1995

Long-Term Effects of Clearcutting and Short-Term Impacts of Storms on Inorganic Nitrogen Uptake and Regeneration in a Small Stream at Summer Base Flow

By FRANK J. TRISKA, VANCE C. KENNEDY, RONALD J. AVANZINO, *and*
KENT C. STANLEY

GEOMORPHIC PROCESSES AND AQUATIC HABITAT IN THE REDWOOD CREEK BASIN, NORTHWESTERN CALIFORNIA

U.S. GEOLOGICAL SURVEY PROFESSIONAL PAPER 1454–V

CONTENTS

ILLUSTRATIONS

TABLES

LONG-TERM EFFECTS OF CLEARCUTTING AND SHORT-TERM IMPACTS OF STORMS ON INORGANIC NITROGEN UPTAKE AND REGENERATION IN A SMALL STREAM AT SUMMER BASE FLOW

By FRANK J. TRISKA, VANCE C. KENNEDY, RONALD J. AVANZINO, and KENT C. STANLEY

ABSTRACT

Uptake and regeneration of dissolved inorganic nitrogen (DIN) in forest streams are controlled by factors operating on time scales of less than 1 day to greater than 80 years. Flux of inorganic nitrogen, primarily nitrate, was estimated in Little Lost Man Creek, Humboldt County, Calif., between 1974 and 1982 and in experimental channels during 1979. Studies were conducted during low flow (May–November) over an approximately 1,500-m reach of the stream flowing through an area clearcut in 1965. The study period coincided with the development of a riparian canopy, dominated by alder (*Alnus rubra*), a nitrogen-fixing species.

Studies in experimental channels indicated a large diel fluctuation in DIN concentration. Nitrate uptake rates decreased as the community aged. Uptake rates varied with canopy cover. Experimental short-term nitrate enrichment of the stream (200 µg/L NO_3-N) in 1975 (open canopy) and 1979 (closed canopy) confirmed reduced uptake under closed canopy conditions.

Background DIN chemistry surveyed weekly to biweekly during 1974 (prior to canopy closure) indicated a maximum uptake of 77 percent available nitrate (NO_3-N) at summer base flow. In 1976 maximum uptake was 87 percent of available NO_3-N under a similar sampling regime. Nitrate concentration at the upstream station (1975) was highest at night (18 µg/L NO_3-N) and lowest at midafternoon (8 µg/L NO_3-N). Nitrate concentrations downstream simultaneously ranged from 5 to 8 µg/L NO_3-N, indicating uptake within the reach. Four years later after canopy closure (1979), a diel study indicated regeneration (6–10 µg/L NO_3-N) rather than uptake in a 265-m section of the same reach. Regeneration was confirmed in June–November 1982.

Laboratory studies of stream sediments using an inhibitor of nitrite oxidation (sodium chlorate) indicated a potential for nitrate regeneration. Nitrate regeneration (measured by difference in upstream-downstream nitrate concentration) was also observed in a 92-percent-shaded experimental channel when the epilithon was senescent.

Development of the alder riparian zone is of long-term importance in nitrogen cycling of Little Lost Man Creek. We hypothesize gradual decline of instream production related to reduced synthesis of protein from inorganic nitrogen thus reducing passage of nitrogen to higher trophic levels. Biotic production will remain low until the canopy is reopened by natural mortality of riparian trees.

INTRODUCTION

Of the major dissolved elements in fluvial environments, nitrogen is especially valuable for studying biotic impacts on element transport. Nitrogen is useful as an indicator because most nitrogen chemistry is biologically mediated in nature, and nitrogen is rare in the mineral structure of sediments. In mountain streams, the biotic interface with solute chemistry is primarily associated with communities attached to benthic surfaces (epilithon). High gradients and current velocity, however, often prevent planktonic water-column communities from having a major impact on nutrient cycling. The instantaneous pool of dissolved elements in the surface water of a reach is usually insignificant; rather, the timing of nitrogen input determines the magnitude of potential chemical-biological interactions.

A myriad of factors, operating on different time scales, determines nitrogen uptake and transport properties of a stream under pristine conditions (table 1). Daylight uptake by photosynthetic algae can produce a diel fluctuation in nitrogen concentration during low flow. Small storms can reset the benthic community during the growing season by partially scouring sediment surfaces. Scouring is often followed by vigorous growth and rapid nitrogen uptake. Seasonal light and temperature fluctuations, due to such factors as spring leafout, bed stability, and fluctuations in discharge, introduce variability within a reach. Finally, canopy development in the riparian zone can control solar input to a reach (and thus uptake by photoautotrophs) for extended periods (Swanson and others, 1982).

This paper examines uptake and transport of dissolved inorganic nitrogen (DIN) from a variety of time perspectives. Biotic control of nitrate transport between storm-induced resets is examined daily and seasonally with

TABLE 1.—*Biological and physical factors that influence nitrate uptake on a stream reach over specified time scales*

<24 hours	1 to 30 days	30 days to 1 year	1 year to <100 years
Increase uptake (decrease transport)			
Diel photoperiod (daylight hours). Small storms that cause slight scour and elevate nitrogen concentration. Existing high bed roughness and porosity.	Epilithon in early successional stage (active growth). Moderate consumption of epilithon by grazing invertebrates.	Seasonal increase in daylight hours (spring-summer). Seasonal increase in temperature. Seasonal discharge pattern: low base flow, high bed contact, high bed stability.	Canopy opening due to natural or storm-induced mortality.
Decrease uptake (increase transport)			
Diel photoperiod (hours of dark).	Epilithon in late successional stage (senescence). Extremely low or high consumption of epilithon by grazing invertebrates. Major storms that cause high scour and high discharge.	Seasonal decrease in daylight hours (autumn, winter). Seasonal decrease in temperature. Seasonal discharge pattern: high base flow, low bed contact, high bed disturbance. Spring leafout of riparian canopy.	Canopy closure due to development of riparian vegetation.

respect to growth, maturity, and senescence of epilithon during summer low flow. The influence of canopy cover is examined in flumes in which shading, discharge, nutrient concentration, and channel geometry can be controlled. Observations from these controlled experiments are used to interpret long-term field variations in dissolved nitrogen (1974–82) during development of a riparian canopy.

STUDY SITE

The study was conducted at Little Lost Man Creek, a third-order pool-and-riffle stream located in Humboldt County in northwestern California (fig. 1). The site is approximately 5 km east of the Pacific Ocean. Soils on the watershed, derived from the rocks of the Franciscan assemblage (Bailey and others, 1964), are unstable, and numerous dormant landslides have been reported along the banks (Iwatsubo and others, 1975). The watershed is 9.4 km^2 and ranges in altitude from 24 to 695 m (387 m mean altitude). The channel gradient if 66 m/km (Iwatsubo and others, 1975; Iwatsubo and Averett, 1981). The area is characterized by cool, wet winters and warm, dry summers. Approximately 92 percent of the vegetation is old-growth, coastal redwood forest (*Sequoia sempervirens*) including associated Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga hetrophylla*). Between 1962 and 1965, and prior to incorporation into Redwood National Park, 8 percent of the watershed was clearcut at two sites. Following clearcutting, alder (*Alnus rubra*), a nitrogen-fixing species, has dominated the riparian vegetation.

Summer streamwater temperature typically varies between 14 and 20 °C. Summer background dissolved inorganic nitrogen and orthophosphate concentrations, which were determined colorimetrically with a Technicon II AutoAnalyzer, were approximately 20 to 40 μg N/L and 10 μg P/L. Summer and early autumn storms can increase DIN concentration to 150 to 175 μg N/L and orthophosphate concentration to 25 μg PO_4-P/L (Kennedy and Malcolm, 1977).

The summer epilithon community is dominated by diatoms including *Achnanthes lanceolata*, *Diatoma vulgare*, *Gomphonema angustatum*, and *Melosira varians*. (For a more complete species list, see Iwatsubo and others, 1976.) A full range of invertebrate functional groups (Cummins, 1973; Merritt and Cummins, 1978) is represented in the benthos with a predominance of collector organisms (Iwatsubo and Averett, 1981). Common fishes include steelhead trout (*Salmo gairdneri gairdneri*), coho salmon (*Oncorhynchus kisutch*), threespine stickelback (*Gasterosteus aculeatus*), and the coast-range sculpin (*Cottus aleuticus*) (Iwatsubo and Averett, 1981).

