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NITROGEN FLUXES IN A HIGH ELEVATION COLORADO ROCKY MOUNTAIN BASIN

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ABSTRACT

Measured, calculated and simulated values were combined to develop an annual nitrogen budget for Loch Vale Watershed (LVWS) in the Colorado Front Range. Nine-year average wet nitrogen deposition values were 1·6 ($s = 0{\cdot}36$) kg NO_3-N ha^{-1}, and 1·0 ($s = 0{\cdot}3$) kg NH_4-N ha^{-1}. Assuming dry nitrogen deposition to be half that of measured wet deposition, this high elevation watershed receives 3·9 kg N ha^{-1}. Although deposition values fluctuated with precipitation, measured stream nitrogen outputs were less variable. Of the total N input to the watershed (3·9 kg N ha^{-1} wet plus dry deposition), 49% of the total N input was immobilized. Stream losses were 2·0 kg N ha^{-1} (1125 kg measured dissolved inorganic N in 1992, 1–2 kg calculated dissolved organic N, plus an average of 203 kg algal N from the entire 660 ha watershed). Tundra and aquatic algae were the largest reservoirs for incoming N, at approximately 18% and 15% of the total 2574 kg N deposition, respectively. Rocky areas and forest stored the remaining 11% and 5%, respectively. Fully 80% of N losses from the watershed came from the 68% of LVWS that is alpine. © 1997 by John Wiley & Sons, Ltd.

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KEY WORDS nitrogen; annual budget; dry and wet deposition; watershed; Rocky Mountains

INTRODUCTION

Historically, nitrogen has been among the nutrients most often limiting to the growth of aquatic and terrestrial organisms (Aber *et al.*, 1989; Stoddard, 1992). Recently, however, there is increasing evidence that N limitation has been overcome in a number of diverse environments (Likens *et al.*, 1977; Ågren and Bosatta, 1988; Aber *et al.*, 1989; Schelske, 1991; Tietema and Verstraeten, 1991; Stoddard, 1992; Stoermer *et al.*, 1993; Galloway *et al.*, 1994). Globally, increased nitrogen availability is due in part to large regional increases in nitrogen oxide emissions (Brimblecombe and Stedman, 1982; Schindler and Bayley, 1993; Galloway *et al.*, 1994), agricultural ammonia emissions (van Breeman *et al.*, 1987; Schlesinger and Hartley, 1991), and waste water and agricultural effluent (Brezonik, 1972; Valiela *et al.*, 1990).

In the Front Range of the Colorado Rocky Mountains a number of alpine and subalpine lakes have high concentrations of nitrate (6·3–16·8 μeq NO_3 l^{-1}; Eilers *et al.*, 1986), including Loch Vale Watershed (LVWS) lakes in Rocky Mountain National Park, with an annual mean 1982–1992 concentration of 16·2 μeq NO_3 l^{-1} (Baron, 1992). Mean deposition rates of N in wetfall in Loch Vale Watershed are 1·6 ($s = 0{\cdot}36$) kg NO_3-N ha^{-1}, and 1·0 ($s = 0{\cdot}3$) kg NH_4-N ha^{-1} for the nine years 1984–1992 (NADP/NTN Data Base, 1993). These values are greater than those that are considered background N deposition values (about 0·2 kg N ha^{-1}) typical of remote, non-industrialized parts of the world (Galloway *et al.*, 1982; Hedin *et al.*, 1995). The plains adjacent to the Colorado Front Range include Denver and other metropolitan areas and a major agricultural region, and, frequently, surface winds flow up into the mountains, drawing agricultural and urban air to high elevations (Parrish *et al.*, 1990; Langford and Fehsenfeld, 1992; Baron and Denning, 1993). Additionally, the predominant westerly winds contribute nitrate to snowpacks from western

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sources (Turk *et al.*, 1992). For this paper, results from a variety of published and original data are synthesized in order to develop a model of nitrogen flux in Loch Vale Watershed, and to explore the fate of atmospherically deposited nitrogen in alpine and subalpine terrestrial and aquatic ecosystems.

Site description

Loch Vale Watershed (LVWS) is a 6·6 km^2 north-east-facing basin located in Rocky Mountain National Park, Colorado. Streams and four lakes are located in a narrow glaciated valley 500–1000 m below surrounding granitic cliffs (Figure 1). Three lakes, Sky Pond, Glass Lake and Andrews Tarn, are alpine, with a combined volume of 173 000 m^3. The Loch is a shallow 61 100 m^3 lake below treeline. A fourth-order stream drains the basin at The Loch outlet, where discharge has been measured since 1983. Two alpine subbasins, Icy Brook (2·8 km^2) and Andrews Creek (1·5 km^2), drain into subalpine Icy Brook, with a watershed area of 2·3 km^2. Although the stream below the confluence is bordered by meadow and forest, the slopes of this subalpine portion are either unvegetated or covered by sparse tundra. The percentage cover by landform for the entire 6·6 km^2 is 81% rock, 11% tundra, 6% forest, 1% meadow and 1% surface waters. The forest is a mature stand of Englemann spruce and subalpine fir, and trees are greater than 500 years in age (Arthur and Fahey, 1992).

The climate is continental and characterized by strong westerly winds, particularly during the winter months. Mean annual temperature is 1·5°C, with January minimum and maximum temperatures of −10·9 and −2.9°C, respectively. July minimum and maximum temperatures are 7·7 and 19·5°C, respectively. Of the approximately 110 cm precipitation per year, 65–80% occurs as snow. Much of the remainder occurs as summertime cloudbursts that originate from up-valley funnelling of warm air from lower elevations. As the uplifted air rises, cools and condenses, thunderstorms often develop (Baron and Denning, 1993).

METHODS

Precipitation

Precipitation is measured with two Belfort rain gauges located at 3160 m elevation adjacent to a solar-powered remote area weather station. One rain gauge is equipped with an alter wind shield, and the other with a nipher wind shield. A comparison of performance of the two shields showed an insignificant difference, so the two have been used interchangeably to create the most complete record (Bigelow *et al.*, 1990).

Precipitation chemistry is measured with an Aerochemetrics collector located adjacent to a meteorological station. Precipitation has been collected weekly since September 1983, as part of the National Atmospheric Deposition Program/National Trends Network (NADP/NTN Data Base, 1993). NADP procedures are described in Peden (1986). Wet deposition is presented as kg per watershed and is calculated as the product of the volume-weighted mean concentration and the total measured precipitation for each time sequence. Precipitation collected in summer 1986 was contaminated; mean summer values from the other nine years were substituted in order to develop a full 1986 deposition year.

