m}^3$ at ALB during the May–October 1999 period. At GL4, this is 6.2% higher than the 1981–98 average; at ALB, it is 1.4% below the 1981–98 average. The GL4 hydrograph peaked at $0.80 \text{ m}^3 \text{ s}^{-1}$ on June 9 when a snow and ice barrier at the Green Lake 5 outlet was breached. At ALB, peak flow of $0.84 \text{ m}^3 \text{ s}^{-1}$ did not occur until July 3 and was delayed and reduced in magnitude by recharge of the Lake Albion reservoir, which had

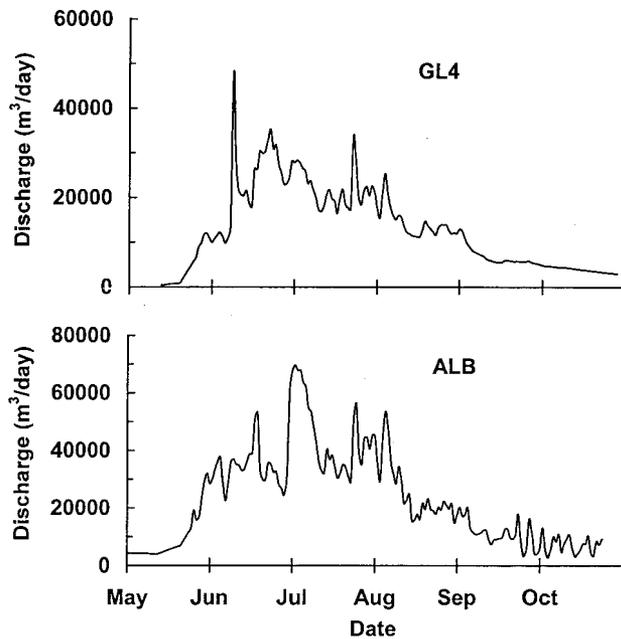


Figure 2. Hydrographs at two gauged sites, GL4 (alpine) and ALB (forested), for the 1999 sampling period. Hydrographs at both sites are dominated by runoff from the seasonal snowpack, which peaks in late June.

been drawn down in fall 1998 and did not reach spillway level until 29 June 1999.

Hydrochemical Characteristics and N Species Concentrations

In general, the dominant chemical constituents in North Boulder Creek were not good predictors of variations in N species concentrations. For all stream samples collected, H^+ was significantly correlated with NO_3^- -N and NH_4^+ -N concentrations, but it did not explain more than 25% of the variation in either of the two inorganic N species (Table 2). Streamwater DOC explained about 27% of the variation in DON concentrations and was also weakly correlated with NO_3^- -N. Base cations (C_B) explained only 12% of the variation in both NO_3^- -N and DON. Silica (Si) was most strongly correlated with DON, explaining 14% of the variation in DON concentrations. SO_4^{2-} explained less than 10% of the variation in concentration of all four N species.

Mass Fluxes of N Species

Estimated yields of the four N species show that leaching of inorganic forms of N varied more than leaching of organic forms of N along the elevational transect (Table 3). Area-weighted export of total N decreased with increasing basin area from 4.96 kg N ha^{-1} at NAV to 1.25 kg N ha^{-1} at ALB. This de-

crease in total N export with increasing basin area was driven primarily by decreases in export of inorganic N, which dropped from 4.5 kg N ha^{-1} at NAV to 0.82 kg N ha^{-1} at ALB in the forested reaches of the catchment.

At the highest reaches of the catchment, total N export was dominated by NO_3^- -N at 4.32 kg N ha^{-1} or 87% of the total. DON made up only 8% (0.4 kg N ha^{-1}) of exported N; NH_4^+ -N and PON export were both below 0.2 kg N ha^{-1} and accounted for less than 5% of total N export. Moving downstream to Green Lake 4, NO_3^- -N remained the dominant form of N exported, although the yield of NO_3^- -N decreased to 2.5 kg ha^{-1} . DON export was nearly unchanged and consequently increased to 13% of total N exported. NH_4^+ -N (0.13 kg ha^{-1}) and PON export (0.09 kg N ha^{-1}) both remained low; together, the two species still accounted for less than 8% of total N export. At the forested ALB site, NO_3^- -N export dropped precipitously to 0.75 kg ha^{-1} but remained the dominant form of N export. DON export of 0.34 kg ha^{-1} was similar to that seen in the alpine (0.41 kg ha^{-1}) but now accounted for nearly 30% of the streamwater N budget. NH_4^+ -N export decreased slightly to 0.08 kg ha^{-1} , which accounted for 6% of streamwater N.

On the whole, organic N export varied little with increasing basin area. As a result, organic forms of N accounted for more than a third of streamwater N export as North Boulder Creek enters the forest. These observations are supported by additional data from 1998 that show that organic N varies between the same three sites by just over 0.1 kg ha^{-1} and accounts for 41% of N export at the Albion site.