MATERIALS AND METHODS

FLUME STUDIES: SHORT-TERM NITROGEN UPTAKE AND REGENERATION

Determinations of short-term inorganic nitrogen uptake and regeneration were made in one set of six clear acrylic plastic channels, or flumes, between August 17 and September 20, 1979 (fig. 2; baseline water chemistry and channel characteristics are listed in tables 2 and 3). A header box with separate mixing chambers and separate V-notched weirs regulated flow (10 L/min) to each channel. Water was supplied through PVC (polyvinyl

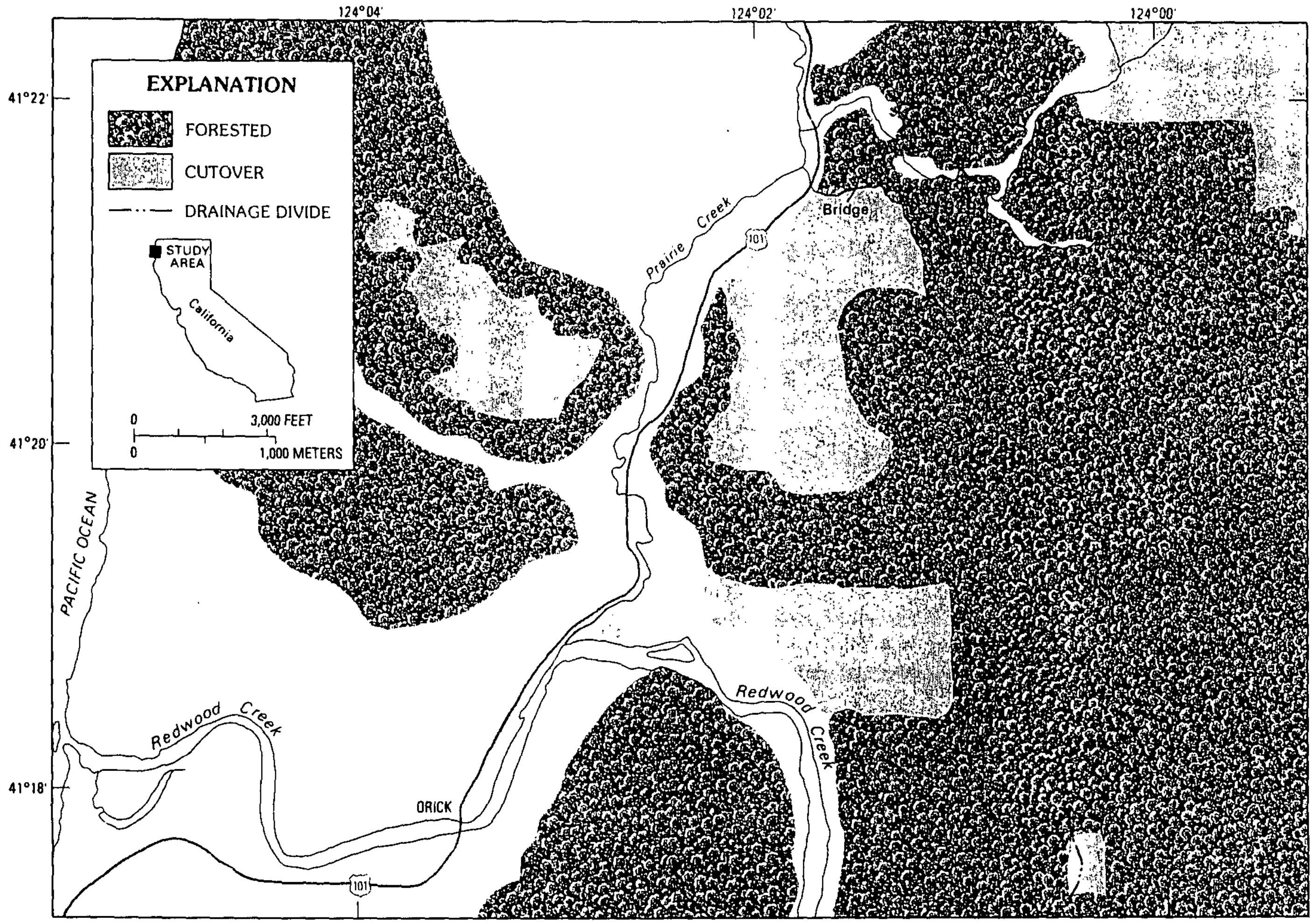


FIGURE 1.—Location of study area and sampling sites along Little Lost Man Creek. Most upstream-downstream dissolved inorganic nitrogen chemistry is compared between sites labeled "Gage" and "Bridge." Flume experiments occurred at the downstream end of the reach labeled "1979." Data from other upstream-downstream studies (1976, 1979) are labeled by year and indicate the approximate reach length. For all studies, the reach passed through an area clearcut on one bank in 1965.

chloride) pipe by gravity and passed through a 300-µm-pore-size filter. Nutrient solutions, when added, were pumped from a common source by using a separate pump for each channel. Nutrient enrichment was targeted at 100 µg/L NO_3-N and 25 µg/L PO_4-P except in the control channel. The nutrient concentrations in enriched channels were 2 to 3 times baseline concentrations (night) and typical of concentrations observed in summer and early autumn storms. Chloride was added with the nutrient solution at an accurately known flow rate and concentration. Since it is conservative with respect to biological uptake and sediment sorption, dilution of the added chloride after mixing was used as a measure of waterflow through the channel. Change in the ratio of chloride to nutrients during transport, which served as the measure of nitrogen flux, was calculated as follows:

$$\text{DIN uptake } (\mu\text{g/h}) = [N_o + (Cl_x - Cl_o \times N_T / Cl_T - N_x] \times Q$$

where:

N_o = DIN upstream concentration,
Cl_x = downstream flume concentration of chloride,
Cl_o = upstream flume concentration of chloride,
N_T = DIN concentration solute tank,
Cl_T = chloride concentration solute tank,
N_x = DIN concentration downstream, and
Q = discharge.

Discharge was determined daily from either daily injection pump rates and ΔCl or by using a calibrated bucket and stopwatch. Nutrient injection began August 24 and ended September 11, 1979.

Light input was estimated by a Licor 500 integrating light meter with a LI 190S sensor, which measured photosynthetically active radiation. Water temperature was measured by a continuous recording sensor placed in the stream.

TABLE 2.—*Channel properties and average background water chemistry (± standard deviation) in 1979 for the experimental acrylic plastic channels set in Little Lost Man Creek*

[DON=dissolved organic nitrogen; DOC=dissolved organic carbon]

Properties of the channel reach studied		Background water chemistry	
Length	9.75 m	DON	62.6±10.5 σ μg nitrogen per liter
Width	152.5 mm	NO_3	41.1±7.3 σ μg nitrogen per liter[1]
Depth	100.0 mm	NO_2	<3.0 μg nitrogen per liter
Volume	148.7 L	NH_4	<4.0 μg nitrogen per liter
Flow	9.5 L/min	PO_4	12.8±1.0 σ μg phosphorus per liter
Surface area (including slides).	12.4 m^2	DOC	1.1±.28 σ mg carbon per liter
Water surface area	1.48 m^2		
Water traveltime through reach.	15–20 min		

[1] Diel fluctuations in nitrate concentration were approximately 25 percent.

TABLE 3.—*Light and temperature data for selected sampling dates at Little Lost Man Creek*

[Light input was estimated by a Licor 500 integrating light meter with a LI 190S sensor that measures photosynthetically active radiation. Water temperature was measured by a continuous recording sensor placed in the stream]

Date (1979)	Temperature (°C)		Light [(μE/m^2)/s] 24-hour average
	Maximum	Minimum	
Aug. 24–25	16.7	15.5	468
Aug. 28–29	16.9	15.6	317
Sept. 6–7	17.2	15.6	363
Sept. 12–13	17.2	16.7	372
Sept. 18–19	15.6	14.4	294

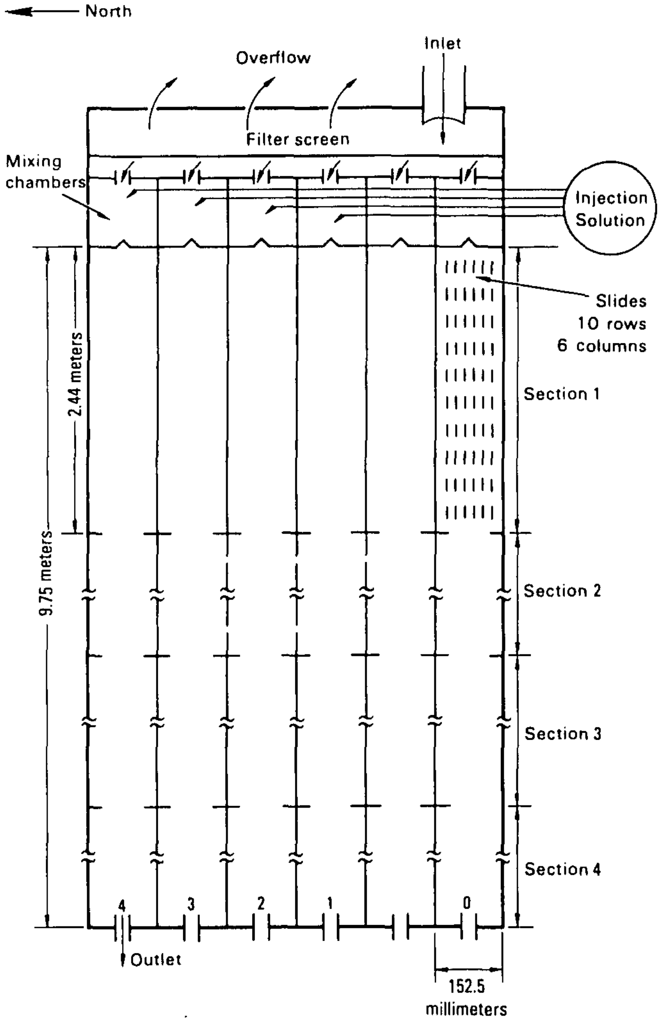


FIGURE 2.—Experimental flumes used to estimate short-term nitrogen flux by the epilithon community. Physical dimensions and arrangement of slides are illustrated.