Stream discharge and chemical composition

Stream discharge is monitored at two alpine tributaries and at the outlet to the entire basin in LVWS (Figure 1). Stage height at the tributaries was recorded at 15 minute intervals beginning in April 1992. Discharge was measured once to twice per week during spring runoff to develop discharge rating curves. The uncertainty associated with this method of calculation is 4% (Winter, 1981). The discharge record was extended through the winter months using a logarithmic extrapolation of stream flow recession. Because the estimates of winter flow were 0·5% of the annual total for Icy Brook and 7·0% for Andrews Creek, the overall uncertainty introduced by the extrapolation was considered insignificant to overall budget estimates.

Stream discharge at The Loch outlet was calculated from continuous measurements of stream stage in a Parshall flume since 1983. The flume was calibrated for stream stages of 6 cm or more; very low flows during the winter were unmeasurable. Stage heights at low flows were assigned, instead, as follows: in October the

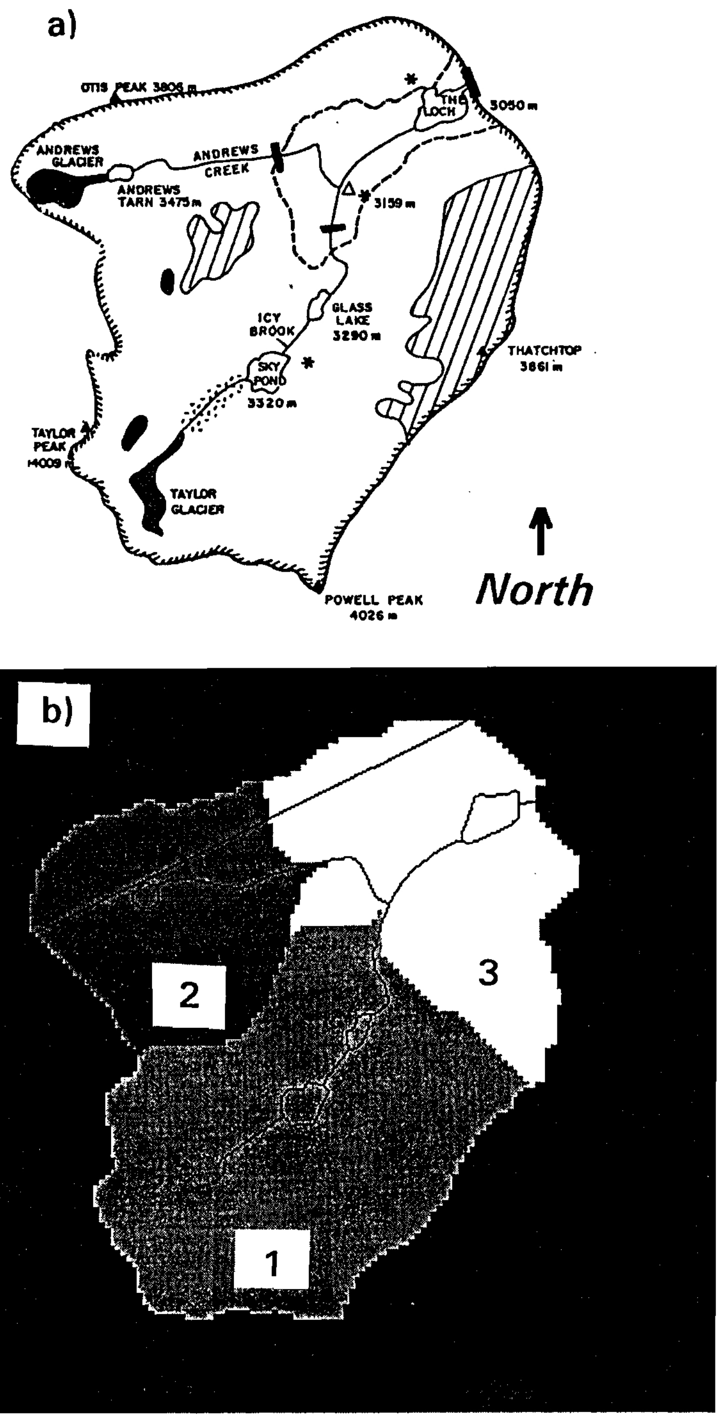

Figure 1. Map of Loch Vale Watershed in Rocky Mountain National Park, Colorado. (a) Major landforms. Hatched areas are alpine tundra, the area within the dotted line is forest, and remaining areas are bedrock or talus. Stream gauging stations are shown by dark rectangles; the meteorological station is shown with an open triangle; (b) Loch Vale Watershed subbasins: Icy Brook (alpine) (1), Andrews, Creek (alpine) (2) and Icy Brook (subalpine) (3). The line running through (b) is the Alva Adams tunnel. This figure was generated with GRASS 4.1

last valid recorded reading was carried through to the end of the month; in November the stage was set to 0·036 m; in December 0·019 m; January and February 0·002 m; March 0·019 m; and April 0·036 m, until the stage increased to measurable values. The uncertainty assigned to Parshall flumes is 5%; another 5% was added to account for slight leakage around the flume (Winter, 1981; Baron, 1992).

Seasons were defined for this paper as winter, spring and summer, based on examination of the measured hydrograph and observed weather parameters (Baron and Bricker, 1987). Winter, the period from 1 October–14 April, corresponds to minimum surface water drainage from the basin. All precipitation that occurred during this time is assumed to have accumulated within Loch Vale as cold snowpack. Spring, from 15 April–14 July, is when that snowpack is released. This is the period of maximum discharge. Summer is defined as the rest of the year, 15 July–30 September, and corresponds to declining flow.

Stream water samples were collected manually and by autosampler at varying time intervals, ranging from daily to weekly. Samples were collected in acid-washed bottles, filtered with 0·45 μm filters and analysed by ion chromatography. The mean relative percentage difference was less than 15% for 80 NO_3 duplicate samples, and less than 42% for 65 NH_4 paired samples over the period 1983–1993. As expected, major constituents of water, such as NO_3, are analysed more precisely than those present in trace amounts, such as NH_4. Ammonium concentrations were close to the 0·166 $\mu eq\ l^{-1}$ detection limit, and NO_3 concentrations were often much greater than the 0·161 $\mu eq\ l^{-1}$ detection limit.

Terrestrial ecosystem processes

Nitrogen imports and exports from alpine tundra and subalpine forest were taken from previously published results of CENTURY model simulations for LVWS (Baron *et al.*, 1994). CENTURY is a general model of plant–soil ecosystems that represents carbon, nitrogen and other nutrient dynamics (Sanford *et al.*, 1991; Parton *et al.*, 1993). Climate data from LVWS for forest, and from Niwot Ridge, Colorado, for alpine tundra, were used to run the model. The separate forest and tundra runs were initialized with previously published measurements from the two sites, such as above- and below-ground plant tissue C and N, percentage soil organic matter and other soil attributes (Webber and May, 1977; Arthur and Fahey, 1992; Baron *et al.*, 1992, 1994). The simulated results at steady state (1066 year runs) compared well with additional, previously unused data from the two sites, as well as measured values from other similar forest and tundra ecosystems (Cole and Rapp, 1981; Vogt *et al.*, 1986; Prescott *et al.*, 1989; Bowman, 1992; Bowman *et al.*, 1993; Baron *et al.*, 1994; Walker *et al.*, 1994).