VWM Nitrogen Concentrations along the Elevational Transect

Seasonal VWM concentrations of the four N species along the elevational transect are indicative of their relative importance in total N export as North Boulder Creek moves from its headwaters above treeline to the downstream forested reaches of the catchment. NO_3^- -N was the dominant form of N in streamwater at all but the lowest site on the sample transect, accounting for 40%–90% of total N (Table 4). In the alpine area, NO_3^- -N concentrations increased sharply between the glacier outflow and the NAV sampling site. Below NAV, NO_3^- -N concentrations decreased downstream by a factor of 5 to less than 5 $\mu moles L^{-1}$ below Silver Lake reservoir. NH_4^+ -N accounted for 10% or less of total N export at every site on the transect except for ARK, where it accounted for 24% of N export (Table 4). The high value for NH_4^+ -N at the ARK site was probably a result of snowmelt release of NH_4^+ -N. Water drain-

Table 2. Slope, R^2 , and Probability (P) of Linear Regression between $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, DON, and PON and Selected Solutes for All Samples

Parameter	$\text{NH}_4\text{-N}$			$\text{NO}_3\text{-N}$			DON			PON		
	Slope	R^2	P	Slope	R^2	P	Slope	R^2	P	Slope	R^2	P
H^+	1.04	0.14	<0.001	6.06	0.23	<0.001	-0.39	0.01	0.04	na	<0.01	0.59
C_B	-0.01	0.05	0.003	-0.04	0.12	<0.001	0.01	0.12	<0.001	na	<0.01	0.27
SO_4^-	na	<0.01	0.27	-0.07	0.03	0.04	0.01	0.02	0.06	0.01	0.07	0.01
DOC	na	<0.01	0.72	-1.45	0.06	0.02	0.70	0.27	<0.001	na	<0.01	0.71
Si	-0.02	0.06	0.001	-0.08	0.04	0.01	0.03	0.14	<0.001	na	<0.01	0.52

DON, dissolved organic nitrogen; PON, particulate organic nitrogen; na, not applicable because of a nonsignificant regression; C_B , sum of base cations; DOC, dissolved organic carbon; Si, silica

($n = 172$, except DOC $n = 82$) All slopes are in $\mu\text{moles L}^{-1}$ except DOC, which is in mg L^{-1} .

Table 3. Seasonal Export (kg ha^{-1}) for Inorganic ($\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$) and Organic (DON and PON) N Species at Three Gauged Sites along the Elevational Transect in 1999

Site	Area (ha)	Inorganic N			Organic N			Total N
		$\text{NH}_4\text{-N}$	$\text{NO}_3\text{-N}$	DIN	DON	PON	ON	
NAV	42	0.19	4.32	4.51	0.40	0.06	0.46	4.96
GL4	221	0.13	2.50	2.63	0.41	0.09	0.51	3.14
ALB	710	0.08	0.75	0.82	0.34	0.08	0.42	1.25

DIN, dissolved inorganic nitrogen; DON, dissolved organic nitrogen; PON, particulate organic nitrogen; ON, organic nitrogen Export of inorganic N was much more variable with location than export of organic N.

Table 4. Mean Concentrations ($\mu\text{moles L}^{-1}$) and Percentage of Total N Concentration by Species (in parentheses) at Nine Sample Sites along the Elevational Transect in 1999, from the Highest (ARK) to the Lowest (SLP) Elevation Site

	ARK	NAV	GL5	GL4	INL	ALB	SLI	SLO	SLP	CC
$\text{NH}_4\text{-N}$	5.8 (24)	0.7 (2)	1.6 (8)	0.8 (4)	0.6 (3)	1.0 (7)	0.7 (5)	1.1 (10)	0.9 (8)	0.5 (7)
$\text{NO}_3\text{-N}$	14.7 (61)	27.1 (90)	13.6 (70)	14.1 (77)	12.1 (71)	7.9 (61)	8.3 (62)	4.9 (48)	4.5 (40)	0.1 (2)
DON	2.8(12)	2.1 (7)	2.7 (14)	2.6 (14)	2.7 (16)	3.3 (25)	3.6 (27)	3.2 (32)	4.9 (45)	5.9 (85)
PON	1.0(4)	0.4 (1)	1.5 (8)	0.8 (4)	1.7 (10)	0.8 (6)	0.9 (6)	1.0 (10)	0.8 (8)	0.4 (6)

The Como Creek site (CC), which drains subalpine forest, is also included.

ing the glacier has limited interaction with underlying soils, as evidenced by extremely low values for silica at ARK (less than $5 \mu\text{moles/L}$) compared to downstream sites; therefore, $\text{NH}_4\text{-N}$ has little chance to be removed by either sorption in mineral soil horizons or by biological assimilation. The Como Creek site proved a sharp contrast to North Boulder Creek, with streamwater $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ together accounting for only 9% of streamwater N.

In contrast to DIN, DON concentrations increased moving downstream into the forested reaches of the catchment. In terms of the total N concentration

in streamwater, DON increased from less than 10% in the high alpine to 45% at the lowest site on the transect. At this site, DON became the dominant form of N in surface waters. DON was highest at the Como Creek site, accounting for 85% of streamwater N. PON accounted for 10% or less of total N concentration at all sites sampled and showed little correlation with changes in basin size or land-cover type.