Each experimental channel consisted of four successive longitudinal sections (fig. 2), and each section contained 10 rows of 102×152-mm clear plastic slides roughened by sandblasting and mounted perpendicular to the bottom. Each row contained six slides spaced 25 mm apart. Each channel contained 240 slides, and the total surface area of each flume was 12.4 m^2. Potential access to nutrients by epilithon was identical in each channel. Slides were placed in various streambed habitats 5 days before mounting in the channels, then acclimated 4 additional days prior to nutrient enrichment. Experimental treatments with regard to nutrient enrichment and canopy were as follows: channel 0 (control)—background nutrient, full sunlight; channel 1—nutrient amendment, full sunlight; channel 2—nutrient amendment, 30 percent shade; channel 3—nutrient amendment, 66 percent shade; channel 4—nutrient amendment, 92 percent shade. Shading was provided by woven nylon greenhouse screen of variable mesh size to produce the respective shade treatments. On each sampling date, 18 slides (6 percent of channel surface area) were randomly removed from each channel, and no location was sampled more than once. Slides were placed in individual plastic bags and returned to a field laboratory where epilithon was harvested by scraping, placed in plastic bags, and frozen. Each sample yielded four subsamples. Scraped slides were returned to the channels. A detailed description of sampling procedures is presented elsewhere (Triska and others, 1983).

At the conclusion of the experiments, chlorophyll α was determined on one sample chosen from each section of each channel on each sampling date. (Three samples were collected per channel.) Chlorophyll α was determined by extraction of algae in 90 percent acetone shaken with magnesium carbonate. Absorbance was read at 665 nm for chlorophyll α and 750 nm to correct for turbidity. Readings were made before and after acidification to correct for phaeopigments (Wetzel and Westlake, 1974). Results were extrapolated from the known surface area of the sample (slide) to the total surface area of the plastic channel.

Biomass was determined by oven drying duplicate nonextracted samples at 50 °C. Ash content was estimated by ignition at 500 °C for 4 hours. From the amount of ash from the acetone-extracted sample and known percent ash from the unextracted samples, biomass was estimated for the acetone-extracted sample. Epilithon transported from the flume or deposited on the bottom was not included. The carbon:nitrogen ratio of epilithon was determined on a Carlo-Erba CHN analyzer at the laboratory of Dr. Wayne Minshall, Idaho State University.

Water was sampled five times daily for background concentrations of NO_3+NO_2, NH_4, PO_4, and Cl and for nutrient concentrations at the outlet of each flume. Samples were collected before sunrise (approximately 6:00 a.m.) and at 10:00 a.m. and 2:00, 6:00, and 10:00 p.m. After collection, samples were filtered (0.45 μm) at streamside. Samples for nitrogen and phosphorus were frozen (−20 °C) until the day of analysis, and samples for chloride were refrigerated. Analyses were made on a Technicon AutoAnalyzer II with a precision for NO_3-N+NO_2-N and NO_2-N of ±1 μg/L below 100 μg/L and ±1 percent above (Technicon Industrial Method no. 158–71W, December 1972). Analytical precision for orthophosphate was ±1 μg/L (Technicon Industrial Method no. 155–71W, January 1973). Analytical precision for chloride was ±1 percent at 5 mg/L and above (Technicon Industrial Method no. 99–70W/B, revised February 1976; O'Brien, 1962). Water samples frozen for extended periods did not show significant loss of nutrients compared to samples analyzed immediately. Nitrite and ammonium were always at or below the limits of detection; thus nitrate and DIN are essentially synonymous.

FIELD STUDIES: LONG-TERM NITROGEN UPTAKE AND REGENERATION

Field studies consisted of both daily and weekly to biweekly surveys of DIN. Samples were taken at midafternoon. When water was sampled more than once the same day, the samples collected closest to 2:00 p.m. were used for comparison. Weekly to biweekly surveys were made at low flow in 1974, 1976, and 1982. Water samples were taken at two sites: Gage, at a gaging station, and Bridge, downstream near the base of the clearcut. Diel fluctuations in chemical constituents were measured in 1975, 1979, and 1982. Diel sampling was conducted at Gage and Bridge and at two subreaches within the clearcut area (designated "1976" and "1979" in fig. 1).

Nitrification potential was estimated from bankside sediments collected at two sites in the clearcut area and at one site in the old-growth forest. Following the method of Belser and Mays (1980), sodium chlorate (10 m*M* final concentration) was added to shaken slurries of stream sediments (20 g fresh weight). Slurries were incubated at room temperature (23 °C) for 48 h. Chlorate inhibits enzymatic oxidation of nitrite to nitrate. Nitrification was estimated by comparing accumulations of nitrite in treated sediment slurries to untreated controls. Organic carbon content of sediments was determined on a Leco carbon analyzer by subtraction of inorganic carbon from total carbon.

RESULTS AND DISCUSSION

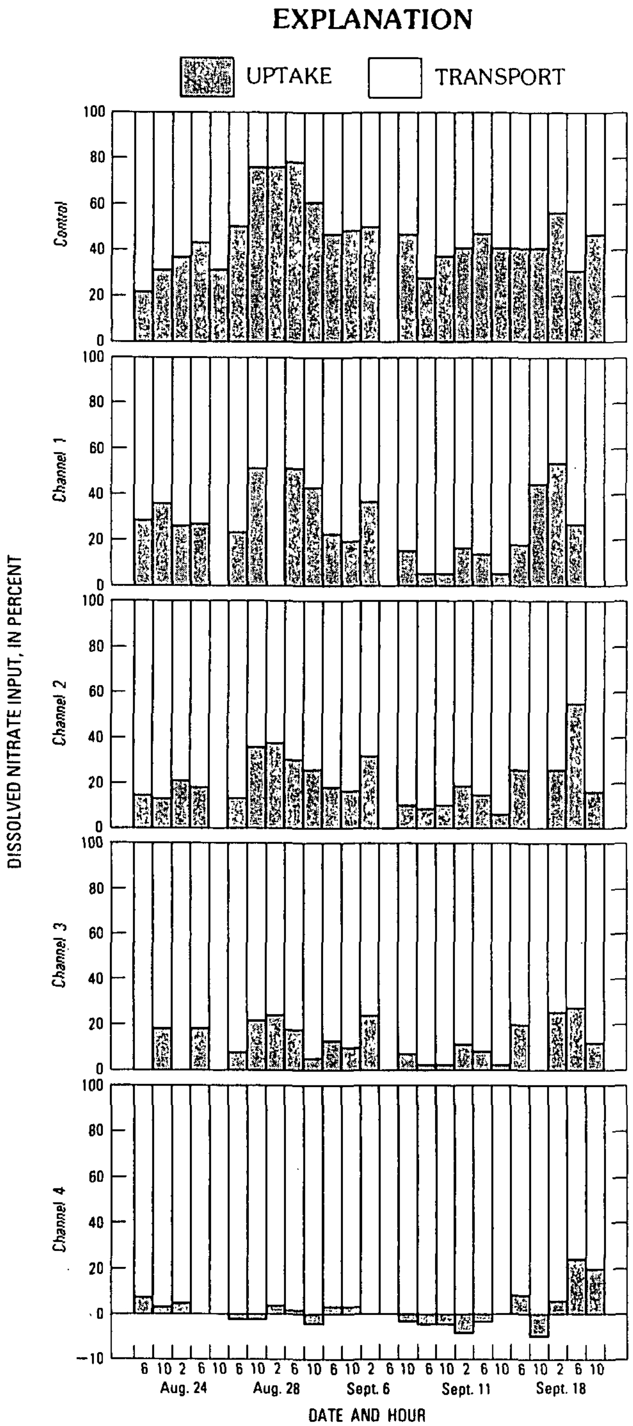
FLUME STUDIES: SHORT-TERM NITROGEN UPTAKE AND REGENERATION

Light and temperatures were regulated by climate, geomorphology, and vegetation of the watershed. Little Lost Man Creek flows through a long narrow valley that has steep slopes that reduce light intensity part of the day. Incident radiation input on sampling days varied from 294 to 468 ($\mu E/m^2$)/s (table 3). Between August 28 and September 12, day length (light input) to the flumes was decreased by morning fog. Fog also helped to moderate temperature. The diel variation in water temperature was about 2 °C. Temperature throughout the experiment ranged between 14.4 and 17.2 °C.