Phytoplankton biomass N

Chlorophyll *a* measurements from 1984 to 1986 (McKnight *et al.*, 1986, 1988) from surface, middle and bottom waters were averaged for each season for The Loch and Sky Pond. Ratios of C: chlorophyll *a* in phytoplankton vary depending on the availability of P. A ratio of C: chlorophyll *a* of 8 $\mu mol\ C\ \mu g\ chl\ a^{-1}$ was used, based on the finding of Morris and Lewis (1992) that Rocky Mountain lake biota have severe P limitations and on C: chlorophyll *a* ratios reported by Hecky *et al.* (1993) for P-deficient phytoplankton. Phytoplankton N was then bracketed using C: N ratios of 7–12, which are similar to C: N ranges found from N-rich, P-poor subarctic or temperate lakes (Hecky *et al.*, 1993). The resulting values were summed by season for the volume times seasonal turnover rates in total water volume of The Loch, and the volume times seasonal turnover rates in total water volume of alpine lakes (Sky Pond plus Glass Lake), to yield phytoplankton N contents. Turnover rates were estimated from Baron (1992) to be 15, 5 and 1 per season, for Sky Pond and Glass Lake, and 60, 22 and 1 per season for The Loch for spring, summer and winter, respectively.

RESULTS

Measured water fluxes

Measured precipitation ranged from 85·1 cm in the driest year (1989) to 125·8 and 125·3 cm in 1984 and 1986, the two wettest years (Table I). The highest discharge was during the years of greatest precipitation,

Table I. Water fluxes (cm) for Loch Vale Watershed, 1984–1993. Water years are 1 October–30 September

Year	Precipitation (P)	Discharge (Q)	$P-Q$	% Evaporation*
1984	125·8	91·3	34·5	0·27
1985	110·7	67·5	43·2	0·39
1986	125·3	93·5	31·8	0·25
1987	102·7	74·8	27·9	0·27
1988	94·3	73·5	20·8	0·22
1989	85·1	65·4	19·6	0·23
1990	119·0	74·6	44·4	0·37
1991	105·9	74·0	31·9	0·30
1992	96·5	58·9	37·6	0·39
1993	120·4	76·5	43·9	0·36

* Evaporation, transpiration and sublimation, calculated by difference between precipitation and discharge.

91·3 cm in 1984 and 93·5 cm in 1986; the lowest discharge of 65·4 cm was during 1989. The difference between measured precipitation and measured discharge ranged between 19·6 and 44·4 cm, or 22–39% of precipitation. This is consistent with the calculated evaporative water losses (evaporation, evapotranspiration, and sublimation) rates of Baron (1992), using a combination of values depending on season and land cover type.

Discharge hydrographs for 1992 were representative of other years (Figure 2). Discharge occurs year round at The Loch outlet and Andrews Creek; in Icy Brook, flow ceases during the winter months and resumes during spring snowmelt. Approximately half of the total discharge of LVWS was from the 290 ha of Icy Brook basin that is above the treeline, and another third came from the 160 ha Andrews Creek sub-basin.

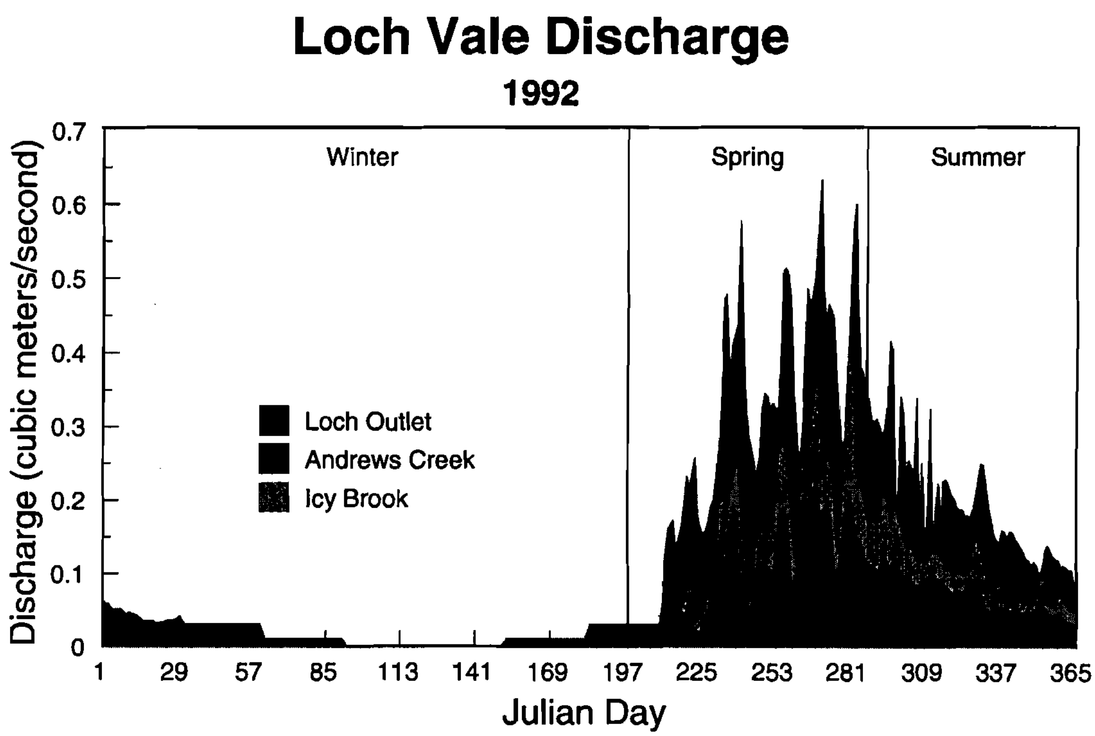

Figure 2. Discharge for water year 1992. Icy Brook and Andrews Creek are alpine tributaries in Loch Vale Watershed. The Loch outlet is the furthest downstream extent of the watershed. Julian days from 1 October 1991 are shown on the x-axis

