

BIOGEOCHEMISTRY OF NITROGEN IN SONORAN DESERT STREAMS

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ABSTRACT

Inputs of inorganic nitrogen to streams of the arid Southwest are dominated by nitrate and ammonium in precipitation and nitrate mobilized from desert soils and transported to stream channels by overland flow. Thus, during flash floods, inorganic nitrogen concentrations are high in stream water. Once in the stream channel, inorganic nitrogen may be exported in surface runoff and subsurface flow to downstream ecosystems, stored and transformed in the hyporheic (deep sediment) zone and later released to the surface stream, or utilized by biota in the surface stream. Important nitrogen transformations within stream ecosystems include autotrophic assimilation by periphyton of surface sediments, and coupled mineralization and nitrification in deep sediments. Stream channels interact with groundwater in this region, thus nitrogen dynamics of streams may affect groundwater quality.

INTRODUCTION

Nitrogen and phosphorus have received much attention in limnological investigations because of their importance in determining aquatic productivity. Early work in lentic systems also was motivated by the realization that in excess, these macronutrients can cause eutrophication (Likens 1972). An eastern North American research bias (attributable to demography of limnologists) led to the generalization that of the two nutrients most likely to limit primary productivity, phosphorus limited freshwater systems (Likens 1972, Schindler 1977) while nitrogen was the limiting nutrient in coastal marine ecosystems (*e.g.*, Ryther and Dunstan 1971). Recent papers focusing on streams (Grimm and Fisher 1986a,b) and lakes (Elser *et al.* 1990) have pointed out this bias and suggested that nitrogen limitation commonly occurs in many freshwater ecosystems, especially those of western North America.

My goal in this review is to synthesize information from a relatively long term (12 y) intensive study of nitrogen dynamics in a northern Sonoran Desert stream, Sycamore Creek, Maricopa County, Arizona. I will begin by summarizing experimental studies demonstrating the importance of nitrogen as a limiting nutrient, then I will describe spatial and temporal variability of nitrogen concentration, and finally, I will present explanations for that variability based on analysis of sources, intrasystem transformations, and sinks of nitrogen in the stream ecosystem. Where possible, I will summarize supporting information from other studies of aquatic ecosystems in western North America, but I will focus primarily on dryland streams and rivers. Because streams are strongly linked with adjacent ecosystems including terrestrial catchments, downstream reservoirs, large rivers, and groundwater, an understanding of nutrient dynamics in streams may be crucial to understanding biogeochemical cycles in these linked systems. This is especially true in deserts, where lotic systems are "hot spots" of productivity in comparatively barren surroundings (Grimm and Fisher 1992).

DESCRIPTION OF DESERT STREAMS

Hydrologic disturbance is a dominant force shaping the structure and function of lotic ecosystems in the Southwest. Flash floods, at one hydrologic extreme, can remove both in-stream and riparian biota and alter channel sediment distributions. As a result, channels are typically wide relative to the wetted stream, and

riparian vegetation does not appreciably shade the stream. Insolation and water temperatures are high, favoring development of high standing crops of algae and macrophytes.

Stream substrata range from coarse sand to boulders, with small amounts of fine silt and a few patches of bedrock. Depth of alluvium over bedrock determines the size of the hyporheic zone, a region of saturated sediments and interstitial water beneath the surface stream. The hyporheic zone exchanges water (and nutrients) with the surface subsystem and also interacts with groundwaters, which in arid regions are recharged through stream channels. This subsystem is important both to ecosystem metabolism (Grimm and Fisher 1984) and to nutrient dynamics (Grimm *et al.* 1991; Valett *et al.* 1990) in the stream ecosystem.

Sycamore Creek, like other desert streams of the Salt River basin in the northern Sonoran Desert, is a moderately hard-water system, with conductivity from 300 to 500 $\mu\text{S}/\text{cm}$ and alkalinity near 250 mg/L as CaCO_3 . Calcium dominates cations, with magnesium and sodium each averaging about half the calcium concentration (as meq/L), while anions are dominated by bicarbonate, with sulfate of secondary importance (Fisher and Grimm 1983). Silica concentrations from 5-10 mg/L are unlikely to limit diatom growth, and soluble reactive phosphorus varies little about a mean of near 50 $\mu\text{g}/\text{L}$. In contrast, inorganic nitrogen concentrations are dynamic and highly variable. Most inorganic N is present as nitrate, although ammonium-N concentrations as high as 50 $\mu\text{g}/\text{L}$ have been recorded in Sycamore Creek's surface water.

IMPORTANCE OF NITROGEN TO AQUATIC PRODUCTIVITY

A limiting factor may be defined as that factor that produces an increase in some response variable when its abundance is changed. Bioassays for limiting nutrients usually involve addition of the suspected limiting nutrient and subsequent evaluation of change in biomass or productivity in comparison to a control (no addition) (Gerhart and Likens 1975; Pringle and Bowers 1984; Fairchild *et al.* 1985). Some authors have (incorrectly) identified limiting nutrients based on relative availabilities in the environment, arguing for example that phosphorus is limiting because environmental nitrogen to phosphorus ratio (N:P) > 16 (the Redfield (1958) ratio). Bothwell (1985) and Grimm and Fisher (1986a) used the term "potential nitrogen limitation" to describe the situation where environmental N:P is lower than optimum N:P of the primary producer community. Nutrient limitation occurs only if absolute concentrations are below limiting levels; potentially limiting nutrients can become limiting if assimilation sufficiently reduces concentrations, in the absence of other inputs.

Grimm and Fisher (1986b) found that at low flow, southwestern streams were *potentially* N-limited, based a mean N:P of 11.4 (Figure 1). In Sycamore Creek, N:P < 17.1 (mean cellular N:P for algae in this system) is the rule rather than the exception (Figure 2), thus this stream is potentially N-limited. To establish whether nitrogen *actually* limits primary production, four nutrient enrichment bioassays were conducted in Sycamore Creek. Results from these experiments indicate that nitrogen is limiting at environmental concentrations as high as 55 $\mu\text{g}/\text{L}$; and that phosphorus is neither primarily nor secondarily limiting (Table 1). In other words, phosphorus availability is adequate to support periphyton growth even when nitrogen is present in excess. In contrast, streams of the tallgrass prairie are so nutrient-poor as to show an enrichment response only to the simultaneous addition of nitrogen and phosphorus (Tate 1990).