Nitrate uptake, the difference between input and output (transport) concentrations in the channels, varied (fig. 3). Uptake was greatest in midafternoon and least after dark. The magnitude of fluctuation depended on nutrient concentration, shading, and the maturity of the biological community.

Nitrate uptake rates in the control channel and in channel 1 were similar prior to nutrient addition (fig. 4; 6:00 and 10:00 a.m., August 24). Once injection of nutrients began, nitrate uptake immediately increased in channel 1 (fig. 4; 2:00 p.m. and 6:00 p.m. samples, August 24). High rates of uptake continued through August 28, as the community grew rapidly. In the control channel, nitrogen uptake increased by 5 to 10 mg/h during daylight hours through August 28 but by an additional 20 to 30 mg/h in channel 1 as a result of nutrient amendment. Differences between the channels decreased as the community matured (September 11). On September 19, 1 week after the end of nutrient amendment, diel uptake patterns were similar in both channels.

Nitrogen uptake in the nutrient-amended channels was also controlled by shading (figs. 3, 5). Over the full experiment, algal uptake on an areal basis was linearly related (r^2=0.95) to shading in the nutrient-amended



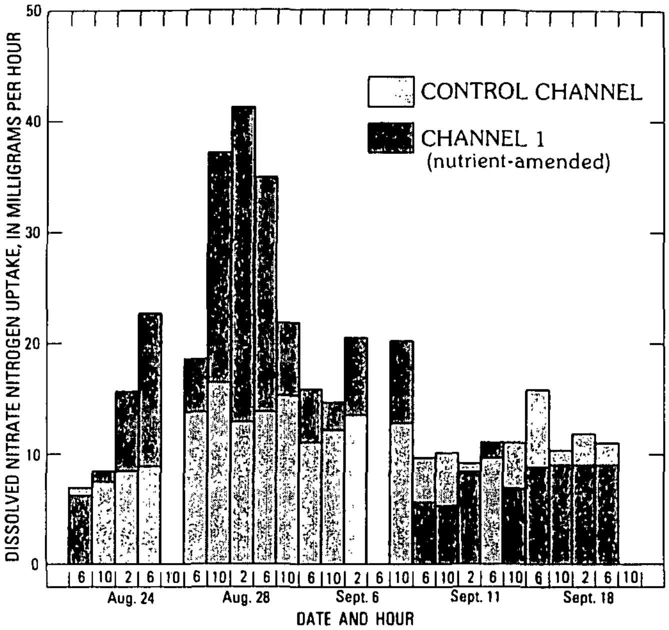


FIGURE 4.—Nitrate uptake in two channels exposed to full sunlight. The *control channel had background nutrient concentrations,* while nitrate and phosphate were added to channel 1.

◀ FIGURE 3.—Diel uptake versus transport as a percent of instantaneously available nitrate on five sampling dates during a 28-day experiment. Uptake is input minus output, and transport is equivalent to output. Nutrient concentration and shading were manipulated as follows: Control—background nutrients, full sunlight; channel 1—nutrient amendment, full sunlight; channel 2—nutrient amendment, 30 percent shade; channel 3—nutrient amendment, 66 percent shade; channel 4—nutrient amendment, 92 percent shade. Negative uptake indicates samples in which dissolved inorganic nitrogen concentration was higher in output than in input water. Nutrient amendment was 100 μg NO_3-N/L and 25 μg ortho PO_4-P/L. Nutrient amendment was cut off on September 12.

channels. Uptake was greatest in channel 1 (0.73 g N/m^2) and least in channel 4 (0.002 g N/m^2).

Transport, nitrate not removed biologically as uptake, was also linearly related (r^2=0.97) to percent shading over the total experiment. In the nutrient-amended flumes, average transport varied between 75 percent (channel 1) to more than 99 percent (channel 4) (fig. 3). In the control, transport was approximately 55 percent of input nitrate (fig. 3). Considering the short flume length (<10 m), small surface area (12.4 m), and continuous input of nitrate, a very short cycling distance under natural conditions is suggested.

Nitrate uptake also was related to community senescence. In both control and nutrient-amended channels, uptake of amended nitrate decreased as the community aged (fig. 3). Maximum nitrate uptake occurred when

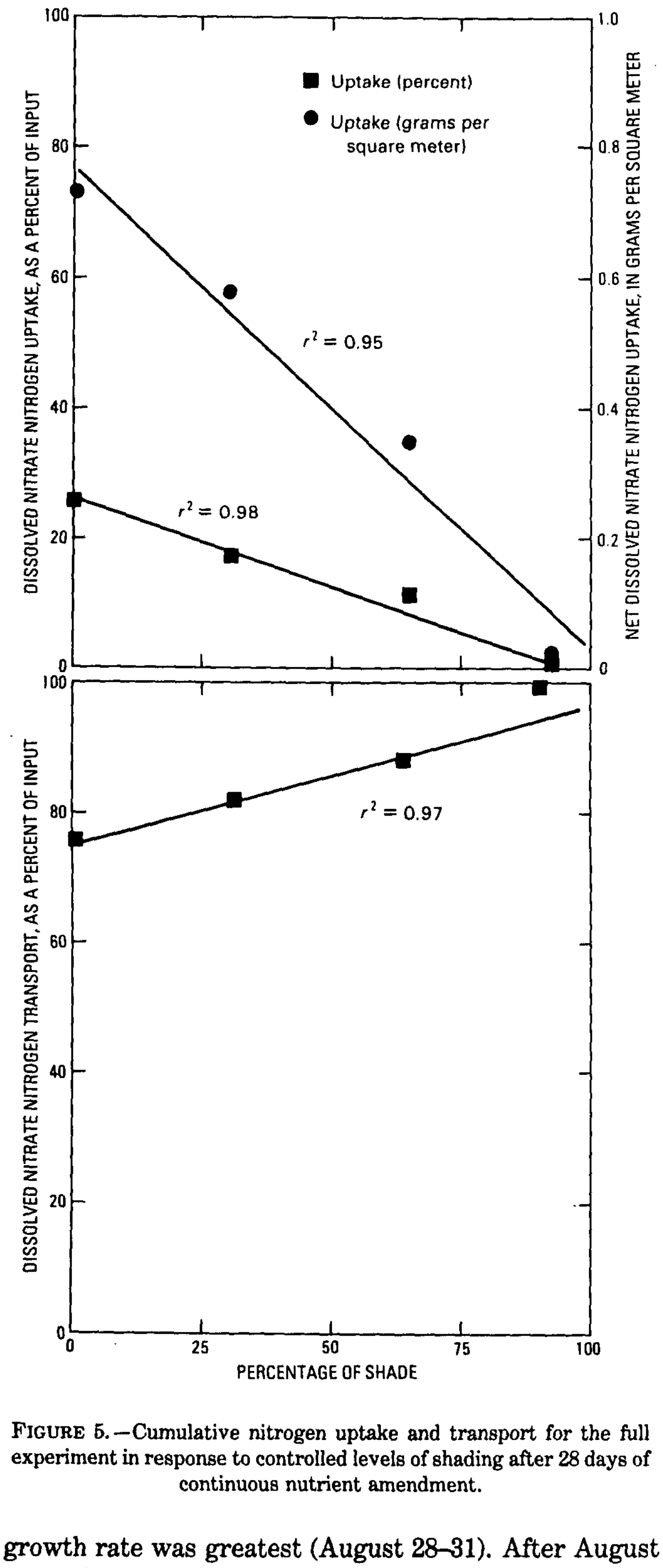


FIGURE 5.—Cumulative nitrogen uptake and transport for the full experiment in response to controlled levels of shading after 28 days of continuous nutrient amendment.

growth rate was greatest (August 28–31). After August 28, midafternoon uptake gradually declined at all levels of shading. By September 11, nitrate uptake in the nutrient-amended channels was less than at the beginning of the experiment, although epilithon biomass was maximum. On September 12, nutrient addition was cut off, thus the higher percentage uptake September 18 is of background nitrate. Net community primary production also declined as the community aged (Triska and others, 1983). Pryfogle and Lowe (1979) report that dead cells can constitute between 20 and 50 percent of the biomass in natural epilithon communities. Thus, dead and senescent tissue can represent a high proportion of organic matter that is physiologically inert to nutrient uptake.

In channel 4 (92 percent shade), many samples had higher output than input of nitrate concentration. Regeneration, 105 to 110 percent of input, is shown as negative uptake on figure 3. Regeneration occurred almost continually from September 6 to 12 (data shown for September 11 only) and is attributed to remineralization of organic detritus. By the end of the experiment, regeneration nearly equaled earlier uptake, explaining the low net uptake for all channels (fig. 5). This regeneration is considered in detail in Triska and others (1985). The influence of nitrate regeneration in flume experiments will be considered later in the discussion of field studies that examine the long-term influence of canopy development.