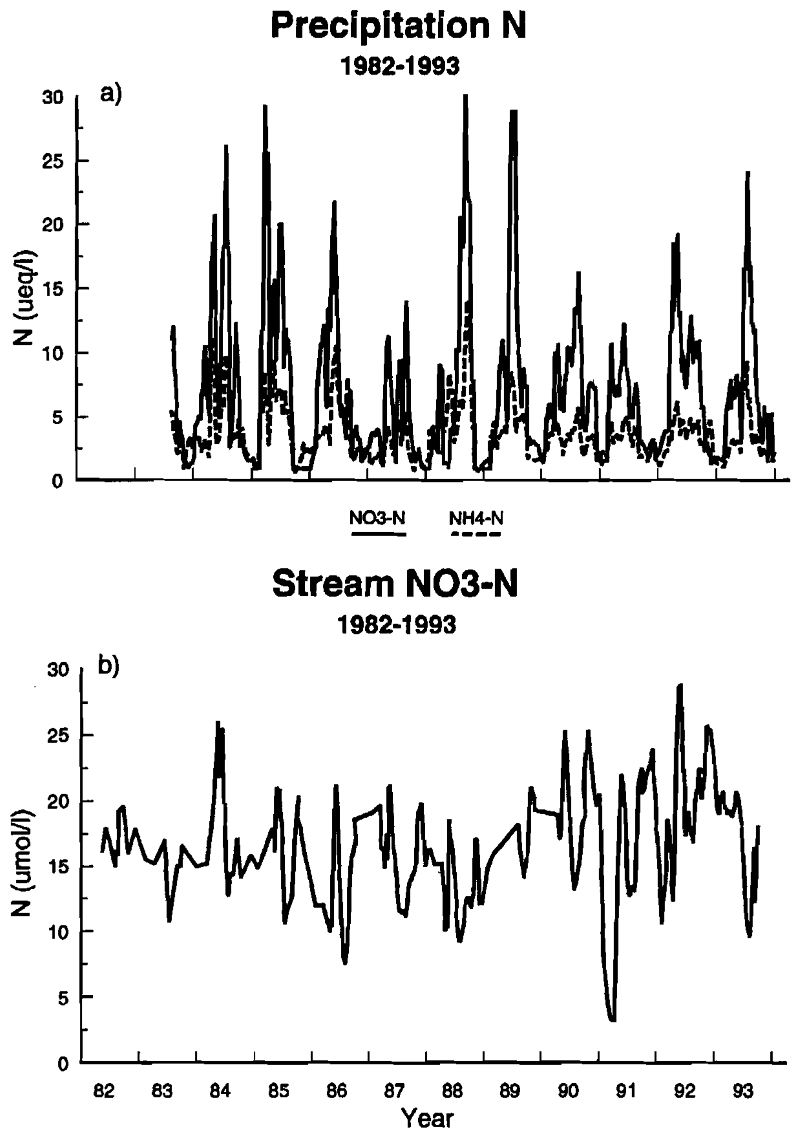

Figure 3. Time series, from 1982 to 1993, of N concentrations (μeq l^{-1}) of (a) precipitation NH_4-N and NO_3-N and (b) stream NO_3-N in Loch Vale Watershed. Stream values are from The Loch outlet

The remaining water was supplied during the spring by snowmelt from the subalpine portion of the basin into The Loch or its tributaries. The subalpine water contribution was negligible during the summer season.

Nitrogen concentrations

Nitrate concentrations in precipitation were greater than ammonium concentrations (Figure 3a). Stream nitrogen was almost exclusively nitrate and, with the exception of low values observed in 1991, fluctuated around 16·2 μeq NO_3 l^{-1} (Figure 3b).

Maximum nitrate concentrations were found in Andrews Creek, intermediate concentrations in Icy Brook and the lowest concentrations were usually measured at The Loch outlet (Figure 4). Nitrate concentrations at all sites were seasonally dynamic; maximum concentrations were measured in early spring just after the

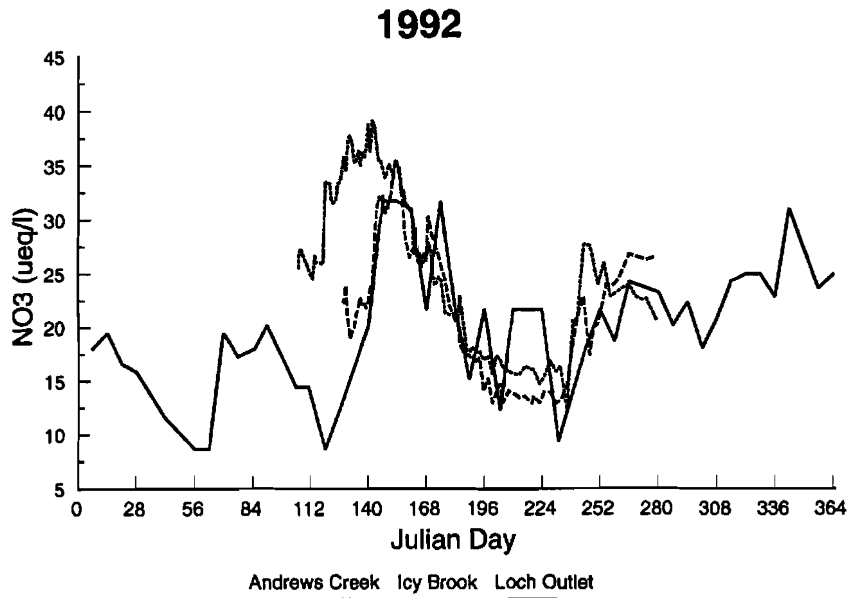

Figure 4. Nitrate concentrations (μeq/l) in Icy Brook, Andrews Creek and at The Loch outlet for water year 1992

beginning of snowmelt. Concentrations declined to their lowest levels during midsummer. Nitrate concentrations increased again at the end of the summer and remained between 8 and 20 μeq l^{-1} for The Loch outlet until the beginning of the spring snowmelt.

Calculated algal N

Algal biomass varied considerably in LVWS from year to year, over the seasons (Spaulding *et al.*, 1993) and from lake to lake (McKnight *et al.*, 1986, 1988). Cell numbers were much greater in Sky Pond (ave. 59 900, $s = 55\,570$, $n = 46$) than in The Loch (ave. 5880 cells ml^{-1}, $s = 4460$, $n = 57$). Mean chlorophyll *a* was more abundant in Sky Pond than The Loch during all seasons; the highest mean value of 5·18 ($s = 4{\cdot}20$) μg l^{-1} occurred in the winter, and the lowest mean value of 3·75 ($s = 1{\cdot}41$) μg l^{-1} was found during the summer (Table II). Winter chlorophyll *a* was also highest for The Loch, with an average of 4·65 ($s = 3{\cdot}92$) μg l^{-1}; but spring season chlorophyll *a* was lower than summer values, with a mean of 1·28 ($s = 0{\cdot}73$) μg l^{-1}, possibly because of rapid lake water turnover during snowmelt (Baron, 1992; McKnight *et al.*, 1990). Chlorophyll *a* values were highly variable, reflecting the dynamic nature of algal populations. The alpine lakes have significantly greater lake volumes, and they turn over less frequently, and this influenced the total amount of N calculated in algal biomass for alpine versus subalpine lakes. We calculated a range of 36–56 kg N ha^{-1} yr^{-1} for Sky Pond and Glass Lake, compared with a range of 13–25 kg N ha^{-1} yr^{-1} for The Loch.