The four N species differed in how concentrations varied between alpine and forested reaches of the catchment (Figure 3). A *t*-test of the 1999 data shows that mean concentrations of $\text{NH}_4\text{-N}$ and PON

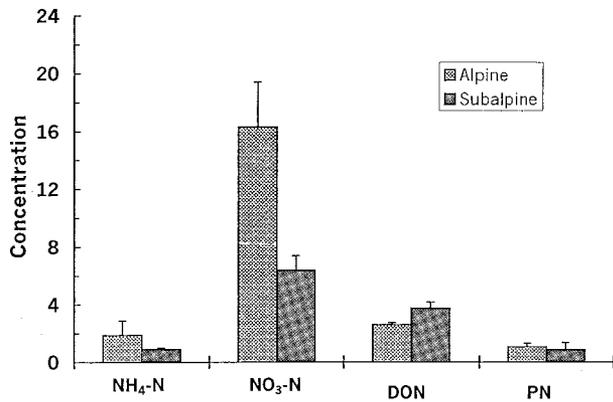


Figure 3. Mean seasonal concentrations (\pm SE) of $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, DON, and PON at alpine ($n = 5$) and forested ($n = 4$) sites in 1999. All concentrations are given in $\mu\text{moles L}^{-1}$. $\text{NO}_3\text{-N}$ and DON concentrations were both significantly different ($P < 0.05$) between the alpine and forested sites. $\text{NH}_4\text{-N}$ and PON concentrations were much lower and did not vary significantly between the alpine and forested reaches of the catchment.

did not differ significantly between the alpine and forested reaches ($P > 0.05$ for both). In contrast to $\text{NH}_4\text{-N}$ and PON, the mean concentration of $\text{NO}_3\text{-N}$ at alpine sites, $16.3 \mu\text{moles L}^{-1}$, was significantly greater than the mean of $6.4 \mu\text{moles L}^{-1}$ for the forested reaches ($P = 0.01$). The mean DON concentration at forested sites, $3.8 \mu\text{moles L}^{-1}$, was significantly greater than the $2.6 \mu\text{moles L}^{-1}$ in the alpine reaches ($P = 0.05$). Results from 1998 were similar (data not shown). Ammonium and PON concentrations in 1998 were not significantly different between alpine and forested reaches, whereas concentrations of $\text{NO}_3\text{-N}$ ($P = 0.02$) and DON ($P = 0.001$) were significantly different. The downstream change in the relative proportion of organic and inorganic N was closely related to the total amount of N in streamwater (Figure 4). For all sites in 1998 and 1999, seasonal VWM concentrations of TDN were significantly related to the DIN:DON ratio ($R^2 = 0.81$, $P < 0.001$). Values for TDN ranged from near $20 \mu\text{moles L}^{-1}$ at NAV to less than $1 \mu\text{moles L}^{-1}$ at SLP. The DIN:DON ratio ranged from about 30 at NAV to 6 at SLP.

Temporal Variations in Streamwater N Concentrations along the Elevational Transect

Results from GL4, SLP, and CC illustrate seasonal differences in N concentrations between the alpine (GL4) and forested (SLP and CC) portions of the catchment. Ammonium-N concentrations were low

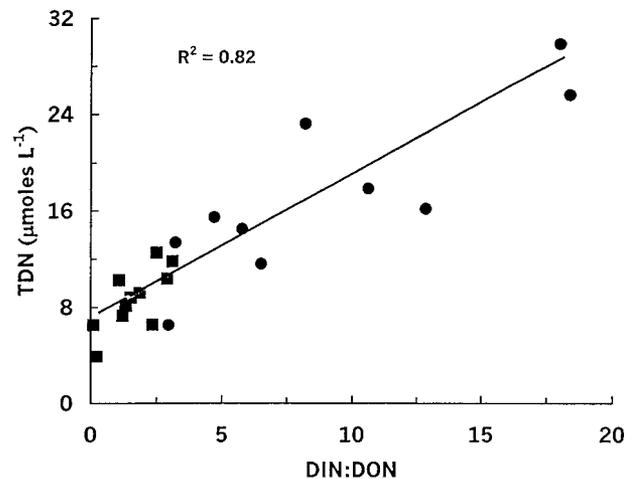


Figure 4. Relationship between mean TDN concentrations and the ratio of DIN:DON for all sampling sites in 1998 and 1999. Alpine sites, denoted by circles, had high DIN:DON ratios and high TDN concentrations compared to forested sites, which are denoted by squares. For all sites, the mean DIN:DON ratio explained 82% of the variation in mean TDN concentrations ($R^2 = 0.82$, $n = 21$, $P < 0.001$). The Como Creek catchment is included in the forested sites.

(less than $3.3 \mu\text{moles L}^{-1}$) at all three sites throughout the season (Figure 5a). Nitrate-N concentrations showed an early season peak and had a higher range ($7.4\text{--}33.5 \mu\text{moles L}^{-1}$) at GL4 than at either of the forested sites (Figure 5b). Nitrate-N concentrations at CC were less than $1.0 \mu\text{mole L}^{-1}$ throughout the season, whereas at SLP $\text{NO}_3\text{-N}$ concentrations increased on the descending limb of the hydrograph and remained at about $8.0 \mu\text{moles L}^{-1}$ throughout the summer (Figure 5b). At GL4, DON concentrations ranged from near detection limits to $5.3 \mu\text{moles L}^{-1}$ (Figure 5c). At SLP and CC, DON concentrations were generally higher, ranging from 2.3 to $10.0 \mu\text{moles L}^{-1}$, with the highest concentrations occurring on the ascending limb of the hydrograph and in the fall (Figure 5c). Similar to $\text{NH}_4\text{-N}$, PON concentrations were low at all sites (Figure 5d). Interestingly, the two forested sites, SLP and CC, were different with respect to $\text{NO}_3\text{-N}$ and DON concentrations. Nitrate-N concentrations were significantly higher at SLP than CC ($n = 15$, $P < 0.001$), while DON concentrations were significantly higher at CC than SLP ($n = 15$, $P = 0.003$).