Inorganic nitrogen concentration is below 55 $\mu\text{g}/\text{L}$ in Sycamore Creek about 53% of the time (Figure 3), especially during summer low-flow periods ($n = 211$, non-flood samples only). This suggests that nitrogen limitation is a common occurrence in this stream. Other streams of the Southwest have similarly low nitrogen concentrations; 82% of stream sites surveyed at low flow (non-flood, continuously flowing streams; $n = 92$) were N-limited if 55 $\mu\text{g}/\text{L}$ is considered a limiting concentration (Grimm and Fisher 1986a). Many streams of the Pacific Northwest are secondarily N-limited, although light is usually the limiting factor in small, heavily-shaded headwater streams (Gregory 1980; Hill and Knight 1988; Triska *et al.* 1983). Nitrogen limitation is not limited to lotic ecosystems; examples abound of N-limited lakes (see Elser *et al.* 1990). We have suggested previously (Grimm and Fisher 1986a) that regional nitrogen limitation may be due less to low nitrogen than to abundant, physicochemically-controlled phosphorus. Phosphorus

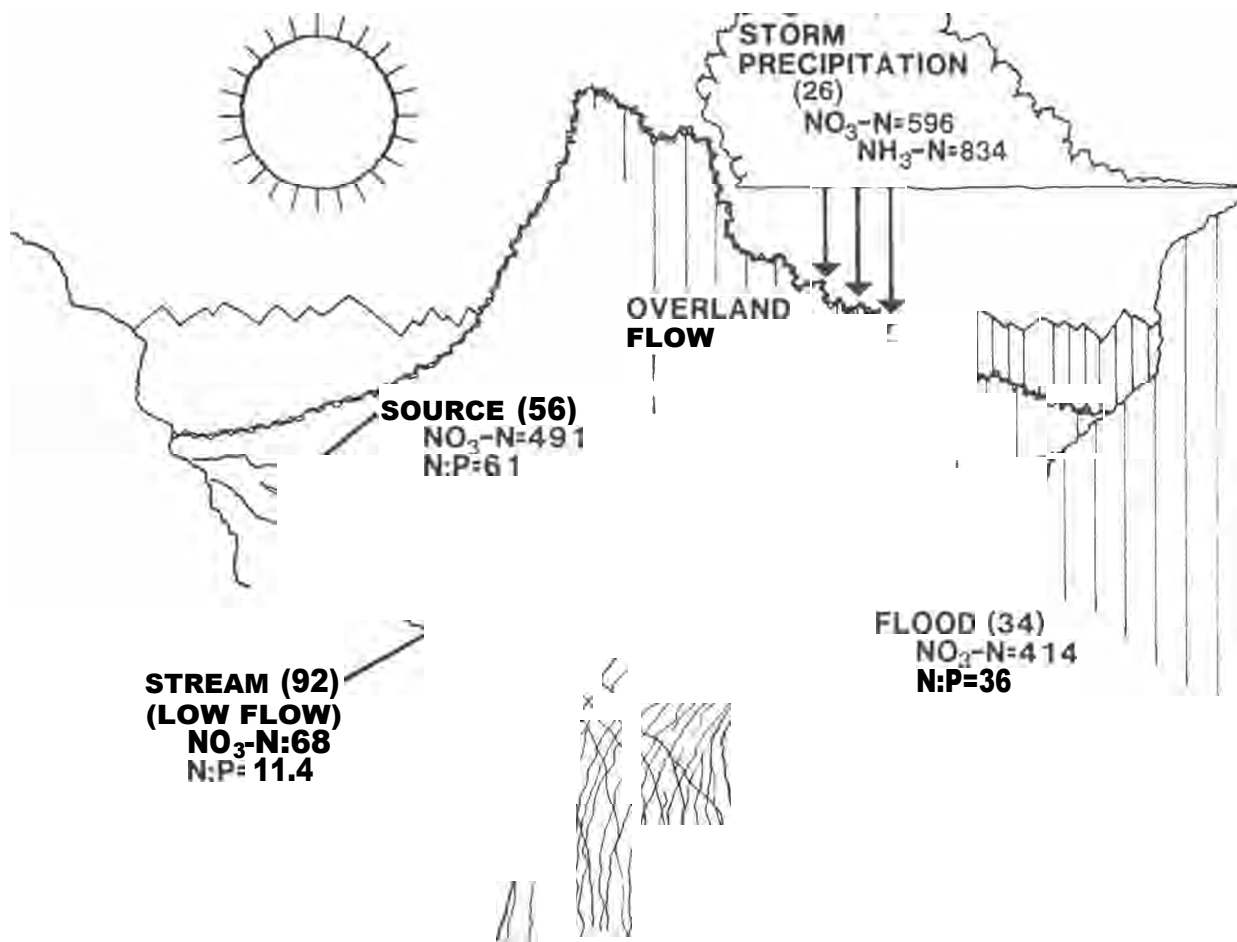


Figure 1. Schematic summary of mean nitrate-N concentration and N:P ratios of precipitation, floodwaters, sources of surface flow in intermittent channels, and continuously flowing streams sampled at points downstream from sources. Data from extensive survey of surface waters in Arizona drainage basins (Grimm and Fisher 1986b), numbers of sites (or precipitation events) in parentheses.

equilibrium (either solubility control or adsorption-desorption equilibrium) allows depletion of nitrogen to occur with continued uptake, whereas phosphorus remains unchanged.

In addition to its importance in controlling productivity, especially during early succession (Grimm and Fisher 1986a), nitrogen availability strongly influences algal assemblage structure and may indirectly limit secondary production of detritivorous macroinvertebrates through limitation of microbial communities that colonize detritus. Cyanobacteria are important components of late-successional assemblages in particular (Grimm and Fisher, unpublished data), but also are endosymbionts of diatoms of the Epithemiaceae, which may colonize during early stages of succession (Peterson and Grimm 1992). Grimm and Fisher (1989) hypothesized that N limitation of microbial production was responsible for dramatic crashes of macroinvertebrate populations observed during 5 post-flood successional sequences. This hypothesis was based, in part, on a positive correlation ($r = 0.74$, $p < 0.001$) of > 30 -d macroinvertebrate densities with nitrogen flux (concentration \times discharge). We suggested that food "quality" of fine particulate materials (which are continually reingested by macroinvertebrates) deteriorates when N supply limits microbial colonization. These studies indicate that nitrogen supply may control both autotrophic and heterotrophic metabolism and thus strongly affect ecosystem productivity.

Table 1. Results of nutrient enrichment bioassay experiments in Sycamore Creek, Arizona. Data from Grimm and Fisher (1986). Two types of experiments were conducted: enrichment of substrata (sub) and overlying water (wat). Symbols: + - response variable significantly > control; 0 - response variable not significantly > control. NT = not tested.