Nitrogen fluxes

Loch Vale Watershed. In general, more N was deposited in wetter years, but there was not a one-to-one relationship between measured amounts of precipitation and annual wet N deposition (Table I, Figure 5). Somewhat less than half of the total annual N in precipitation was deposited during the winter season; the remainder was distributed evenly between spring and summer.

Measured efflux from the watershed did not fluctuate as greatly as influx, although there was some indication that more N left during high precipitation years (Figure 5). The bulk of the N efflux was during spring, although a significant fraction was also lost during the summer season. An average of 43% of the total N entering the basin from wet deposition flushed out of LVWS in any given year.

Table II. Ranges of N in algal biomass calculated from the average (and standard deviation) of measured chlorophyll *a* values (McKnight *et al.*, 1986, 1988). Values are derived assuming a C : chlorophyll *a* ratio of 8, and a range of C:N of 7–12 (Hecky *et al.*, 1993). Chlorophyll *a* was measured in Sky Pond and The Loch. Volumetric calculations were made using a total of 147 374 m^3 and 4·04 ha for alpine lakes (Sky Pond and Glass Lake), and 61 100 m^3 and 4·98 ha for The Loch. Seasonal turnover rates from Baron (1992) of 15, 5 and 1, for Sky Pond and Glass Lake, and 60, 22 and 1 for The Loch for spring, summer and winter, respectively, were used to determine seasonal algal N

	Spring		Summer		Winter		Total	
	n	Average (s)	*n*	Average (s)	*n*	Average (s)	*n*	Range
Sky Pond and Glass Lake	45		34		10		89	
chlor *a*		4·85 (2·97)		3·75 (1·41)		5·18 (4·20)		
μmol N l^{-1}		3·23–5·50 (1·98–3·39)		2·50–4·29 (0·94–1·61)		3·45–5·92 (2·80–4·80)		9·18–15·71
kg N ha^{-1}		27·38–42·15		7·30–10·95		1·83–3·03 (1·43–2·45)		36·50–56·13
The Loch	67		37		10		114	
chlor *a*		1·28 (0·73)		2·22 (2·00)		4·65 (3·92)		
μmol N l^{-1}		0·85–1·46 (0·38–0·65)		1·48–2·54 (1·33–2·29)		3·10–5·31 (2·61–4·48)		5·43–9·30
kg N ha^{-1}		7·26–14·52		5·44–9·79		0·49–0·91		13·19–25·21

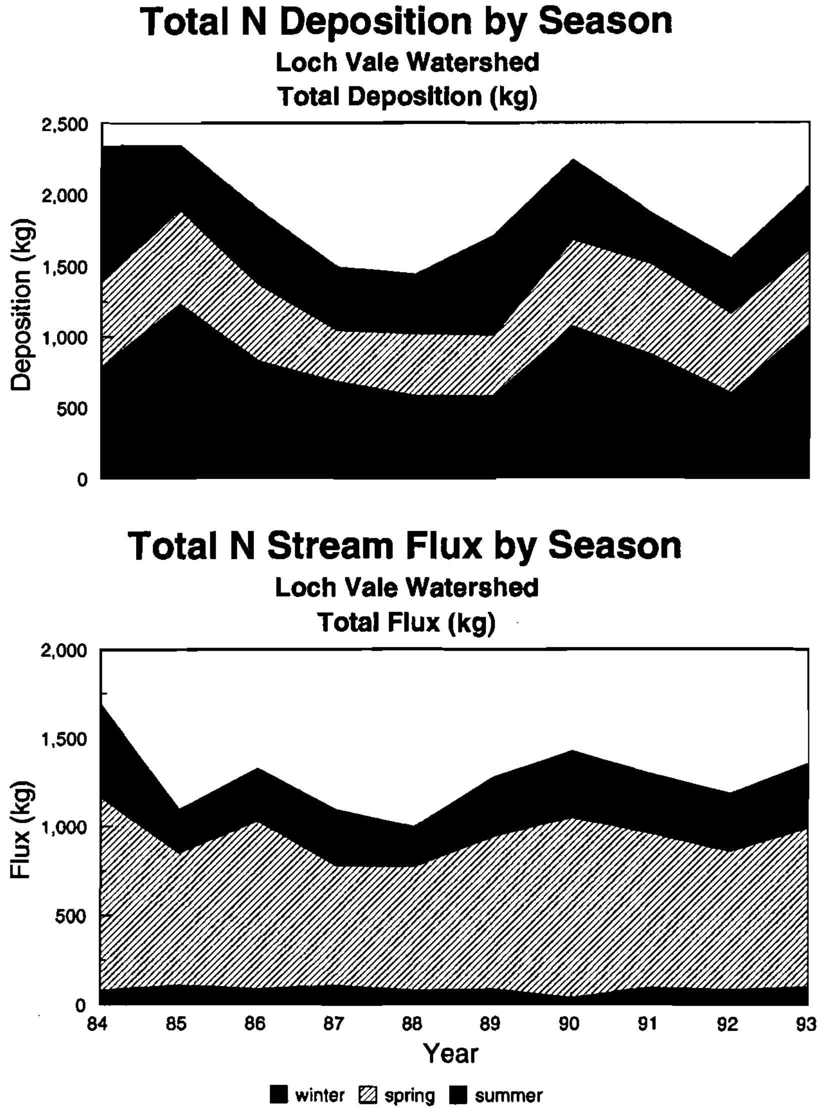

Figure 5. Measured nitrogen in wet deposition and stream efflux from The Loch outlet, water years 1984–1993. Fluxes are separated by seasons of the water year, with winter being 1 October to 14 April, spring 15 April to 14 July and summer 15 July to 30 September

Sub-basins. Most (62%) of the N efflux from the two alpine basins in 1992 occurred during snowmelt. For Icy Brook the efflux was 383 kg N out of the total yearly N flux of 618 kg N, and for Andrews Creek, 289 kg N out of the total flux of 464 kg N. The remaining 38% efflux occurred during the summer. For the whole LVWS basin, 55% of the total 1125 kg N loss was from Icy Brook, and an additional 41% came from Andrews Creek (Table III).

Only 4% of the measured N leaving the basin was contributed by the area below the treeline (calculated by difference between loss from the alpine sub-basins and loss at The Loch outlet), and this subalpine contribution of 43 kg N occurred only during the spring. During the summer there was net consumption of N in the aquatic system below the treeline, since more N passed from the two alpine basins into the subalpine basin than left at The Loch outlet.

Table III. Dissolved inorganic nitrogen losses (in kg) measured from 660 ha Loch Vale Watershed and its alpine sub-basins Icy Brook (290 ha) and Andrews Creek (160 ha) for water year 1992. The subalpine N loss was calculated by the difference between the alpine losses (Icy Brook and Andrews Creek) and the watershed as a whole. A negative value denotes N retention

	Loch Vale Watershed ($n = 53$)	Icy Brook ($n = 87$)	Andrews Creek ($n = 107$)	Subalpine
Winter	79	—	—	—
Spring	730	383	289	59
Summer	315	235	175	−95
Annual	1124	(618)	(464)	−36

DISCUSSION

Dynamics of inputs and outputs

Nitrogen fluxes (Figure 5) suggest that, although wet deposition values fluctuated with precipitation, measured stream N outputs were less variable. The stability of N outputs could be a result of one factor, or a combination of several: dry-deposited N species that may make overall deposition less variable than observed only in wet deposition; a large groundwater reservoir that releases N throughout the year; or biological (vegetative, algal or microbial) N demand that serves to dampen the amplitude of surface water N dynamics.