Data from June 17 (ascending limb) and August 19 (baseflow) illustrate longitudinal differences in $\text{NO}_3\text{-N}$ and DON concentrations during early-season and late-season flows (Figure 6). Concentrations of $\text{NH}_4\text{-N}$ and PON showed little change with

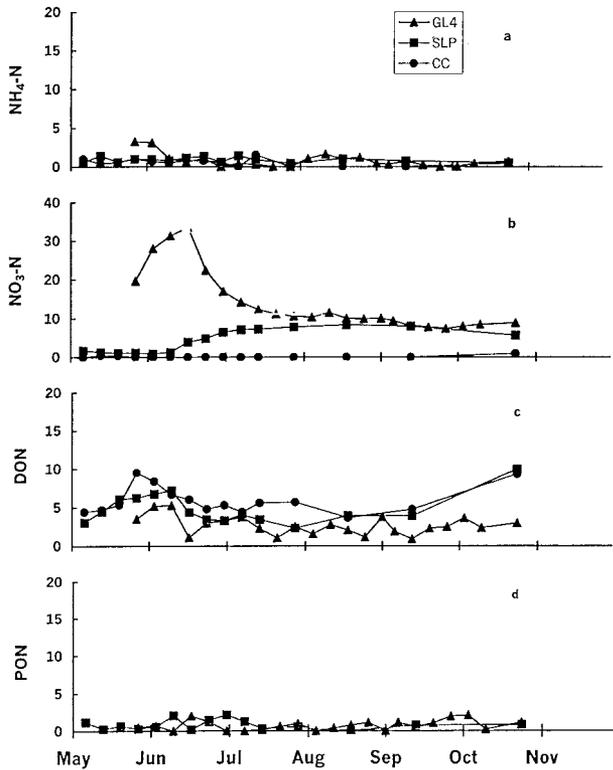


Figure 5. Streamwater N concentrations at an alpine site (GL4) and two forested sites (SLP and CC) during the 1999 sampling season. All concentrations are in $\mu\text{moles L}^{-1}$; note the difference in scale for $\text{NO}_3\text{-N}$. Streamwater could not be sampled at the GL4 site until May 27 because of deep snow and ice cover at the sampling site. GL4 had higher concentrations of $\text{NO}_3\text{-N}$ (b) and $\text{NH}_4\text{-N}$ (a) early in the season. The increase in $\text{NO}_3\text{-N}$ concentrations at SLP in June suggests that the alpine portion of the catchment may be subsidizing the streamwater inorganic N load in the subalpine. The forested SLP and CC sites had higher DON (c) concentrations for most of the season, particularly in the early summer and fall. PON concentrations (d) were low at all sites.

increasing basin area (data not shown). DON and $\text{NO}_3\text{-N}$ concentrations demonstrated relatively large changes with basin area that became less pronounced later in the season. On the rising limb of the hydrograph, $\text{NO}_3\text{-N}$ concentrations ranged from 33 to 52 $\mu\text{moles L}^{-1}$ at the five alpine sites but did not exceed 9 $\mu\text{moles L}^{-1}$ at the four forested sites (Figure 6a). During baseflow, there was little difference between alpine and forested sites with respect to $\text{NO}_3\text{-N}$ concentrations; all sites except NAV were between 7 and 11 $\mu\text{moles L}^{-1}$. DON concentrations on the rising limb of the hydrograph were lower in the alpine (0–3 $\mu\text{moles L}^{-1}$) than the forest (4–6 $\mu\text{moles L}^{-1}$) (Figure 6b). During late-season flows, there was an increase in DON concentrations with

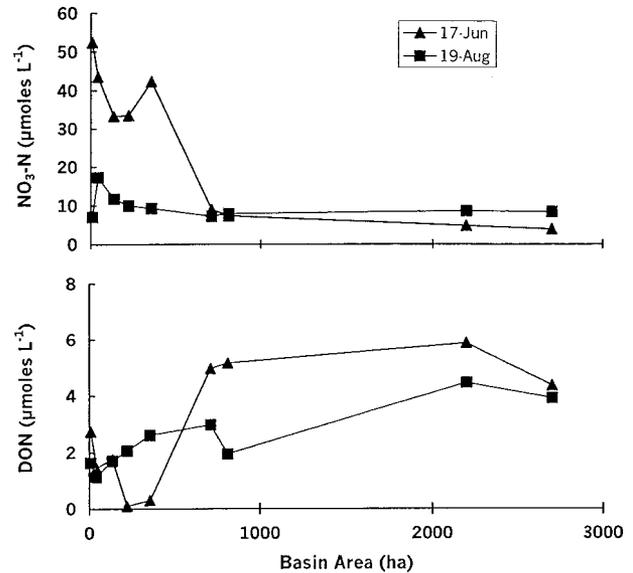


Figure 6. Relationship between streamwater $\text{NO}_3\text{-N}$ concentrations and basin area (a) and streamwater DON concentrations and basin area (b). Relationship is shown during the rising limb of the hydrograph (June 17) and during late season low flows (August 19). At both points on the hydrograph, $\text{NO}_3\text{-N}$ concentrations decreased with increasing basin area, whereas DON concentrations increased with increasing basin area.

increasing basin area although the differences between the alpine and forested sites were less pronounced.