TYPE	TREATMENTS	AMBIENT CONCENTRATION ($\mu\text{g/L}$)				RESPONSE		
		NH ₄ -N	NO ₃ -N	SRP	N:P	+N	+P	+N+P
1	SUB C, N	8	55	54	2.6	+	NT	NT
2	SUB C, N, P, N+P	14	29	45	2.1	+	o	+
3	WAT C, N, P, N+P	11	18	40	1.6	+	o	+
4	WAT C, N	12	27	47	1.8	+	NT	NT

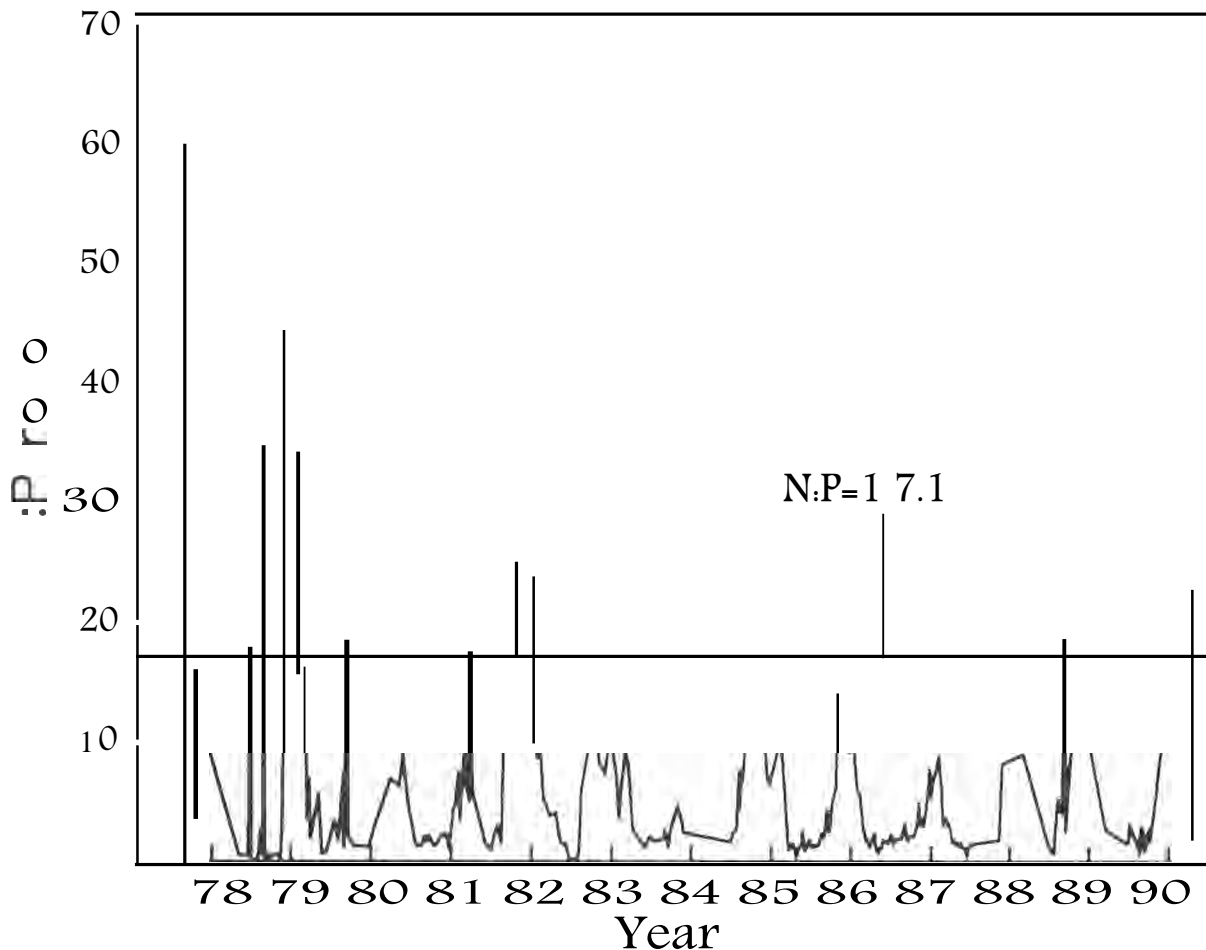


Figure 2. Atomic ratio of inorganic N (NO₃-N+NH₄-N) to soluble reactive P in surface waters from Sycamore Creek, Arizona, 1978-1990, n = 279. Horizontal line indicates N:P = 17.1, a mean algal N:P and an estimate of the point of transition from potential P limitation (N:P > 17.1) to potential N limitation (N:P < 17.1).

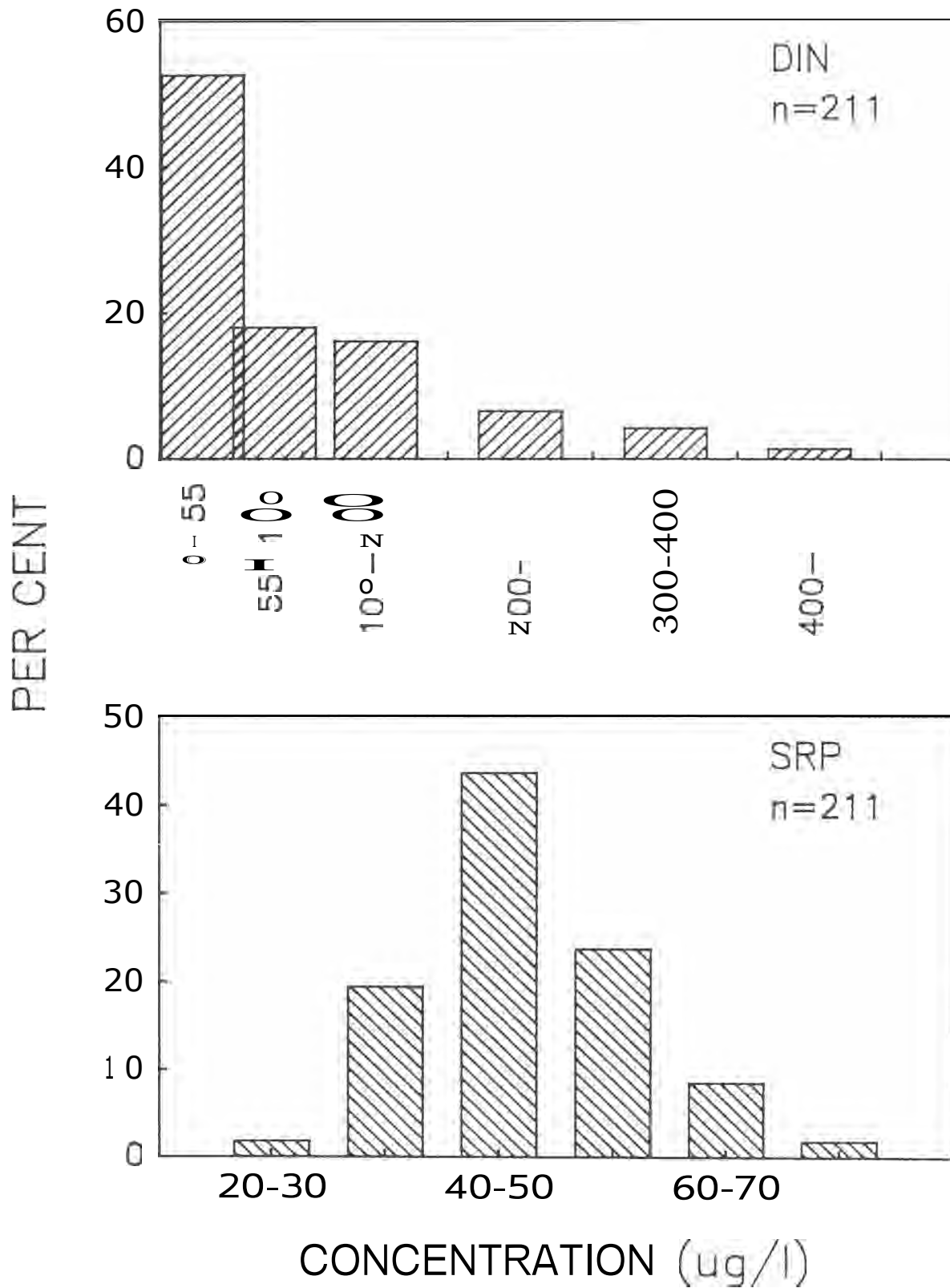


Figure 3. Frequency distributions of interflow dissolved inorganic N and soluble reactive P concentration in Sycamore Creek, Arizona, 1978-1990, n = 211. Note distributions do not include floodwater samples.