The relation of nitrate uptake to three measurements, biomass, chlorophyll, and carbon:nitrogen ratio, was also examined. When nutrient enrichment commenced, epilithon biomass (ash free) ranged from 2.43±0.5 to 7.77±0.68 g/channel (table 4). After 4 days of nutrient enrichment, the heavily shaded channel 4 (92 percent) had little biomass accumulation. Biomass in this channel thereafter remained significantly lower than that in channel 1 (student's *t*-test, $p < 0.01$). Two weeks after the nutrient amendment began, channel 1 was significantly higher ($p < 0.05$) in biomass than either the 30-percent-shaded or the 66-percent-shaded channels. On September 11, 19 days after nutrient addition began, biomass in all shaded channels was significantly lower than that in channel 1; (channel 2, $p < 0.05$; channel 3, $p < 0.01$). On September 12, nutrient addition ended, and nutrient concentration in all treated channels returned to background levels. Immediately before cutoff, both fully lighted channels supported nearly equal biomass (52.2±7.0 g/channel for the control channel vs. 49.0±2.3 g/channel for channel 1). After cutoff, biomass declined equally in both channels (17.6±2.6 g vs. 16.8±0.3 g biomass remaining, respectively, for channel 0 and channel 1).

Although the accumulation of biomass was nearly identical in the control and in channel 1, chlorophyll α content of the control channel at nutrient cutoff was less than half that of channel 1 (table 4). From a base of 31 mg, chlorophyll α increased to 182 mg/channel in the control. In channel 1, however, chlorophyll α rose from a base of 22 mg to a maximum of 403 mg/channel. Channel 2 (30 percent shade) produced slightly more chlorophyll α

TABLE 4.—*Biotic characteristics of the epilithon in the experimental flumes*

Date		Aug. 24	Aug. 28	Sept. 6	Sept. 11	Sept. 20
Channel treatment		**Biomass, in grams ash-free dry weight (± standard deviation)[1]**				
0......................	Control	7.77±0.68	13.34±0.60	31.27±4.53	52.15±6.99	17.63±2.64
1......................	0 shade	5.13±.55	14.82±2.36	40.50±2.94	49.02±2.34	16.83±.31
2......................	30 percent shade	4.76±.66	11.62±1.63	23.25±1.43	39.59±1.01	23.91±2.93
3......................	66 percent shade	3.71±1.23	9.72±1.08	21.33±2.80	28.18±4.70	25.53±3.36
4......................	92 percent shade	2.43±.50	3.27±.48	3.94±1.43	7.45±2.42	4.54±2.00
Channel treatment		**Chlorophyll α in milligrams [2]**				
0......................	Control	30.98	63.47	167.42	181.86	64.77
1......................	0 shade	21.59	135.20	270.87	402.52	104.34
2......................	30 percent shade	20.64	134.74	332.65	410.34	170.68
3......................	66 percent shade	20.10	132.85	178.32	278.05	130.06
4......................	92 percent shade	14.60	54.51	59.42	92.77	51.78
Channel treatment		**Carbon:nitrogen[3] (± standard deviation)**				
0......................	Control	11.58±0.67	14.06±0.26	10.56±0.62	8.11±0.21	7.18±0.07
1......................	0 shade	12.76±.29	8.21±.15	7.39±.22	7.79±.07	7.49±.02
2......................	30 percent shade	11.13±.48	9.15±.71	7.35±.55	6.83±.31	6.91±.01
3......................	66 percent shade	9.22±.14	7.74±.17	7.30±.07	7.47±.06	7.39±.06
4......................	92 percent shade	9.72±.11	9.19±.62	6.92±.06	8.47±.30	8.08±.06

[1] Biomass estimates for the total channel.

[2] *Chlorophyll α in the total channel.*

[3] Carbon:nitrogen is determined from samples taken at midflume.

than channel 1 but had approximately 20 percent less biomass, possibly indicating shade adaptation (Meeks, 1974; Lyford and Gregory, 1975). Chlorophyll α was lower in the 66-percent-shaded and 92-percent-shaded channels.

Carbon:nitrogen ratios varied between 9.2 and 12.8 when the experiment began (table 4). C:N was lower in most nutrient-amended flumes than in the control channel. Nutrient amendment resulted in reduction of C:N by August 28, and C:N generally continued to decline throughout the experiment. In the control flume, however, C:N increased when community growth was most rapid, indicating potential nitrogen limitation. By September 20, C:N was similar in all flumes.

After 1 week, the cumulative nitrate uptake in channel 1 (0.358 g NO_3-N/m^2) was 1.8 times higher than that of the control (0.198 g NO_3-N/m^2). This cumulative nitrate uptake is consistent with the observed lowering of C:N. Cuker (1983) reported an increase in chlorophyll α levels in the epilithic algal community of an arctic lake after addition of nutrients. Chlorophyll α may partially serve as a reservoir of nitrogen, because the chlorophyll molecule contains significant nitrogen. This possibility is also consistent with our own observations of chlorophyll α enhancement as a result of nutrient amendment. Rhee (1978) observed that protein was the major storage pool of cellular nitrogen. Protein also serves an important function in the structural arrangement of chlorophyll in chloroplasts. Wherever the intracellular location of nitrogen, however, the decline in C:N and high cumulative uptake indicate a rapid epilithon response to increased nitrate.

Although the highest rates of nitrate uptake occurred in midafternoon, indicating a primarily algal response, significant uptake also was observed afterdark. Afterdark uptake varied by shade treatment and was greatest during the period of most active epilithon growth, August 24 to 28. Afterdark uptake was maximum in the control channel at about two-thirds the uptake of daylight, possibly indicating nitrogen limitation. Eppley and others (1971) reported afterdark uptake of nitrate in nitrogen-limited chemostat cultures of two marine phytoplankton. Grant and Turner (1969) observed afterdark uptake but found light uptake was 23 times greater. This observation was presumably due to the fact that nitrate uptake and reduction by algae are energetically linked to photosynthesis (Eppley and Coatsworth, 1968; Eppley and others, 1971; Healy, 1973; Cloern, 1977), possibly through the reversible inactivation of nitrate reductase during light-dark cycles (Hodler and others, 1972; Griffiths, 1979). Nitrate reductase activity rapidly increases in *Chlorella* sp. cultures during the light period and may begin to fall even before the dark period begins. The rapid response following illumination may result from conversion of a preformed macromolecule into an active enzyme (Tischner and Hutterman, 1978). These previous studies on *Chlorella* sp. in chemostats used pure and synchronous algal cultures. Because afterdark uptake was proportionally higher in our field experiments, significant nitrogen flux also may occur through bacteria and fungi in natural epilithon.

The channel experiments illustrate how biological uptake can regulate the distance that a nitrate ion travels downstream. Temporally, uptake was controlled on a daily basis by irradiance and on a week-to-week basis by physiological senescence that reduced uptake at all levels of shading. In natural channels, physical factors, including sloughing, animal grazing, and small summer and early autumn storms, reset the community and partially mitigate the effect of senescence. Tissue removal, whether directly by consumption or indirectly by sloughing or scouring, may enhance both nitrogen passage to higher trophic levels and the DIN uptake per unit area.

Spatially, canopy cover (percent shading) controlled the overall magnitude of uptake. Under natural conditions canopy cover is a function of stream order, with almost complete coverage in lower order streams and less coverage downstream.

FIELD STUDIES: LONG-TERM NITROGEN UPTAKE AND REGENERATION

In this section, we will apply conclusions from the flume studies to longer term DIN chemistry by comparing years when the riparian canopy was open, 1974 to 1976, to years when it was largely closed, 1979 to 1982. We will approach canopy effects on inorganic nitrogen transport from a diel and seasonal perspective, as in the flume studies, and briefly speculate about the long-term impact of canopy closure on the structure of biological communities.

Diel nitrate patterns in September 1974 and 1982 are compared in figure 6 for two stations, Gage and Bridge. The Gage site was at the head of the clearcut area and indicates dissolved inorganic nitrogen input from the upstream virgin forest. The Bridge site was located about 1,500 m downstream near the base of the clearcut area and upstream of the junction of Little Lost Man Creek and Prairie Creek (fig. 1). Diel variation in background nitrate concentration at Gage was typically 10 to 20 µg NO_3-N/L in both 1974 and 1982 but was higher in 1982. The diel pattern of nitrate concentration at Gage was similar to the pattern seen in our experimental channels (highest after dark and lowest between noon and 4:00 p.m.). In 1974 (fig. 6), the riparian canopy was open, and full sunlight reached the stream. At the Bridge site, nitrate concentration was typically reduced to between 5 and 8 µg NO_3-N/L due to biological uptake. Absence of a diel pattern at Bridge is attributed to continuous biotic uptake. Uptake of approximately 77 percent of transported nitrate occurred between the two stations in 1974. Opposite results were observed at the same sites in 1982 (fig. 6). Rather than a reduction in nitrate concentration, a threefold increase in nitrate was observed at the downstream site. The canopy was nearly closed in 1982, except for a few large pool reaches that allowed light infiltration.