Soil Characteristics along the Elevational Transect

There was little variation in KCl-extractable DIN from the valley floor soils in 1999 (Table 5). KCl-extractable $\text{NO}_3\text{-N}$ was near or below detection limits at all sites. Similarly, KCl-extractable $\text{NH}_4\text{-N}$ was also low, ranging from 0.26 to 1.09 mg N kg^{-1} , and was not significantly different between the alpine and subalpine reaches of the catchment ($P = 0.42$, $n = 15$). Microbial N values were much higher than KCl-extractable DIN, ranging from 8.39 to 27.70 mg N kg^{-1} . Microbial N was slightly higher in the alpine compared to the subalpine ($P = 0.03$, $n = 15$), primarily because of high values at GL4.

In contrast to microbial properties, soil C:N ratios showed a consistent increase with increasing vegetation moving downstream in the catchment (Table 5) and were significantly higher in the subalpine compared to the alpine ($P < 0.001$). Soil C:N ratios in the alpine were low and tightly clustered, ranging from 13 to 16. The soil C:N ratio was 18 at the treeline site (ALB) and increased to 30 below tree-

Table 5. Soil Characteristics at three Alpine and three Subalpine Sites along the Elevational Transect

Site	Soil C:N	NH ₄ ⁺ (mg N kg ⁻¹)	NO ₃ ⁻ (mg N kg ⁻¹)	Microbial N (mg N kg ⁻¹)
Alpine				
NAV	13.0	0.51	0	9.28
GL4	12.9	1.09	0	27.70
INL	15.6	0.37	0.03	11.12
Forested				
ALB	18.0	0.88	0.02	13.43
SLI	19.9	0.49	0	9.41
SLP	30.1	0.26	0	8.39

Soil C:N ratios showed a consistent relationship with elevation and basin area, unlike inorganic N and microbial N.

Table 6. Mean DOC Concentrations and Streamwater DOC:DON Ratios along the Elevational Transect in 1998 and 1999

Site	DOC (mg L ⁻¹)		Streamwater DOC:DON	
	1998	1999	1998	1999
ARK	0.4	NA	16.0	NA
NAV	0.6	NA	25.3	NA
GL5	0.6	NA	30.1	NA
GL4	1.1	1.4	42.0	36.4
INL	1.5	1.4	44.2	36.6
ALB	2.2	2.1	49.5	45.3
SLI	2.1	2.3	46.7	46.0
SLO	2.6	2.5	55.2	54.5
SLP	2.9	3.6	54.7	52.5

DOC, dissolved organic carbon; DON, dissolved organic nitrogen

line. Moreover, regression analysis showed that soil C:N ratio was highly correlated with landscape position in the catchment as represented by elevation ($R^2 = 0.80$, $P < 0.01$).

Relationships between Streamwater N and C and Soil C:N Ratios

DOC in streamwater was measured concurrently with N at nine sites along the elevational transect in 1998 and again at six sites in 1999. Mean DOC concentrations ranged from 1.4 to 3.6 mg C L⁻¹ and showed a similar pattern to DON with higher values at the forested sites than the alpine sites (Table 6). Similarly, annual streamwater DOC:DON ratios increased moving downstream from 36–39 in the alpine to 52–54 at forested sites. Simple regression analyses show that soil C:N ratios (independent variable) along the transect explained 78% of the

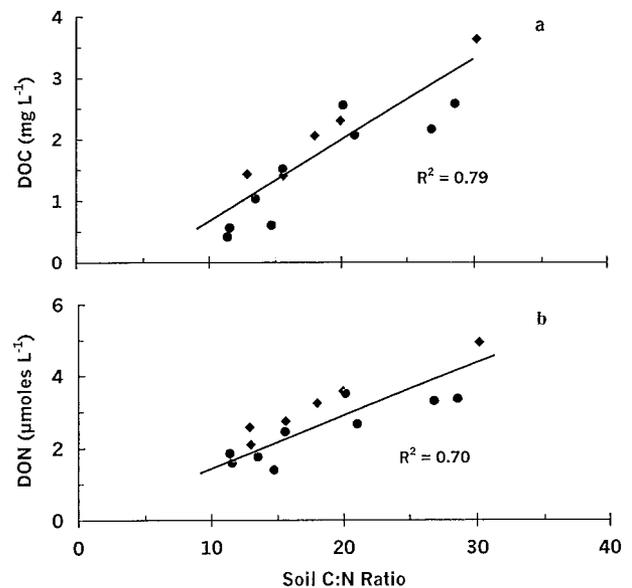


Figure 7. Relationship between soil C:N ratios and streamwater DOC (a) and DON (b) concentrations along the elevational transect in 1998 and 1999. DOC and DON were highly correlated to the relative amounts of C and N in soils along the transect. The slope of the relationship between soil C:N and both DOC and DON were not significantly different between years (t -test, $P < 0.05$), so data from both years are shown together. 1998 data are shown as circles; 1999 data are shown as diamonds.

variation in mean DOC concentrations ($P < 0.01$, $n = 14$) in 1998 and 1999 (Figure 7a). Similarly, soil C:N ratios explained 70% of the variation in mean DON concentrations ($P < 0.001$, $n = 15$) for the 2 years (Figure 7b).