TEMPORAL AND SPATIAL VARIABILITY OF NITROGEN CONCENTRATION

Spatial variability of nitrogen incorporates both within- and among-stream differences. Pronounced longitudinal variation in concentration of nitrate-N has been observed in several streams (Stockner 1968; Owens *et al.* 1972; Kaushik and Robinson 1976; Grimm *et al.* 1981; Grimm and Fisher 1986b; Tate 1990). Longitudinal decline of nitrate-N concentration is common among a wide variety of southwestern streams; thus sources or springs have significantly higher concentration (mean $\text{NO}_3\text{-N} = 491 \mu\text{g/L}$) than do streams below sources at low flow (mean $\text{NO}_3\text{-N} = 68 \mu\text{g/L}$; Figure 1). Nitrate-nitrogen concentration also differs between surface and hyporheic waters, with subsurface concentration generally exceeding that of the surface stream (Valett *et al.* 1990).

Differences among streams may be attributable to catchment geology and soils, time since flooding, or instream processes. Variability of a biologically conservative variable, such as conductivity, provides an indication of the extent to which 157 southwestern streams surveyed by Fisher and Grimm (1983) differed chemically: coefficient of variation was 128%. Regional variability of soluble reactive phosphorus (SRP) was remarkably similar to this ($\text{CV} = 132\%$), suggesting that SRP may be relatively conservative. Nitrate-N concentration, however, was highly variable among streams ($\text{CV} = 221\%$). This high variability may be explained by temporally varying processes (both biotic and abiotic) that alter inorganic nitrogen concentration in streamwater.

Temporal variation must be considered at several scales. Diel variation occurs in response to algal and riparian uptake (Manny and Wetzel 1973; Triska *et al.* 1983; Sebetich *et al.* 1984; Grimm 1987; Tate 1990), diel changes in hydrology (Valett, in review), and diel difference in other processes for which inorganic nitrogen is a substrate or product. At the scale of the interflood period (the period between floods, averaging ≈ 60 d in Sycamore Creek; Grimm and Fisher 1989), dissolved inorganic nitrogen (DIN) exhibits a wide

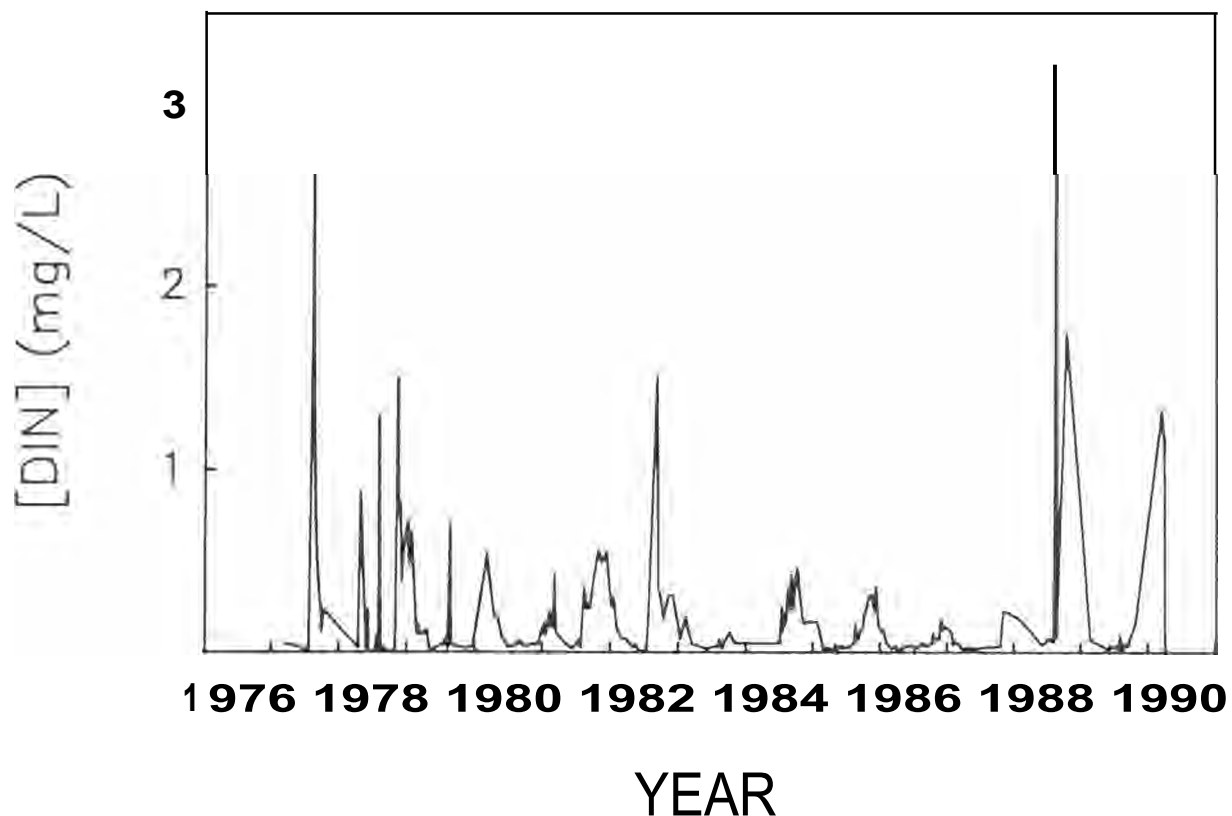


Figure 4. Dissolved inorganic N (DIN) concentration of surface water from Sycamore Creek, Arizona, 1978-1990, $n = 284$.

range of concentration when compared with SRP (Figure 3). In addition, the distribution of interflood DIN concentration is highly skewed towards low or limiting levels ($< 55 \mu\text{g/L}$). In contrast, SRP concentration shows a normal distribution, and does not fall below $20 \mu\text{g/L}$ (Figure 3).

At an annual scale, flash floods are included in the distribution, and temporal variability increases dramatically (Figure 4). Peak concentrations are associated with flood peaks, while valleys are associated with summer low-flow conditions. Wintertime non-flood concentration tends to be slightly higher than that of summer (Grimm and Fisher 1986b).