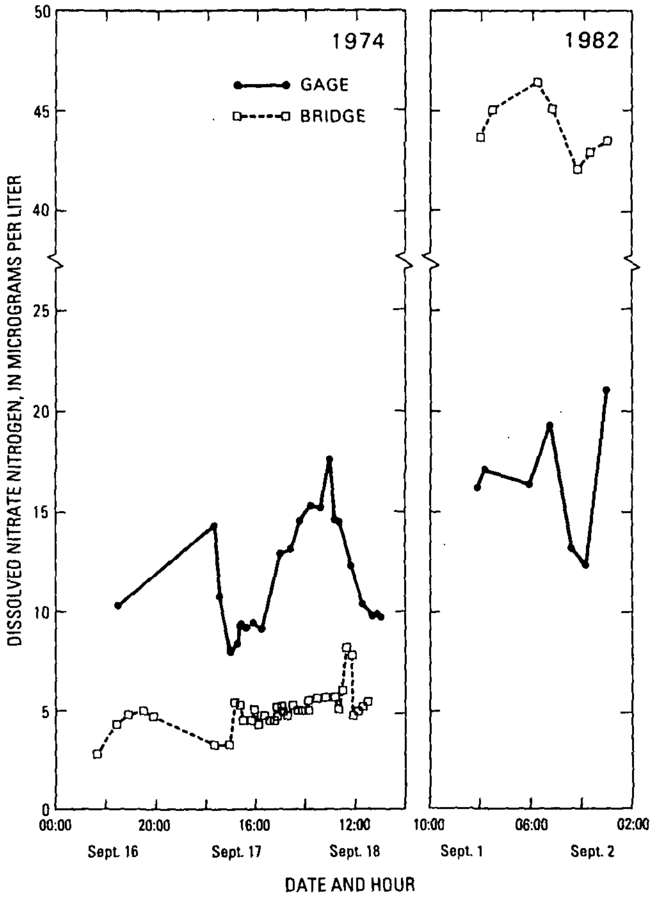


FIGURE 6.—Diel difference in NO_3-N concentrations during late summer between an upstream (Gage) and a downstream (Bridge) study site. Concentration differences prior to canopy closure (September 16–18, 1974) are indicated on the left, and differences after canopy closure (September 1–2, 1982) are indicated on the right. Location of the Gage and Bridge study sites is shown in figure 1.

By 1982, nitrate regeneration was observed over the whole summer-autumn period of declining discharge (fig. 7). Except for the mid-August sample, the pattern of background nitrate concentration at the Gage site was similar in both 1974 and 1982; DIN concentration was low during early summer (June and July), usually between 10 and 15 µg N/L in 1974 and 5 and 10 µg N/L in 1982. Maximum midday nitrate concentration at the Gage site was approximately 40 µg N/L during 1974 (mid-August sample) but less than 20 µg N/L during 1982. Concentrations at the Gage site during 1976 were intermediate, but as in 1974, the Gage site samples had a higher concentration in late summer. Comparison of data from the Bridge and Gage sites indicates nitrate disappearance during the late spring and summer in 1974 and 1976 but nitrate regeneration throughout the summer of 1982.

During the low-flow period, uptake in the reach was greatest during July in 1974 and in mid-July and early

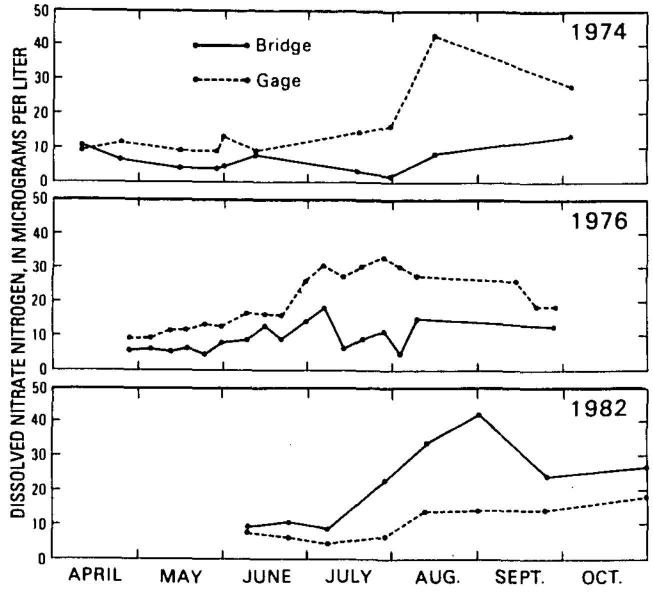


FIGURE 7.—Seasonal differences in midday NO_3-N concentration between an upstream study site (Gage) and a downstream study site (Bridge). The riparian canopy was open above the stream during 1974 and 1976 and closed by 1982. Study site locations are shown on figure 1.

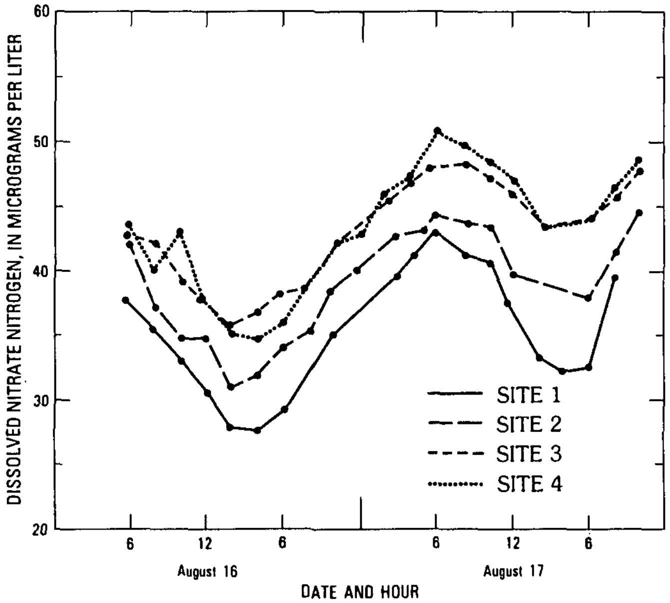


FIGURE 8.—Diel change in background NO_3-N concentration at four stations within a 265-m reach of Little Lost Man Creek under low-flow conditions, August 16 to 17, 1979. Distance between sites 1 and 2 is 64 m; between sites 2 and 3 is 58 m; and between sites 3 and 4 is 143 m. This 265-m reach is labeled "1979" on figure 1.

August in 1976. Differences between study sites were less in early summer, presumably because higher discharge and increased velocity shortened traveltime and lessened contact with the epilithon. Nitrogen uptake declined in September and October. Declines in uptake, despite low flow, may indicate community senescence as observed in the experimental channels. Possible causes of senescence include emergence of many grazer invertebrates by late summer and extremely low flows, which allow metabolites to accumulate and minimize physical sloughing. Nitrate regeneration also declined by mid-September in 1982.

The nitrate regeneration currently observed at Little Lost Man Creek is not uniform throughout the reach. A diel study at four sites in a 265-m section of the clearcut reach (labeled "1979" in fig. 1) indicated significant increase in nitrate concentration within short distances (fig. 8). For example, the distance between sites 1 and 2 was 64 m and between sites 2 and 3, 58 m. The greatest observed increase in nitrate concentration occurred between sites 1 and 3. The distance between sites 3 and 4 was 143 m but was characterized by net nitrate uptake during daylight and by slight nitrate regeneration after dark and until noon the next day. This reach contained one unshaded riffle and two long unshaded pools.

The flume studies indicate two potential sources of nitrate increase in 1979 and 1982: (1) regeneration within the bed and (2) decrease of algal uptake of nitrate from inflowing ground water as a result of canopy development (increase in shading). To test the hypothesis that nitrification was actually occurring in stream sediments, we collected submerged bankside soils at three sites along the stream: (1) adjacent to an alder stand where nitrogen-fixing nodules were not observed on roots, (2) adjacent to an alder tree where roots were definitely nodulated, and (3) adjacent to an old-growth maple tree. Nitrification potentials were measured as an increase in nitrite by inhibition of the enzyme that facilitates the final oxidation of nitrite to nitrate. Samples from all three sites indicated nitrification potential when compared to uninhibited controls (fig. 9). In conjunction with our observations in the experimental channels, this preliminary survey of bankside sediments indicates a biological potential for nitrate regeneration.