Several investigators have documented elevated concentrations of aerosol and particulate N species in ambient air above 3000 m in the Colorado Front Range (Heubert *et al.*, 1983; Parrish *et al.*, 1990; Sievering *et al.*, 1994). Measurements of ambient atmospheric HNO_3, particulate NO_3 and particulate NH_4, coupled with elevated snowpack N over wet-only deposition, suggest that dry-deposited N along the Colorado Front Range may be significant, although less so than measured wet deposition (Sievering *et al.*, 1992, 1994; Campbell *et al.*, 1995).

Smoothed stream fluxes could be related to groundwater storage of high N snowmelt waters, and subsequent release as baseflow. Despite the absence of a source of deep groundwater along the Continental Divide, and thin and sparsely distributed soil cover in the watershed, subsurface water may play an important role in regulating concentrations of nitrate in LVWS (Campbell *et al.*, 1995; Kendall *et al.*, 1995). Evidence supporting this idea comes from Back (1994), who found that the ^{18}O and D isotopic signatures of lake waters during the summer months were indistinguishable from those of snowmelt. Measurements of glacial meltwater from high in LVWS showed high NO_3 concentrations (30 μeq l^{-1}) even after a prolonged dry period in which no rain fell (Martin, 1994).

Examination of hysteresis patterns for nitrate and other solutes in concentration–discharge relationships in Andrews Creek and Icy Brook showed that the hysteresis patterns were consistent with piston-type flow through a reservoir of soil or groundwater (Campbell *et al.*, 1995). During late spring snowmelt, large day to day variations in stream flow were accompanied by little or no change in solute concentrations. The most likely reservoir of groundwater storage is in the interstices of talus fields that make up a substantial portion of the alpine zone of LVWS. In the talus, vegetation to take up nitrogen is sparse, allowing nitrate concentrations to remain high throughout the growing season. A large supply of N to streams from groundwater could serve to dampen interannual variability. This is an area of active research, as we do not know the residence times of water in talus.

Several investigators attributed the lack of a relation between N deposition and stream losses to terrestrial N demand (Johnson, 1992; MacDonald *et al.*, 1992). In the systems studied by these investigators, N from deposition was apportioned first to terrestrial vegetation and microbial processes, with the remainder available for export. Lajtha *et al.* (1995) suggest that this applies particularly to aggrading forests or those that are chronically N limited.

Nitrogen fluxes

If wet-only deposition is considered, as in Figure 5, net N retention is 25% of inputs in LVWS. Of the mean annual wet N deposition of 1716 kg N ($s = 354$; or 2·6 kg N ha^{-1}, $s = 0{\cdot}5$) to the watershed, 1125 kg inorganic N ($s = 200$; or 1·7 kg N ha^{-1}, $s = 0.3$) was lost via stream flow. This loss is very similar to reported fluxes from an alpine watershed in the southern Sierra Nevada Mountains of California, where an influx of 4·1 kg N ha^{-1} versus an efflux of 2·9 kg N ha^{-1} resulted in 29% accumulation (Williams *et al.*, 1995). Using the wet-only deposition values, Baron (1992) previously postulated that steep mountain basins behaved as 'flow-through' systems where most atmospheric inputs were flushed rapidly downstream. The reasons given for this included the low ratio of vegetative cover to bedrock, the short growing season and a snowmelt-dominated hydrological regime that rapidly removed 70–80% of water and total solutes from the watershed during a three-month period each year. However, a more realistic assessment of total deposition, including dry as well as wet, brings deposition closer to the range of 2574 kg N total, or 3·9 kg N ha^{-1}. Nearly half of the total N input is immobilized within the watershed at this level of deposition.

Immobilization of N can occur within tundra, forest, rock or aquatic areas. Using previously published work, the results described above and an aerial weighting of ecosystem components, an annual N mass balance was calculated (Table IV, Figure 6). In order to compare the calculations with direct measured values presented in this paper, the watershed was somewhat arbitrarily divided into alpine and subalpine units discharging into an aquatic unit. By constraining the N dynamics of these three units with measured, modelled or calculated values, we balanced the budget by calculating the flux through a fourth unit, bedrock, by difference. Given the smoother efflux than influx (Figure 5), and the growing evidence of dynamic subsurface storage reservoirs for water and N, an annual budget may be too short a time to capture LVWS N dynamics. However, calculation of the annual budget as a first approximation is a useful exercise to identify the relative importance of the different nitrogen cycling components, and to recognize that the relative importance of some processes may change as a function of the time-scale considered.

Tundra and meadow. Tundra and wet meadows comprise about 76 ha of the total 660 ha in LVWS; therefore, 12% of total N deposition, or 296 kg N, was deposited directly on tundra. Additionally, 12 kg N were added to account for direct deposition to surface water area that is above the treeline. Tundra systems are highly organic (Bowman *et al.*, 1993), and are the largest pools of both C and N in LVWS, storing 98 400 kg N in biomass and 824 000 kg N in soil organic matter. According to the CENTURY model results, 3600 kg N is taken up yearly, 3120 of which comes from mineralization. Because the model predicted 160 kg N leached from tundra into surface waters, 316 kg N was taken as runoff from bedrock on to tundra to meet the tundra N requirement. The measured N flux from Icy Brook and Andrews Creek in 1992 was 1080 kg N. To account for this difference an additional 908 kg N was routed from bedrock directly into alpine streams (Table IV, Figure 6).

Forests. Only 6%, or 40 ha, of LVWS is forested, so 156 kg N was routed on to forest directly from deposition. Another 11 kg N was added to account for deposition to surface water area that is below the treeline. The CENTURY model predicted 36 kg N volatilized from forest soils as N_2O (Baron *et al.*, 1994). Forest biomass, according to the model, held 16 000 kg N, while soil organic matter was a repository for 312 800 kg N. Soil organic matter values reported here are much higher than those previously reported, because earlier values were for forest floor N only, instead of for total soil to 60 cm (Arthur and Fahey, 1992; Baron, 1992). Forest N inputs and outputs were well balanced. The simulated amount of forest leachate to streams was 30 kg N, from Baron *et al.* (1994).