The high variability in DIN concentration at the annual scale, when spates are included, may be explained by considering the chemistry of precipitation and runoff (Figure 1). Precipitation is frequently high in both nitrate and ammonium, thus DIN varies from 200 to over $4000 \mu\text{g/L}$. Inorganic nitrogen concentration in rain varies seasonally, contributing to additional variability of inputs (Emmerich 1990). When precipitation amount and intensity exceed a threshold, runoff occurs as overland flow and flashy discharge from small catchments (Osborn and Renard 1970; Yair *et al.* 1978; Fisher and Grimm 1985). Although concentration in rain is high, concentration in runoff often exceeds that in precipitation, suggesting that additional DIN is mobilized from desert soils. Runoff from small catchments feeds larger channels, where flood response depends in part on channel storage capacity. Floods insufficient to fill storage pools in channel alluvium may recharge dry hyporheic sediments rather than produce increased discharge (see also Stanley and Valett 1992). This scenario explains in part why sources of surface flow (which are points of hyporheic discharge onto the surface) have similar chemistry to floodwaters (Figure 1).

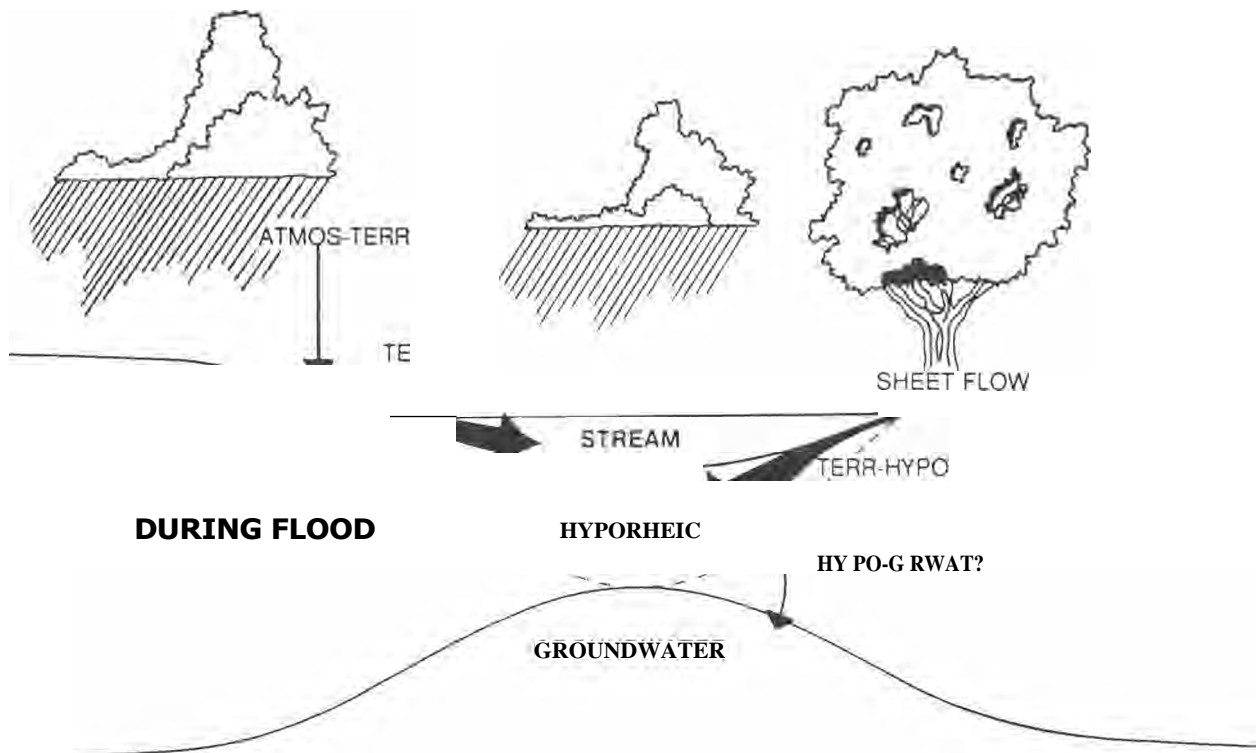


Figure 5. Major intersystem nitrogen transfer pathways during flash floods in desert catchments. Thickness of arrows indicates importance of flux.

NITROGEN SOURCES, SINKS, AND TRANSFORMATIONS

During flood events, the primary direction of nitrogen transfer is toward the stream, from the surrounding desert catchment (Figure 5). This input may represent the most important nitrogen source for the ecosystem over the long term. Of course, floodwaters high in nitrogen may simply be carried to downstream systems (larger streams, reservoirs, canals), but if recharge of the hyporheic zone is appreciable some of the nitrogen is likely to be retained. Hyporheic-groundwater exchange is probably the only significant N output, and this linkage is unlikely to be enhanced during flood. Because biotic standing crops are severely reduced by spates (Fisher et al. 1982; Grimm and Fisher 1989), intrasystem biotic transformations and intersystem transfers mediated by biota are insignificant during flash floods.

In contrast, between floods the predominant direction of nitrogen transfer is away from the stream (Figure 6). Nitrogen linkages between the stream and the terrestrial ecosystem include riparian uptake, emergence of aquatic insects, and stranding of algae along stream margins during drying. Hyporheic zone to groundwater transfer of nitrogen is an additional sink. Finally, during late successional periods, two conditions favoring atmospheric-aquatic linkage are prevalent in dryland streams: Cyanobacteria become abundant or even dominant taxa (Fisher et al. 1982), and anaerobic zones increase in abundance. Nitrogen fixation by Cyanobacteria (several nitrogen-fixing genera, including *Anabaena*, *Calothrix*, and *Nostoc*, are common in desert streams) may represent the sole input of nitrogen during interflood periods (Grimm 1987). High productivity coupled with intense decomposition may promote the establishment of anoxic zones immediately beneath the sediment surface, where denitrification may occur. This microbially-mediated reduction of nitrate to nitrous oxide or dinitrogen (both gaseous), is a potentially important nitrogen sink.