The stoichiometry of both terrestrial and aquatic organic matter were also somewhat useful predictors of NO₃-N concentrations in surface waters. Seasonal VWM NO₃-N concentrations along the transect were inversely correlated with soil C:N ra-

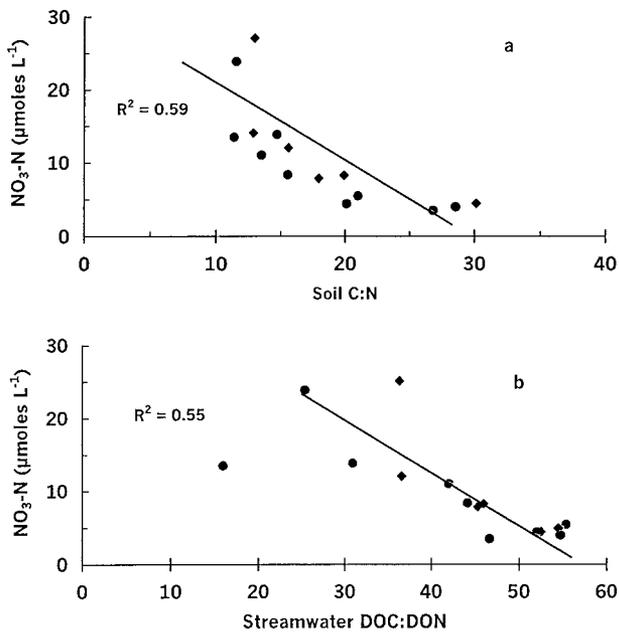


Figure 8. Seasonal mean $\text{NO}_3\text{-N}$ concentrations were correlated with organic C:N ratios in both soil and streamwater along the elevational transect. The slope of the relationship between $\text{NO}_3\text{-N}$ and C:N ratios in soil (a) and streamwater (b) were not significantly different between years (*t*-test, $P < 0.05$), so data from both years are shown together. 1998 data are shown as circles; 1999 data are shown as diamonds.

tios for the 2 years of sampling (Figure 8a). During this time period, soil C:N ratios explained about half of the variation in $\text{NO}_3\text{-N}$ concentrations ($R^2 = 0.58$, $P = 0.001$, $n = 15$). This relationship suggests a link between near-surface soil C and N pools and $\text{NO}_3\text{-N}$ export. Interestingly, streamwater DOC: DON ratios were nearly as effective as soil C:N ratios in terms of predicting streamwater $\text{NO}_3\text{-N}$ concentrations ($R^2 = 0.55$, $P = 0.002$, $n = 15$) (Figure 8b).

The slopes of the regression lines between soil C:N ratios and DOC, DON, and $\text{NO}_3\text{-N}$ varied by less than 15% between 1998 and 1999. These results suggest that there may be an interannual consistency in the relationship between soil organic matter stoichiometry and yields of organic matter and $\text{NO}_3\text{-N}$ in streamwater. Unlike DON and $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ and PON concentrations showed no significant relationship to soil C:N ratios in either 1998 or 1999 ($R^2 < 0.15$, $P > 0.3$ for all comparisons).

DISCUSSION

Major Solutes and N Species Concentrations

Concentrations of all four N species in surface waters were at best only weakly correlated with DOC

($R^2 = 0.06$ for $\text{NO}_3\text{-N}$, $R^2 = 0.27$ for DON). These results suggest that the controls on the export of N species to surface waters may be different from those for DOC. The low correlation between DOC and DON in surface waters is somewhat surprising and deserves further explanation. The ratio of streamwater DOC: DON in headwater catchments changes dramatically during snowmelt runoff, with the highest DOC: DON ratios occurring close to peak runoff (Williams and others 2001; Stepanauskas and others 2000). Our results show that there is also a longitudinal change in the DOC: DON ratio in streamwater, with substantially higher DOC: DON ratios in the subalpine compared to the alpine. Taken together, these findings suggest that the lack of correlation between DOC and DON concentrations is a result of both seasonal and longitudinal changes in the C:N ratio of dissolved organic matter (DOM). Although the mechanisms behind these shifts in the elemental ratio of DOM are not well understood, it is likely that there are temporal and elevation changes in the pools of DOM precursor material that are hydrologically connected to North Boulder Creek.

Concentrations of N species in North Boulder Creek were poorly correlated with both base cations (C_B) and Si ($R^2 \leq 0.14$ for all tests). This is not surprising given that the primary source of C_B and Si is geochemical weathering of bedrock (Garrels and McKensie 1967). Interestingly, nitrate was most strongly correlated with H^+ ($R^2 = 0.23$). Driscoll and others (1987) report a strong negative correlation between NO_3^- concentrations and acid-neutralizing capacity (ANC) in a forested headwater stream in the Adirondacks and suggest that nitric acid inputs to the stream were a primary control on ANC. On North Boulder Creek, Caine (1995) and Williams and Tonnessen (2000) have documented a decreasing trend in ANC at high-elevation sites during the last 2 decades coincident with increasing inorganic N in wet deposition. Thus, it is possible that increased rates of $\text{NO}_3\text{-N}$ leaching to the hydrologic system are in part responsible for the long-term decline in ANC.