A second hypothesis for the observed nitrate increase is absence of nitrate uptake from inflowing ground water. If ground water is higher in NO_3-N than stream water due to upstream removal of NO_3-N during transit, then an apparent increase in NO_3-N in the shaded clearcut areas may result from lack of uptake from newly contributed ground water rather than from actual nitrification. To test this hypothesis, two experiments involving passage of a 3-hour midmorning pulse of nitrate in two reaches were compared between 1976 when the canopy was open and 1979 when it was closed (for location see fig. 1). Calculated nitrate uptake relative to nitrate concentration (based on chloride as a conservative tracer) is presented in figure 10. The results indicate

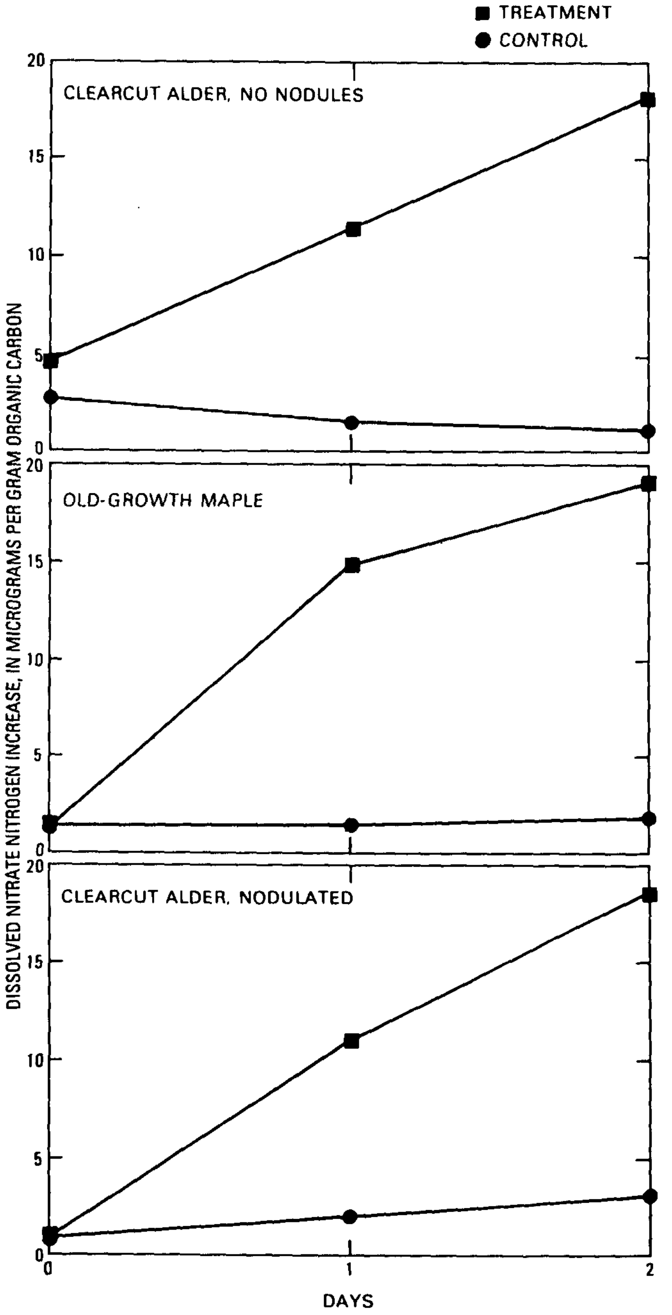


FIGURE 9.—Nitrification potential along Little Lost Man Creek, August 1981, measured by chlorate inhibition. Bankside sediments were collected adjacent to an alder tree where nitrogen-fixing nodules were not observed, adjacent to an old-growth maple, and adjacent to an alder tree where nitrogen-fixing nodules were observed on the roots.

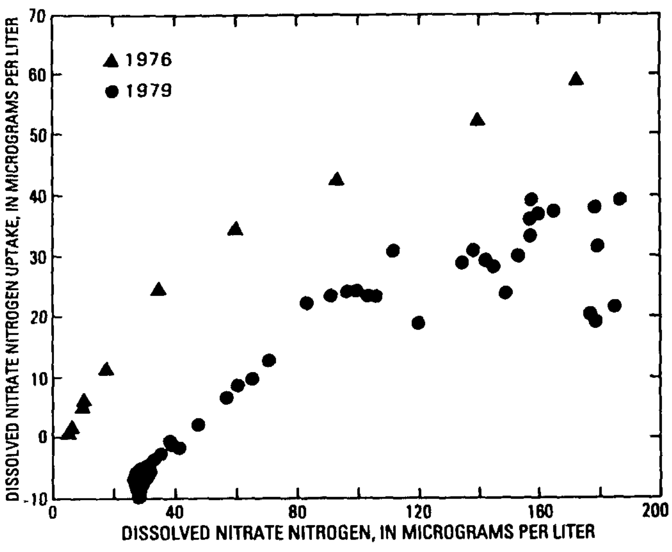


FIGURE 10.—Nitrate uptake at concentrations between 5 and 200 μg NO_3-N/L after passage through two reaches of Little Lost Man Creek (labeled "1976" and "1979" on fig. 1). Experimental injections of nitrate were conducted during 1976 when the riparian canopy was open and during 1979 after canopy closure. Concentration was varied by passage of a nitrate pulse down the channel; chloride was used as a conservative tracer to correct for dilution.

less nitrate uptake at all concentrations between approximately 30 and 180 μg NO_3-N in 1979. The negative uptake observed in 1979 around 30 μg NO_3-N/L is due to regeneration. Decreased uptake was observed in 1979 despite the fact that the minimum traveltime was shorter in 1976 (2.2 hours compared to 7 hours in 1979). The longer traveltime should have enhanced contact with periphyton in 1979. Even with better contact, less nitrate uptake after canopy closure indicates significantly reduced capacity for nitrogen uptake by biota. Thus both mechanisms, nitrification in the bed and reduced uptake by the epilithon, contribute to the current increase in DIN transport from the watershed.

At Little Lost Man Creek, the atomic N:P ratio (NO_3-N+NO_2-N)/ortho PO_4-P) was extremely low in 1974 (approx 1.75) but rose to approximately 7.8 by 1979. Although N:P has risen due to less nitrogen uptake and greater regeneration, both ratios indicate potential nitrogen limitation relative to phosphorus (Redfield and others, 1963; Rhee, 1978). Under the former (1974–76) conditions of high light input and nitrogen limitation, nitrate regeneration would have been difficult to observe in place, because nitrogen-limited algae can remove nitrogen both night and day (Conway and Whitledge, 1979; Triska and others, 1983; Sebetich and others, 1984), obscuring any potential contribution of nitrate regeneration. Since 1979, however, canopy shading has limited light infiltration, thereby lowering algal growth and nutrient uptake. At the same time, enhanced input of particulate organic matter (for example, alder leaf litter and decomposing root tissue) provides an additional source of organic nitrogen for regeneration. Dense shading also optimizes conditions for nitrate regeneration

cteria are inhibited by light (Olson,
iers, 1982). The result has been a
reach from a net loss of nitrogen in
n.

ARY AND CONCLUSIONS

The channel and stream studies in combination indicate that uptake and regeneration of inorganic nitrogen can be regulated on variable time scales in the stream. In experimental control, midafternoon nitrate uptake was up to 75 percent during the period of most active growth and approximately 40 percent by senescent communities under full sunlight. In the stream, maximum diel uptake was greater than 75 percent of the available nitrogen (77 percent in 1974, 87 percent in 1976) in an approximately 1,500-m open reach of Little Lost Man Creek. These levels of uptake indicate the potential of the biotic community to control diel nitrate transport under low-flow conditions.

Within longer term resetting periods (such as between storms), the epilithon community varied in its ability to influence nitrate transport in experimental channels. In an unshaded, nutrient-amended channel, the major factor controlling uptake was the maturity of the algal community. Actively growing epilithon had high nitrogen uptake per unit biomass compared to senescent films, under identical solute nitrogen concentration and channel discharge. In the control, a high C:N of periphyton during active growth presumably reflected nitrogen limitation. In the absence of periphyton removal, nitrogen uptake and C:N of periphyton generally decreased as the community aged. Under natural conditions of full sunlight in the stream, uptake increased from May through August. As discharge fell, background nitrogen concentrations rose, but nitrogen was effectively removed through most of the low-flow period. Toward late August and September, uptake declined although discharge was at its annual low. Community senescence was a possible cause.

Reduction in canopy density, such as from lower to higher order streams or through time as a result of canopy development, also influenced nitrate transport. The canopy increased solute nitrogen concentrations by at least two mechanisms: (1) by promoting nitrification in bankside sediments and (2) by decreasing algal uptake due to light limitation. In our experimental flumes, nitrate regeneration presumably occurred as benthic communities became senescent. However, the process could be verified only under highly darkened conditions, perhaps conditions simulating intragravel sites having high organic matter mineralization. Historically, nitrate regeneration did not produce an observable impact at Little Lost Man Creek until 14 years after clearcutting, when closure of the riparian canopy was nearly complete. The impact of nitrate regeneration was slight early in the growing season but increased throughout the summer to a peak in early September. Regeneration declined in late September, although discharge remained constant. The role of other sources and sinks, such as nitrogen fixed by riparian vegetation or lost via denitrification, is not known.