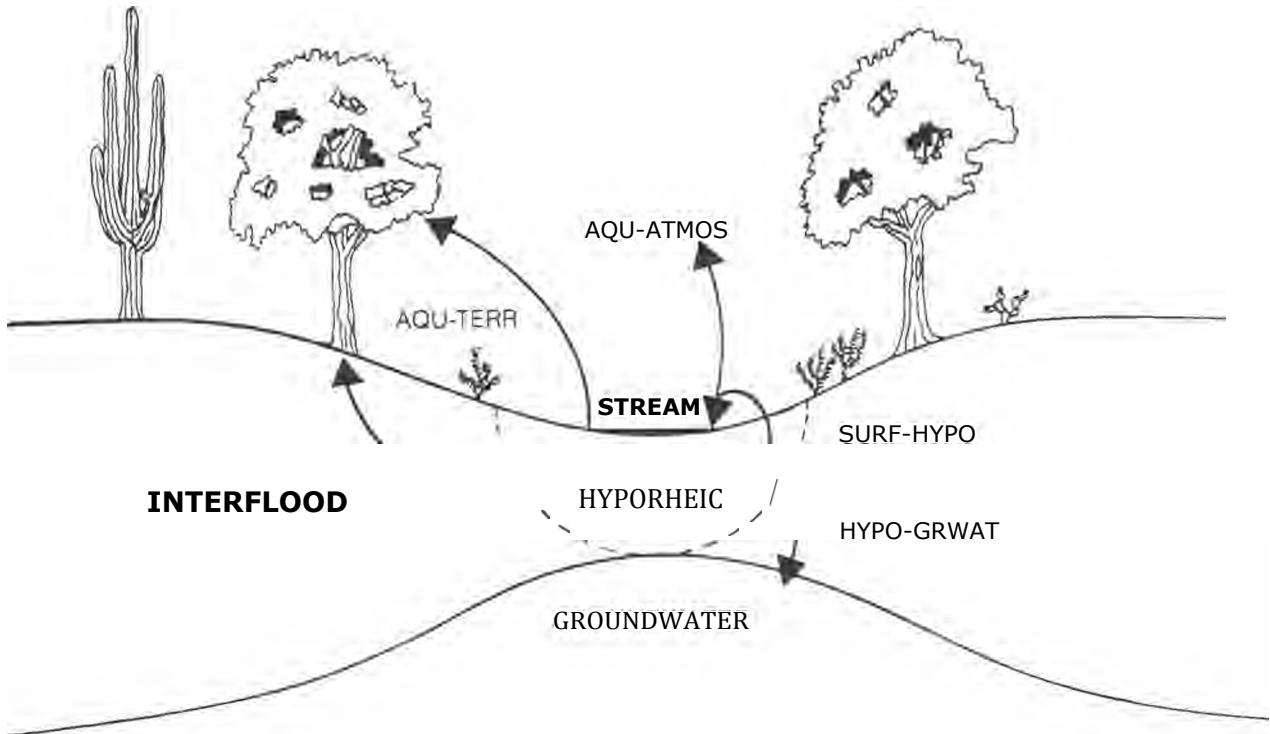


Figure 6. Major intersystem nitrogen transfer pathways during interflood periods in desert catchments.

Distinct intrasystem transformations of nitrogen occur in two important subsystems: the hyporheic and surface zones. In dark hyporheic sediments, primary production is negligible and high rates of microbial respiration could potentially drive oxygen concentration to low levels. When gravels are free of clogging silt or organic matter, however, interstitial flow velocities can be high (1-50 mm/s; Grimm and Fisher 1984, Valett *et al.* 1990); thus oxygen is replenished by recharge from the surface zone. Oxygen concentration in the hyporheic zone probably depends upon residence time, concentration in surface water at recharge sites (which is affected by both production and respiration), and rates of microbial oxygen consumption (Valett, in review). Because few processes dictate oxygen concentration, this variable can be used to infer hyporheic flow patterns and the degree of surface-hyporheic linkage (Valett, in review). Oxygen levels in the subsurface environment also dictate the types of nitrogen transformations that can occur there.

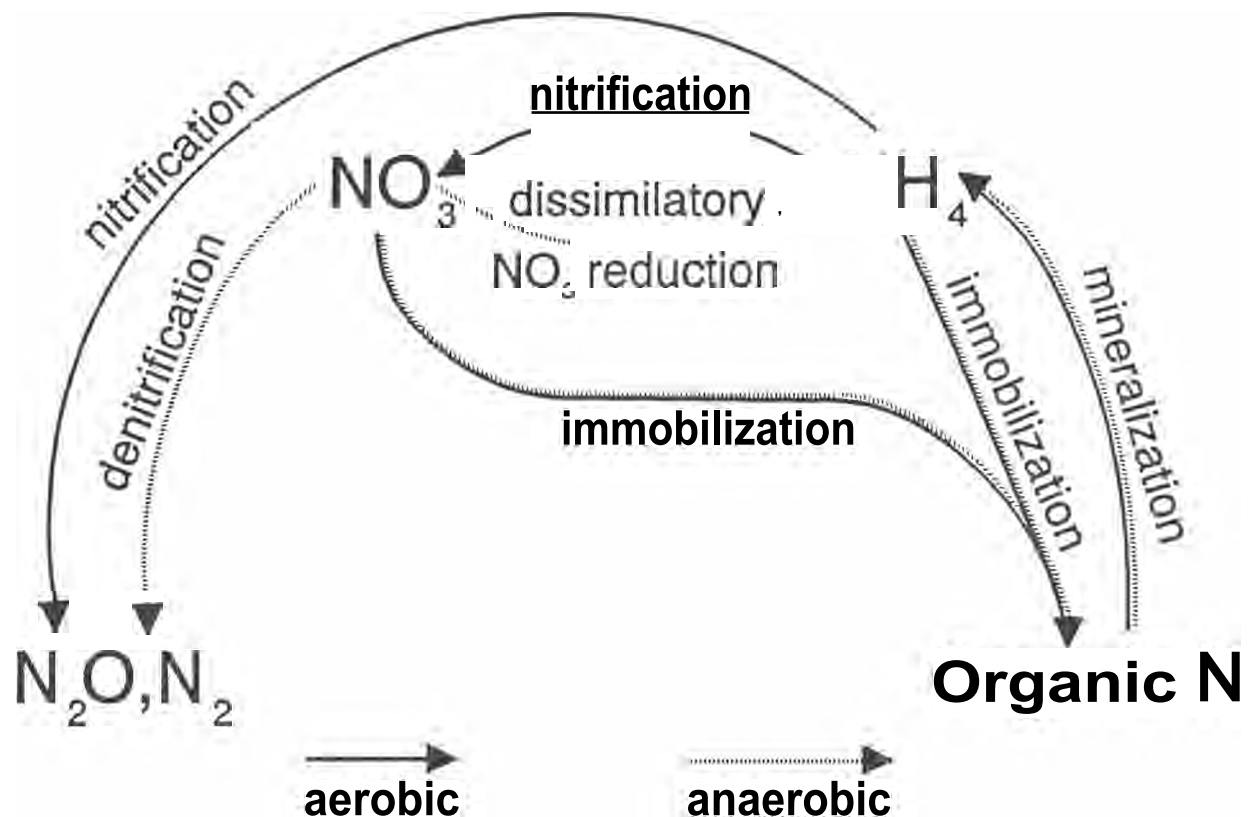


Figure 7. Nitrogen transformations of the hyporheic (deep sediment) zone in desert streams. Predominantly aerobic transformations are expected when coarse sediments are unobstructed by fine materials and coarse interstitial velocities are high.

Sediment nitrogen transformations. --Transformations of N occurring within sediments include several microbial processes: degradation of organic matter (mineralization and immobilization), nitrification, dissimilatory nitrate reduction, and denitrification (Figure 7). A common but simplistic approach to

measuring N transformations in sediments is to quantify net changes in nitrogen concentration of water passed through a sediment core (e.g., Sain *et al.* 1977; Chatarpaul and Robinson 1979). The disadvantage of this approach is that assignment of net changes to specific microbial transformations can be made only on the basis of correlation and inference from supporting studies. For this reason as well, it is difficult, if not impossible, to infer hyporheic flow patterns or residence times from an analysis of concentration (Valett, in review).