Concentrations and Yields of N

Inorganic N. In many forested (Campbell and others 2000a; Kortelainen and others 1997) and pristine (Hedin and others 1995) catchments, concentrations of organic N are higher than DIN concentrations in surface waters. For example, high-elevation catchments at Lake Tahoe (Coats and Goldman 2001) and the southern Sierra Nevada (Williams and others 1995) have organic N concentrations in streamwater that are 1.5–4 times higher

than DIN concentrations. However, in watersheds in the Colorado Front Range, DIN concentrations are typically elevated during snowmelt and often exceed DON concentrations (Campbell and others 1995; Baron and Campbell 1997; Williams and others 2001). On North Boulder Creek, mean annual DIN concentrations were higher than organic N concentrations in streamwater at every sampling site except SLP and CC, the lowest subalpine sites. The dominance of DIN was particularly striking at the five alpine sites, where DIN concentrations comprised 74%–92% of the N in streamwater.

NO₃-N was the dominant form of N in streamwater and yields and concentrations of DIN decreased sharply across the alpine/subalpine ecotone, indicating that catchment retention of DIN increases dramatically as the areal extent of soil and vegetative cover increases. This finding is consistent with the hypothesis that during snowmelt alpine soils are a net source of inorganic N whereas subalpine soils are a net sink (Stottlemeyer and others 1997; Heuer and others 1999). Headwater streams frequently retain and transform more than 50% of the inputs of inorganic N from their watershed (Peterson and others 2001). This is particularly true of smaller streams, which have a high surface to volume ratio that facilitates the rapid uptake and processing of N. Thus, it is likely that the removal of NO₃-N by biological assimilation and denitrification within channelized flow also contributed to the downstream decrease in NO₃-N yields. Yields and concentrations of NH₄-N were quite low, reflecting strong sorption and/or rapid nitrification of NH₄-N in catchment soils.

The fact that DIN concentrations on North Boulder Creek remained elevated (5–10 µeq L⁻¹) nearly 5 km below treeline suggests that DIN leaching in the alpine was affecting the N balance of downstream aquatic sites. To illustrate, a paired *t*-test showed that seasonal NO₃-N concentrations at SLP, the lowest elevation subalpine site on North Boulder Creek, were significantly higher than at Como Creek, the forested control catchment ($P < 0.001$). The SLP site is nearly identical to the CC site in terms of aspect, elevation, and land cover, although the catchment area is approximately four times larger. However, the SLP site receives streamflow from the alpine headwaters of North Boulder Creek, whereas the Como Creek watershed is almost entirely subalpine forest (Figure 1). As a result, it appears that the DIN concentrations at SLP were being subsidized by NO₃-N export from the alpine reaches of the catchment. As alpine areas become N-saturated from increasing N deposition, more NO₃-N is expected in streamwater (Baron and

others 1994; Williams and others 1996a; Campbell and others 2000b). Consequently, downstream aquatic systems will receive additional NO₃-N, with the possibility that the episodic acidification that now occurs at alpine sites on North Boulder Creek during snowmelt (Caine 1995) may extend into the subalpine.

Organic N. Concentrations of DON in the alpine and subalpine reaches of North Boulder Creek were substantially higher than typical DON concentrations in the seasonal snowpack (Williams and others 2001), suggesting that much of the organic N in streamwater is produced within the catchment. On the whole, DON comprised a substantial amount of total N at alpine (12%–16%) and particularly subalpine sites (25%–45%) on North Boulder Creek. These losses of N via DON as a percentage of total N losses in streamwater, though significant, are quite low compared to unpolluted primary forests where N losses are overwhelmingly dominated by DON (Perakis and Hedin 2002).

Few studies have reported concentrations and yields of organic N species in high-elevation catchments. The mean concentrations of DON that we report for the alpine reach of North Boulder Creek are similar to values estimated from fulvic acid concentrations in streamwater at the alpine/subalpine Loch Vale watershed in Colorado (Baron and Campbell 1997). The late season increase in DON concentrations apparent at the forested, subalpine sites is consistent with the findings of Currie and others (1996), who attributed seasonal increases in DON in forest floor leachates at Harvard Forest to the flushing of decomposition products accumulated during late summer. In our study catchment, increased phytoplankton growth in alpine lakes during the late summer and fall (McKnight and others 1993) may also contribute to instream DON concentrations.

PON concentrations were two to ten times lower than DON concentrations at all sites. This is likely a result of low levels of overland flow and minimal direct vegetative inputs into the stream. McKnight and others (1993) documented a similar seasonal relationship between suspended organic carbon (SOC) and DOC in the subalpine Deer Creek catchment in central Colorado. In Deer Creek, SOC concentrations were typically an order of magnitude lower and much less variable than DOC concentrations over the course of one snowmelt season.