Experimental shading in the flume studies reinforced our conclusion that development of the riparian zone is of long-term importance in nitrogen cycling at Little Lost Man Creek and similar creeks. Our results suggest that canopy development will result in a long-term decline in epilithon production because of limitation of the synthesis of algal protein. Epilithon production is a major interface between DIN and the passage of nitrogen to higher trophic levels. Heterotrophic processes such as the decomposition of leaf litter will gain in importance due to greater litter input. However, nutrient flux associated with these heterotrophic processes is slow compared to nutrient flux associated with epilithic communities. As a result, animal species dependent on epilithic films are likely to decline in abundance. Other species that filter sloughed tissue from the water column or consume it as organic detritus are also likely to be affected. Decrease in protein synthesis low in the food chain may even extend to higher level carnivores such as fishes. Murphy (1979), who surveyed 20 small streams in Oregon, found trout biomass (g/m^2) to be lowest in streams covered by dense second-growth riparian cover, highest in open streams, and intermediate in the mixed canopy cover of old-growth forests. Thus the net result of lower DIN flux may be a large decline in biotic production until natural mortality in the riparian zone reopens the canopy (Triska and others, 1982). Development of an alder canopy is a typical response to clearcutting in coastal watersheds of northern California and the Pacific Northwest. As a result, more long-term data are needed for clearcut reaches like Little Lost Man Creek, to adequately assay the long-term impacts of current land management practices.

REFERENCES CITED

Bailey, E.H., Irwin, W.P., and Jones, D.L., 1964, Franciscan and related rocks, and their significance in the geology of western California: California Division of Mines and Geology Bulletin 183, 177 p.

Belser, L.W., and Mays, E.L., 1980, Specific inhibition of nitrite oxidation by chlorate and its use in assessing nitrification in soils and sediments: Applied and Environmental Microbiology, v. 39, p. 505–510.

Cloern, J.E., 1977, Effects of light intensity and temperature on *Cryptomonas ovata* (Cryptophyceal) growth and nutrient uptake rates: Journal of Phycology, v. 13, p. 389–395.

Conway, H.L., and Whitledge, T.E., 1979, Distribution, fluxes, and biological utilization of inorganic nitrogen during a spring bloom in the New York Bight: Journal of Marine Research, v. 37, p. 657–668.

Cuker, B.E., 1983, Grazing and nutrient interactions in controlling the activity and composition of the epilithic algal community of an arctic lake: Limnology and Oceanography, v. 28, p. 133–141.

Cummins, K.W., 1973, Trophic relations of aquatic insects: Annual Review of Entomology, v. 18, p. 183–206.

Eppley, R.W., and Coatsworth, J.L., 1968, Uptake of nitrate and nitrite by *Ditylum brightwelii*—Kinetics and mechanisms: Journal of Phycology, v. 4, p. 151–156.

Eppley, R.W., Rogers, J.N., and McCarthy, J.J., 1971, Light/dark periodicity in nitrogen assimilation of the phytoplankters *Skeletonema costatum* and *Coccolithus huxleyi* in N-limited chemostat culture: Journal of Phycology, v. 7, p. 150–154.

Grant, B.R., and Turner, I.M., 1969, Light stimulated nitrate and nitrite assimilation in several species of algae: Comparative Biochemistry and Physiology, v. 29, p. 995–1004.

Griffiths, D.J., 1979, Factors affecting nitrate reductase activity in synchronous cultures of *Chlorella*: New Phytology, v. 82, p. 427–438.

Healey, F.P., 1973, Inorganic nutrient uptake and deficiency in algae: Critical Reviews in Microbiology, v. 3, p. 69–113.

Hodler, M., Morgenthaler, J.J., Eichenberger, W., and Grob, E.C., 1972, The influence of light on the activity of nitrate reductase in synchronous culture of *Chlorella pyrenoidosa*: Federation of European Microbiological Societies, Letters, v. 28, p. 19–21.

Iwatsubo, R.T., and Averett, R.C., 1981, Aquatic biology of the Redwood Creek and Mill Creek drainage basins, Redwood National Park, Humboldt and Del Norte Counties, California: U.S Geological Survey Open-File Report 81–143, 115 p.

Iwatsubo, R.T., Nolan, K.M., Harden, D.R., and Glysson, G.D., 1976, Redwood National Park studies, data release number 2, Redwood Creek, Humboldt County and Mill Creek, Del Norte County, California, U.S Geological Survey Open-File Report 76–678, 247 p.

Iwatsubo, R.T., Nolan, K.M., Harden, D.R., Glysson, G.D., and Janda, R.J., 1975, Redwood National Park studies, data release number 1, Redwood Creek, Humboldt County, California, September 1, 1973–April 10, 1974: U.S. Geological Survey open-file report, 120 p.

Kennedy, V.C., and Malcolm, R.L., 1977, Geochemistry of the Mattole River of northern California: U.S. Geological Survey Open-File Report 78–201, 324 p.

Lyford, J.H., Jr., and Gregory, S.V., 1975, The dynamics and structure of periphyton communities in three Cascade Mountain streams: Theoretische und angewandte Limnologie Verhandlungen, v. 19, p. 1628–1639.

Meeks, J.C., 1974, Chlorophylls, chap. 5, *in* Stewart, W.P., ed., Algal physiology and biochemistry: Berkeley and Los Angeles, University of California Press, p. 161–175.

Merritt, R.W., and Cummins, K.W., 1978, An introduction to the aquatic insects of North America: Iowa, Kendall/Hunt Publishing Company, 441 p.

Murphy, M., 1979, Determinants of community structure and impacts of logging on predator communities in streams of the western Cascades: Corvallis, Oregon State University, unpublished M.S. thesis, 73 p.

O'Brien, J.E., 1962, Automatic analysis of chlorides in sewage: Wastes Engineering, v. 33, p. 670–672.

Olson, R.J., 1981, Differential photoinhibition of marine nitrifying bacteria: A possible mechanism for the formation of the primary nitrite maximum: Journal of Marine Research, v. 39, p. 227–238.

Pryfogle, P.A., and Lowe, R.L., 1979, Sampling and interpretation of epilithic lotic diatom communities, *in* Weitzel, R.L., ed., Methods and measurements of periphyton communities: A review: American Society for Testing and Materials, STP 690, 183 p.

Redfield, A.C., Ketchum, B.H., and Richards, F.A., 1963, The influence of organisms on the composition of seawater, *in* Hill, M.N., ed., The sea: New York, Wiley-Interscience, v. 2, p. 26–77.

Rhee, G.Y., 1978, Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition and nitrate uptake: Limnology and Oceanography, v. 23, p. 10–25.

Sebetich, M.J., Kennedy, V.C., Zand, S.M., Avanzino, R.J., and Zellweger, G.W., 1984, Dynamics of added nitrate and phosphate compared in a northern California woodland stream: Water Resources Bulletin, v. 20, p. 93–101.

Swanson, F.J., Gregory, S.V., Sedell, J.R., and Campbell, A.G., 1982, Land-water interactions: The riparian zone, chap. 9, *in* Edmonds, R.L., ed., Analysis of coniferous forest ecosystems of the Western United States: Stroudsburg, Pa., Hutchinson/Ross Publishing Company, p. 267–291.

Tischner, R., and Hutterman, A., 1978, Light-mediated activation of nitrate reductase in synchronous *Chlorella*: Plant Physiology, v. 62, p. 284–286.

Triska, F.J., Kennedy, V.C., and Avanzino, R.J., 1985, Uptake and regeneration of nitrate by epilithic communities in a nearly pristine lotic environment: U.S. Geological Survey Water-Supply Paper 2270, p. 91–98.

Triska, F.J., Kennedy, V.C., Avanzino, R.J., and Reilly, B.N., 1983, Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages, chap. 7, *in* Fontaine, T.D., III, and Bartell, S.M., eds., Dynamics of lotic ecosystems: Michigan, Ann Arbor Science Publishers, p. 129–159.

Triska, F.J., Sedell, J.R., and Gregory, S.V., 1982, Coniferous forest streams, chap. 10, *in* Edmonds, R.L., ed., Analysis of coniferous forest ecosystems of the Western United States: Stroudsburg, Pa., Hutchinson/Ross Publishing Company, p. 292–332.

Ward, B.B., Olson, R.J., and Perry, M.J., 1982, Microbial nitrification rates in the primary nitrite maximum off southern California: Deep-Sea Research, v. 29, no. 2A, p. 247–255.

Wetzel, R.G., and Westlake, D.F., 1974, Periphyton, chap. 2.3, *in* Vollenwieder, R.A., ed., A manual for measuring primary production in aquatic environments, IBP Handbook no. 12 (2d ed.): London, Blackwell Scientific Publication, 225 p.