Breakdown of organic material ultimately results in release (mineralization) of nitrogen, although the balance of mineralization and microbial immobilization (uptake of inorganic N) during decomposition is determined by the C:N ratio of the organic matter (Melillo *et al.* 1984). The product of organic nitrogen mineralization is ammonium, which in aerobic sediments may be rapidly nitrified. I determined net nitrogen fluxes associated with sediments from Sycamore Creek in January and February 1984. Sediments were fine gravels containing 0.12-0.31% organic matter (ash-free dry mass, AFDM). Cores were collected, capped underwater, and connected to a reservoir of streamwater. Streamwater of known inorganic nitrogen (iN) concentration was circulated through the sediment cores at realistic interstitial velocities (0.014-0.156 cm/s) for 1-4 h in darkness. Concurrent measurements of oxygen consumption by sediments were made using methods outlined in Grimm and Fisher (1984). In a later study, I measured nitrification potentials of sediments in the laboratory (Grimm *et al.* 1991). My goal was to determine net nitrogen mineralization rates and nitrification potential for comparison with rates of sediment respiration and with whole ecosystem budget parameters (nitrogen retention, algal iN uptake). These comparisons may reveal whether hyporheic nitrogen mineralization could represent an important source of nitrogen to the surface system.

In sediment core experiments, net release of both $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ occurred at mean rates of 6.55 (SE = 1.55, n = 12) and 0.84 (SE = 0.76, n = 12) $\mu\text{g N mg AFDM h}^{-1}$, respectively (Table 2). Ammonium release was highly variable (limits = -4.75 to +5.67 $\mu\text{g N mg AFDM h}^{-1}$), and in two cases ammonium was immobilized. Duff *et al.* (1984) reported comparable rates of release associated with surface stream periphyton communities under dark, aerobic conditions. Since my sediment core systems were aerobic, the relatively large changes in nitrate can be ascribed to mineralization of organic nitrogen with rapid nitrification of ammonium, minus unmeasured losses to microbial assimilation and nitrification to nitrous oxide (Figure 7). Oxygen consumption of sediment cores averaged 123.6 $\mu\text{g O}_2 \text{ mg AFDM h}^{-1}$ (SE = 16.4, n = 5). Assuming a respiratory quotient of 1.0, C:N of mineralization was 7.3. This is a low but not unreasonable value for benthic particulate organic matter, when compared with measured algal and detrital C:N of 9-12 (Grimm 1987).

Potential nitrification rates measured by Grimm *et al.* (1991) were similar to net iN release rates (Table 2). Nitrate-N release of control sediment exceeded that of sediments with inhibitor (nitrapyrin) added, while $\text{NH}_4\text{-N}$ was released in the presence of inhibitor yet consumed in control sediments. Nitrate was neither released nor taken up when inhibitor was added, suggesting that nitrification was the dominant process affecting nitrate in these aerobic sediments (Figure 7), *i.e.*, losses to denitrification, dissimilatory nitrate reduction, and immobilization were insignificant. Triska *et al.* (1989) suggested nitrification was the major nitrogen transformation in aerobic hyporheic sediments, but found anaerobic transformations were important in riparian zone sediments that were more isolated from streamflow (Duff and Triska 1990).

Net iN mineralization and potential nitrification rates were compared with whole ecosystem utilization of iN (Grimm 1987) by multiplying by dry mass of a 1 m² x 50 cm depth sediment column. This conversion expresses N release on an areal basis; 50 cm is a reasonable mean sediment depth for Sycamore Creek (Grimm and Fisher 1984; Fisher *et al.*, unpublished data). Comparison reveals that sediment-mediated recycling of iN represents a significant fraction of surface stream iN utilization (Table 2). Thus where the hyporheic zone is linked to the surface stream through hydrologic exchange, inputs from the hyporheic zone may alleviate surface nitrogen limitation.

Nitrogen transformations in the surface stream. --I previously pointed out that much of the interflow

variability in nitrogen concentration is due to longitudinal changes in concentration below sources (or, in continuously flowing reaches, below hyporheic discharge points). Grimm *et al.* (1981) argued on the basis of correlations of whole stream retention with algal biomass (as chlorophyll *a* and AFDM) that algal assimilation was the process causing longitudinal declines. To further test this hypothesis, I measured algal uptake rates in *in situ* chambers, developed multiple regression model equations that predict uptake as a function of initial concentration and chlorophyll *a*, and used these relationships to predict whole system uptake for 7 dates on which ecosystem nitrogen retention was determined independently (see Grimm 1987). I reasoned that if algal uptake is the process causing concentration declines, then predicted uptake rates should be similar to measured retention.

Nitrate-N uptake by isolated algal assemblages was measured on 19 occasions between 1979 and 1983. Assemblages were of 3 types: diatom-dominated (on gravel or unglazed clay tile substrata); filamentous green algal mats (primarily *Cladophora glomerata* or *Hydrodiayonreticulatum*); or mixed cyanobacteria (primarily

Table 2. Rates of net inorganic nitrogen mineralization (iN *min*, measured as NO₃-N + NH₄-N release) and nitrification potentials (measured as difference between NO₃-N and NH₄-N release in the presence vs. absence of the nitrification inhibitor, nitrapyrin) for Sycamore Creek sediments per unit dry mass, AFDM, and stream bottom area. Areal rates calculated assuming sediment AFDM=0.2% DM (for mineralization measurements) and dry mass = 1,000 kg/m² (to 50 cm depth). Areal rates of ecosystem inorganic nitrogen (iN) retention and algal nitrate uptake included for comparison.

FLUX	N/DM ($\mu\text{g me h}^{-1}$)	N/AFDM ($\text{Ag mg}^{-1} \text{h}^{-1}$)	N/area ($\text{mg m}^{-2} \text{h}^{-1}$)
iN <i>min</i>		7.39	15
NO ₃ -N		6.55	13
NH ₄ -N		0.84	2
Nitrification			
NO ₃ -N	0.047		47
NH ₄ -N	0.021		21
Ecosystem iN retention			-1.4 - 38
Algal NO ₃ uptake ² - low NO ₃ -N			-7.8 - 7.6
Algal NO ₃ uptake - high NO ₃ -N			5.8 - 51.7

¹ Data from Grimm *et al.* (1981).

² Low NO₃-N: <0.2 mg/L; high NO₃-N: 0.2 mg/L.

Calothrix sp.)-diatom assemblages (on gravel-coated tile substrata). Algal samples were either enclosed within chambers *in situ* or moved to streamwater-filled enclosures on the stream bank. Uptake was measured as the change in $\text{NO}_3\text{-N}$ concentration over incubation time (usually ≤ 30 min; adjusted downward to prevent depletion when initial concentration was low), expressed per unit area and per unit chlorophyll *a*. Some chambers were enriched with $\text{NO}_3\text{-N}$, providing a range of initial $\text{NO}_3\text{-N}$ concentrations. Model equations relating uptake per unit chlorophyll *a* to chlorophyll *a* and initial $\text{NO}_3\text{-N}$ concentration were developed using stepwise multiple regression (BMDP Statistical Software).