Yields of DON at our high-elevation site (0.34–0.41 kg N ha⁻¹) were comparable to the average yield of 0.57 kg ha⁻¹ reported for 10 streams in the subalpine Lake Tahoe basin (Coats and Goldman 2001). However, the DON yields on North Boulder

Creek were lower and less variable than results from 10 forested watersheds in the northeast United States, which had a range of 0.5–2.4 kg ha⁻¹ for DON export (Campbell and others 2000a; Meyer and others 1981). Yields of PON on North Boulder Creek were similar to the 0.2 kg ha⁻¹ documented at Bear Brook, New Hampshire (Meyer and others 1981), but less than half of the 0.47 kg ha⁻¹ documented in the Lake Tahoe basin (Coats and Goldman 2001).

Landscape Controls on Organic and Inorganic N Leaching

The sharp decline in DIN yields and concentrations moving downstream on North Boulder Creek appears to reflect the shift in landcover type across the alpine/subalpine ecotone. The alpine portion of the catchment is characterized by large areas of talus and exposed bedrock, which do not retain inorganic N (Williams and others 1997; Campbell and others 2000b). In addition, highly variable snow distribution above treeline can affect both N loading within the catchment and N retention by subniveal microbial populations. In contrast, the subalpine reach of the catchment has extensive vegetation and well-developed soils that facilitate the retention of inorganic N via root and microbial uptake.

Our data appear to support the “leaky faucet” hypothesis: that DON losses persist at a relatively steady rate despite ecosystem demands for N (Hedin and others 1995; Vitousek and others 1998). Yields of DON remained relatively constant as basin area increased along our sampling transect, particularly in comparison to DIN yields, which decreased by a factor of 5 moving from the highest reaches of the catchment downstream to treeline. These findings indicate that although DON acts as an important vector for the hydrologic loss of N in both the alpine and subalpine portions of the catchment, the ability of DON losses to balance N inputs is being overwhelmed at the highest reaches of the catchment. Further, the fact that yields of NO₃-N were much higher than yields of DON at sites above treeline is consistent with previous experimental studies indicating that nitrate losses respond more rapidly than DON losses to inorganic N fertilization (Currie and others 1996).

Interestingly, concentrations of DON on North Boulder Creek demonstrated a close correspondence to soil C:N ratios within the catchment. Previous work has demonstrated a link between soil C:N ratios and DOC flux at the basin scale; however, the mechanisms responsible for this relationship are difficult to pinpoint (Aitkenhead and McDowell 2000). Our results suggest that DON losses

in streamwater are related to the standing stocks of C and N in catchment soils. The fact that DON losses in streamwater were correlated with soil C:N ratios but were not related to either microbial N or soil pools of inorganic N lends further support to the hypothesis that DON production is largely free of immediate microbial control (for example, see Neff and others 2001; Perakis and Hedin 2001).

Indicators of Ecosystem N Status

The North Boulder Creek catchment shifts from being N-saturated, with inorganic N in excess of biotic demands (for example see Aber and others 1998), at its alpine headwaters to being N-limited in the downstream subalpine forest. This contrast within the catchment provides the opportunity to substitute space for time to evaluate several proposed indicators of ecosystem N status, including (a) the organic C:N ratio in soil (Gunderson and others 1998), (b) the organic C:N ratio in streamwater DOM (Kortelainen and others 1997; Campbell and others 2000a, Goodale and others 2000), and (c) the DIN:DON ratio in streamwater (Williams and others 2001).

Organic C:N Ratio in Soil. Our results suggest that the soil C:N ratio is a useful indicator of ecosystem capacity to retain NO₃-N in high-elevation catchments. On North Boulder Creek, the low C:N ratios in the alpine were reflected in high NO₃-N concentrations in streamwater. This is consistent with the increase in net nitrification seen at soil C:N ratios below 25 (Gunderson and others 1998). Below treeline, higher soil C:N ratios were reflected in consistently lower NO₃-N concentrations in streamwater.

Organic C:N Ratio in Streamwater. Campbell and others (2000a) contend that streamwater organic C:N ratios provide a more integrated watershed signal than soil C:N ratios. In our study, DOC:DON ratios in streamwater explained nearly the same amount of variation (55%) in annual NO₃-N concentrations as the soil C:N ratio. This finding indicates that streamwater DOC:DON ratios may be reflective of spatial patterns of soil C:N and net nitrification within the catchment. However, the fact that soil and streamwater C:N ratios explained only about half of the variation in NO₃-N leaching suggests that factors other than catchment soil organic matter stoichiometry play an important role in NO₃-N retention in the North Boulder Creek watershed. In high-elevation watersheds, the timing and depth of snow accumulation may also be an important control on catchment-scale losses of inorganic N (Brooks and others 1998; Brooks and Williams 1999).

DIN:DON Ratio in Streamwater. The annual ratio of DIN:DON in streamwater in North Boulder Creek decreased by more than an order of magnitude between the catchment headwaters and the downstream subalpine forest. This consistent shift in the DIN:DON ratio suggests that this metric effectively captures the change in ecosystem N status from N-saturated (high DIN:DON) above treeline to N-limited (low DIN:DON) downstream in the subalpine forest. Furthermore, the Como Creek control catchment, which is strongly N-limited, had the lowest DIN:DON ratio of any sampling site in our study.

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