Aquatic systems. The inputs to aquatic systems from direct deposition (23 kg N), and measured from the alpine unit (1080 kg N) was 1103 kg N. Inorganic outputs measured in 1992 at The Loch outlet were 1125 kg N. The pool of inorganic N in surface waters was calculated to be 30 kg N based on 1982 concentrations. Calculated phytoplankton N ranged from 280 to 490 kg after conversion of values per ha

Table IV. Summary of nitrogen (N) values used to develop The Loch Vale Watershed N budget depicted in Figure 6

	Area of landform (ha)	N (kg ha^{-1})	N (kg $watershed^{-1}$)	Reference
Wet deposition	660	2·6	1716	NADP, 1993
Dry deposition	660	1·3	858	Sievering *et al.*, 1994
Tundra and meadow				
Inputs				
Deposition	76	4·0	308	NADP, 1993; Sievering *et al.*, 1994
From bedrock	76	4·2	316	Calculated by difference, this study
Pools				
Biomass	76	1295·0	98 400 (6400)	Baron *et al.*, 1994
Soil organic matter	76	10 842·0	824 000 (8000)	Baron *et al.*, 1994
Internal fluxes				
Plant uptake	76	47·0	3600 (1040)	Baron *et al.*, 1994
Mineralization	76	41·0	3120 (640)	Baron *et al.*, 1994
Net loss				
Inorganic N	76	2·1	160 (160)	Baron *et al.*, 1994
Forest				
Inputs				
Deposition	40	4·2	167	NADP, 1993; Sievering *et al.*, 1994
Pools				
Biomass	40	400·0	16 000 (4)	Baron *et al.*, 1994
Soil organic matter	40	7820·0	312 800 (4)	Baron *et al.*, 1994
Internal fluxes				
Plant uptake	40	31·0	1240 (360)	Baron *et al.*, 1994
Mineralization	40	28·0	1120 (320)	Baron *et al.*, 1994
Volitilization	40	0·9	36	Baron *et al.*, 1994
Net loss				
Inorganic N	40	0·8	30 (20)	Baron *et al.*, 1994
Bedrock				
Inputs				
Deposition	540	3·9	2100	NADP, 1993; Sievering *et al.*, 1994
Retention	540	0·5	279	Calculated by difference, this study
Net loss				
Via alpine	540	2·3	1236	Calculated by difference, this study
Via subalpine	540	1·1	585	Calculated by difference, this study
Lakes and streams				
Inputs				
From alpine	450	2·4	1080	Measured, this study
From subalpine	210	2·8	585	Calculated by difference, this study
Pools				
Inorganic N	6	5·0	30	Baron, 1992
Algal biomass	6	46·6–81·6	280–490	Calculated using McKnight *et al.*, 1988
Internal fluxes				
Algal uptake	6	73·0–123·0	438–738	Calculated, this study
Denitrification	6	0·2–0·3	1–2	Calculated, this study
Net loss				
Dissolved inorganic N	660	1.7	1125	Measured, this study
Dissolved organic N	6	0·1–0·3	1–2	Calculated, after Hedin *et al.*, 1995
Algal N flushed	6	26·3–41·3	158–248	Calculated, after McKnight *et al.*, 1990

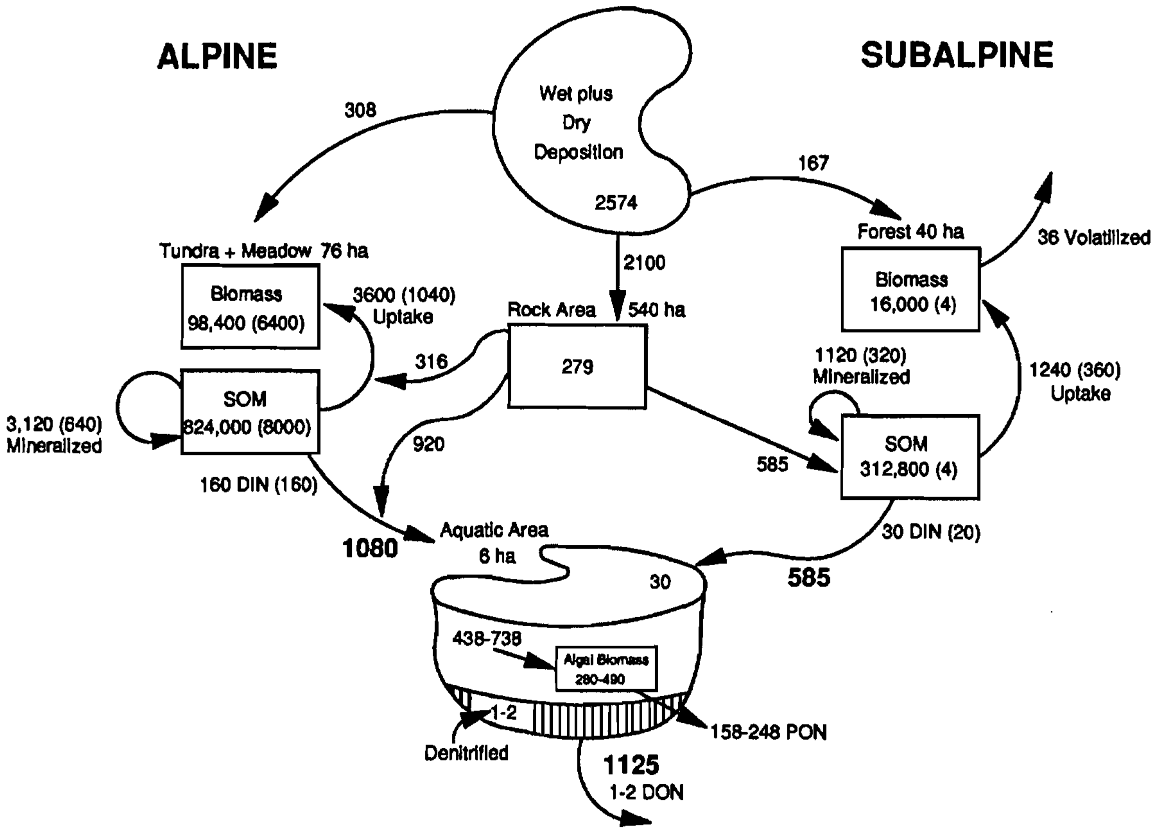

Figure 6. Nitrogen budget for LVWS. Values are estimates, in kg watershed^{-1}. Areas of each ecosystem component are shown in hectares. The budget is divided into an alpine side (tundra and meadows) and a subalpine side (forest). The vegetation is divided into biomass and soil organic matter (SOM). The 'Rock Area' is made up of bedrock and talus fields; runoff from this unit supplies alpine or subalpine areas. Stream fluxes are divided into dissolved inorganic nitrogen (DIN), which is mostly NO_3, dissolved organic nitrogen (DON) and particulate organic nitrogen (PON), calculated from estimates of phytoplankton flushed downstream. Measured values are shown in bold type; all others are either calculated or the results of CENTURY model simulations (Baron *et al.*, 1994). Values in parentheses are standard deviations about the mean of the last ten years of a 1060 year simulation. See text and Table V for further explanation

from Table II to total suface water area (6 ha). Additional aquatic N processes were conversion to organic N, microbial denitrification in lake sediments or uptake into algae and subsequent sedimentation, flushing or consumption by zooplankton.