Nitrate-N uptake ranged from -7.76 to $51.7 \text{ mg m}^{-2} \text{ h}^{-1}$ (negative uptake = release; Table 2), comparable to the whole system rates reported by Grimm *et al.* (1981) for a variety of desert streams (limits: -1.4 to $38 \text{ mg m}^{-2} \text{ h}^{-1}$; Table 2). Nitrate-N uptake in a productive, Cyanobacteria-dominated Washington thermal spring was similar ($12.9 \text{ mg m}^{-2} \text{ h}^{-1}$; Stockner 1968). Chlorophyll-specific uptake was variable, but significantly higher rates were generally observed under enriched conditions (7 of 9 comparisons, t-test, $p < 0.05$). In 3 cases, enriched uptake was an order of magnitude higher than unenriched, suggesting that stream periphyton may have a capacity similar to that observed for marine phytoplankton (McCarthy and Goldman 1979) to rapidly assimilate added nitrogen. Triska *et al.* (1983) also reported 3- to 4-fold enhancement of nitrate-N uptake in experimental channels enriched with N and P.

Chlorophyll-specific $\text{NO}_3\text{-N}$ uptake was dependent upon standing crop for all algal types and upon initial $\text{NO}_3\text{-N}$ concentration for diatoms and Cyanobacteria-diatom assemblages, with these variables explaining 55-66% of the variance in uptake (Table 3). Coefficients for initial concentration were positive, suggesting that chlorophyll-specific uptake becomes saturated at high $\text{NO}_3\text{-N}$ concentration, as is expected for an enzyme-controlled process such as nitrate reduction. Coefficients for chlorophyll *a* standing crop were negative, thus chlorophyll-specific uptake decreased exponentially with increasing standing crop, perhaps as a result of reduced access to nutrients and light of "understory" cells as algal mat thickness increased (Fraleigh and Wiegert 1975; Gregory 1980; Bothwell 1989). $\text{NO}_3\text{-N}$ uptake rates calculated from data of Triska *et al.* (1983) similarly show a decline with periphyton community development from $200\text{-}960 \text{ jig mg}^{-1} \text{ h}^{-1}$ at $2\text{-}10 \text{ mg/m}$ chlorophyll *a* to $15\text{-}37 \text{ } \mu\text{g mg}^{-1} \text{ h}^{-1}$ at 32 mg/m chlorophyll *a*.

To test whether whole system $\text{NO}_3\text{-N}$ retention could be predicted from algal $\text{NO}_3\text{-N}$ uptake, I applied multiple regression equations to data from 7 dates on which retention had been independently measured (Grimm 1987). Equations 1-3 and equation 4 (Table 3) generated similar results, so for clarity only predictions from Equation 4 are reported. Limits of observed $\text{NO}_3\text{-N}$ retention in nearly all cases were within confidence limits of predicted uptake (Table 4); confidence intervals were wider for high chlorophyll *a* standing crops than for low standing crops, but actual retention on those dates was more variable as well. In general, this analysis supports the hypothesis that algal assimilation is the process accounting for retention of $\text{NO}_3\text{-N}$ by desert stream ecosystems. The complexity of the nitrogen cycle undoubtedly increases with time after disturbance, however, as algal mats develop, microzone nutrient and light limitations develop, anaerobic zones increase in extent, and system heterogeneity increases.

SUMMARY AND CONCLUSIONS

There has been much interest in nutrient dynamics and nutrient limitation of aquatic systems because of the aesthetic, public health, natural resource, and recreational importance of clean water supplies. In the Southwest, water quality issues have received less attention than elsewhere; yet, we know that the health of natural streams and rivers in the region is crucial to maintenance of quality of intensively managed surface waters, such as reservoirs and canals, and we are beginning to recognize the importance of vertical hydrologic linkages (*via* the hyporheic zone) to groundwater quality. Our studies in Sycamore Creek and other southwestern streams have indicated that nitrogen is the critical element in terms of ecosystem

Table 3. Model equations relating NO₃-N uptake per unit chlorophyll to initial NO₃-N concentration ([N]) and chlorophyll *a* standing crop (CHL) for three algal types common in Sycamore Creek. Equations are of the form: uptake/chl=(e^{-a [N]} - b CHL) - 100, where a, b, and c are coefficients (standard errors in parentheses), e is the base of natural logarithms, and 100 is a constant permitting utilization of negative uptake values. Algal types are: equation 1 - filamentous Chlorophyta; equation 2 - diatoms; equation 3 - cyanobacteria/diatoms; equation 4 - all considered as a single group (some Chlorophyta excluded because chlorophyll *a* data were not available on an areal basis). Ranges of initial concentrations and algal standing crops to which regression equations are applicable are given in columns 7 and 8.

Equation	a	b	c	partial r ²		range		n	multiple r ²
				[N]	chl	[N] (Ag/L)	chl (mg/m ²)		
1	4.99		-0.220 (0.037)		0.56	19-100	0.03- 2.141	30	0.55
2	7.15	0.242 (0.026)	-0.331 (0.041)	0.22	0.38	5-1000	6-565	73	0.60
3	8.49	0.294 (0.027)	-0.587 (0.071)	0.32	0.34	12-800	6-166	70	0.66
4	7.35	0.271 (0.019)	-0.344 (0.036)	0.33	0.25	5-1000	6-565	158	0.58

* Standing crop for this algal type expressed in mg total chlorophyll *a*

Table 4. Predicted and observed hourly uptake of $\text{NO}_3\text{-N}$ in Sycamore Creek, Arizona, 1981-1983. Predicted values are based on equation 4 from Table 3 (minimum and maximum represent 95% confidence limits); observed values are the minimum and maximum hourly $\text{NO}_3\text{-N}$ retention rates observed over a 24-h period. All uptake values in $\text{mg N m}^{-2} \text{ h}^{-1}$.

DATE	CHL mg/m^{-2}	[N] mg/L	PREDICTED UPTAKE			OBSERVED UPTAKE	
			MEAN	MIN	MAX	MIN	MAX
3 Aug 81	82.5	0.146	8.5	0.6	23.3	-3.0	6.3
18 Aug 81	228.2	0.027	-2.2	-12.0	16.1	2.2	5.5
3 Sept 81	295.0	0.063	1.2	-13.2	15.5	3.5	8.7
6 July 82	342.6	0.030	-6.6	-19.6	18.0	-1.2	0.3
26 Aug 82	7.1	0.028	1.4	0.4	3.3	0.5	1.6
29 Aug 82	17.5	0.015	1.5	0.0	4.4	0.1	0.4
4 Nov 83	99.0	0.049	4.1	-2.5	16.6	-1.5	12.8

productivity. Nitrogen is also highly variable in space and time due to: 1) variation in instream processes (especially algal assimilation in the surface stream and mineralization-nitrification in the hyporheic zone); and 2) temporally variable aquatic-atmospheric coupling within the biogeochemical cycle of nitrogen. We should focus on brief, intensive hydrologic events in the desert as the principal periods of significant movement of nitrogen from atmospheric to terrestrial to aquatic systems. With this perspective, erroneous assumptions such as that made by Peterjohn and Schlesinger (1990) of no net loss of N from semiarid catchments to streamflow, can be avoided. We must also recognize that ribbons of aquatic riparian productivity embedded in barren, arid surroundings are potentially important sources of N to linked ecosystems during the relatively long periods between storms.

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