Dissolved organic nitrogen. The contribution of dissolved organic nitrogen (DON) to total stream N flux was calculated from known organic carbon measurements (Hedin *et al.*, 1995). In many waters organic anions are dominated by fulvic acids, and N concentrations can be derived using 1·6–3·0% N relative to fulvic acid carbon (Aiken *et al.*, 1990; McKnight *et al.*, 1992). In LVWS fulvic acid comprised 25–50% of dissolved organic carbon above the treeline, and 14–69% in stream and lake samples below the treeline (Baron *et al.*, 1992). The DON associated with fulvic acids therefore ranged 0·02–0·15 and 0·02–0·60 kg ha^{-1} for alpine and subalpine waters, respectively (Table V). This quantity is lower than the 1·9 kg ha^{-1} inorganic N losses from LVWS, and is much lower than DON terms reported from other studies. Hedin *et al.* (1995) found DON to be the major form of stream nitrogen in old-growth temperate forest of southern Chile, where inorganic N deposition is extremely low. Even if all the dissolved organic carbon were fulvic acids, maximum DON losses from 6 ha of surface waters would be 2·3 kg watershed^{-1},

Table V. Calculated dissolved organic nitrogen (DON) fluxes from above and below the treeline in Loch Vale Watershed, using methods described by Hedin *et al.* (1995). Dissolved organic carbon (DOC) and % fulvic acid values are from Baron *et al.* (1992). Fluxes are calculated using an average yearly 75 cm water loss from the watershed

	Range of DOC ($mg\ l^{-1}$)	Range of fluvic acid (%)	Range of DON ($mg\ l^{-1}$)	Range of DON ($kg\ ha^{-1}$)
Above treeline	0·8–1·2	25–50	0·003–0·02	0·023–0·15
Below treeline	1·0–3·7	14–69	0·002–0·08	0·015–0·60

a very small amount. Given that 81% of LVWS is exposed rock and, of the remainder, only 7% has well-developed soils, the DON values seem reasonable.

Microbial denitrification. Lake sediments can serve as major sinks for N through microbial denitrification processes (Likens *et al.*, 1985), but in LVWS sediments do not appear to be significant. Measured rates of denitrification in the Canadian Experimental Lakes Area ranged from 232 to 602 μeq NO_3 m^{-2} d^{-1} (Rudd *et al.*, 1986). If these calculations are applied to LVWS, denitrification and loss to lake sediments could account for 0·7–1·8 kg N, or a small amount. These values agree remarkably well with calculated denitrification values of 0·2–0·5 kg N based on epilimnetic to hypolimnetic NO_3 gradients in LVWS lakes (from Baron, 1992, The Loch and Sky Pond, respectively, and assuming 75 cm water discharge).

Algal uptake. Algal cells are rapidly flushed downstream during snowmelt. During all seasons cells can sink to sediments or be consumed by other organisms. But because more cells are constantly replacing this loss, the standing stock of algae is a significant pool of watershed nitrogen. McKnight *et al.* (1990) calculated that even during the rapid snowmelt flushing, the diatom *Asterionella formosa* had a net rate of increase of 0.34 d^{-1} in The Loch. In this study, a net aquatic N consumption of 95 kg in The Loch alone was observed. The flushing rate during snowmelt ranged from 0·55 to 0·66 kg N during the 1985 study (McKnight *et al.*, 1990). Using the 0.60 average rate of flushing during the three-month snowmelt period, a 0.30 average flushing rate during the three-month summer period and an assumption that spring and summer (15 April–30 September) algal biomass constituted 95% of the total annual algal N pool (47–77 kg N ha^{-1} in spring and summer algal biomass, Table II), algal N uptake was calculated. For simplicity the algal population was assumed to be in steady state. By increasing the spring and summer algal pool by 0·6 and 0·3, respectively, and summing up the rest of the year, algal uptake of N is 438–738 kg ha^{-1}; flushing of cells accounts for 144–246 kg N ha^{-1}. Consumption of phytoplankton by higher organisms, sedimentation of cells or microbial activity in the water column was not taken into account. Nevertheless, at 73–123 kg N uptake ha^{-1}, phytoplankton constitute the largest biological consumer of N within LVWS.

Bedrock and talus. Eighty-two percent of LVWS (540 ha) is exposed bedrock and boulder fields, so 82% of total N deposition (2110 kg N) was routed directly from precipitation into this rock unit (Table IV, Figure 6). Nitrogen residing in the bedrock pool was then used to balance the rest of the watershed N budget. As previously stated, 316 kg N was used to balance the internal tundra and meadow N budget. An addition 920 kg N was routed into streams for alpine losses to match measured N fluxes from streams draining tundra. Finally, 585 kg N was taken from bedrock to satisfy the average algal N demand and the measured N losses from the watershed outlet. The remainder of 279 kg N within rock could be utilized by lichens or microorganisms, or stored in subsurface reservoirs.

SUMMARY

The amount of dry deposited nitrogen to LVWS is unknown, but if it is slightly less than measured wet deposition, approximately 52% of the N was flushed downstream in dissolved inorganic or organic form. Dissolved organic nitrogen appeared to be insignificant to the overall N budget, making up less than 1% of the total efflux of N. Based on calculations, particulate organic N as phytoplankton flushed downstream could make up as much as 18% of the total efflux.

Alpine tundra immobilized 18% of the N inputs. Only 5% was incorporated into forest vegetation or soils, in part owing to the low aereal coverage of forests in LVWS, and in part because these forests, at 500 years of age, are not aggrading. Algal uptake processes consume about 22% of total inputs. Short-lived algae do not remain in the water column; they settle to the bottom, are consumed by other organisms, or are flushed downstream as particulate organic matter. Roughly 7% of nitrogen fixed by phytoplankton is washed out of the watershed because of hydrological flushing, leaving 15% within the LVWS aquatic system. Denitrification at the sediment–water interface accounted for up to 2 kg N stored: or an insignificant amount.

We cannot place a high degree of confidence in the bedrock N retention values, because they were derived by difference. The budget calculation exercise suggests, however, that biological processes or subsurface storage within the large bedrock area is significant, accounting for about 10% of total annual N inputs. This finding is consistent with the findings of Kendall *et al.* (1995) and Campbell *et al.* (1995) that suggest both water retention and biological activity in talus significantly influences stream water chemical and isotopic composition.

This study points out that algal N uptake is important to the overall watershed N budget, despite large watershed N fluxes during spring and summer growing seasons. Better measurements are necessary, but the study results suggest that the range of algal consumption of N, at 45–75 kg N ha^{-1}, is equal or greater per unit area than that for alpine tundra and subalpine meadows. The study also suggests large areas of bedrock are biologically active.

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