

Pre- and post-flood retention efficiency of nitrogen in a Sonoran Desert stream

EUGÈNIA MARTÍ, NANCY B. GRIMM, AND STUART G. FISHER

Department of Biology, Arizona State University, Tempe, Arizona 85287-1501 USA

Abstract. The objectives of this study were 1) to compare Sonoran Desert streams with other streams in terms of retention efficiency of nitrate; 2) to examine the effects of a flood on nitrate retention and to determine which factors control nitrate retention in the surface stream subsystem in Sycamore Creek, Arizona; and 3) to compare the short-term nutrient addition technique with computations based upon natural nutrient gradients. From June to September 1995, we did 8 short-term nitrate and chloride additions (4 additions before and 4 after a flood) in a 240-m reach to measure nitrate uptake length as an index of surface stream retention efficiency of nitrate. We also calculated nitrate uptake lengths based on a natural downstream decline in nitrate concentration, using data from the addition dates and from previous studies.

Nitrate uptake lengths measured in Sycamore Creek were short (<120 m) compared to published values from other streams, indicating a high retention efficiency of nitrate in this nitrogen-limited stream. A midsummer flood caused a 2-fold decrease in retention efficiency of nitrate in the reach (i.e., nitrate uptake length increased from 61 to 124 m); however, this change was within the range of variation measured before the flood. Rapid algal recovery (23 d), the dramatic decrease in discharge, and a large transient storage zone may account for the apparent high resilience of nutrient retention efficiency to disturbance. Most of the temporal variation in nitrate uptake length during the study period was attributed to changes in the algal assemblage. In particular, retention efficiency of nitrate decreased when nitrogen fixers were abundant. Uptake lengths calculated from additions were always shorter than those from natural nitrate declines, supporting our hypothesis that nutrient uptake lengths from short-term nutrient additions reflect gross, rather than net, nutrient uptake. Uptake rates from short-term additions and from natural declines of nitrate over post-flood succession showed a similar temporal pattern, but the ratio between them increased late in succession. This result suggests that, during late successional stages, nutrient release processes became more important than nutrient uptake processes, a prediction that is consistent with the ecosystem succession and nutrient retention hypothesis.

Key words: nitrate, nutrient uptake length, nutrient retention, disturbance, transient storage zone, algae, resilience.

All ecosystems are open to some extent, exchanging materials and energy with their surroundings. Streams and rivers are especially open ecosystems dominated by downstream transport. Yet streams also retain and transform some of this transported material through various physical, chemical, and biological mechanisms. Nutrients in transport may change dramatically in form and in concentration, depending on the hydrologic route followed (i.e., as reflected in water residence time) and on the biologically mediated changes that occur within different subsystems. The net effect of flow path, heterogeneity, and biological processing determines the extent to which the ecosystem retains transported material. The spiraling concept (Newbold et al. 1981) provides a theoretical and mathematical framework to estimate the influence of biotic and abiotic instream processes

on surface-stream nutrient retention. Actual measurements of spiraling length for stream ecosystems are rare because of the difficulty of quantifying inputs and outputs of all compartments in the ecosystem; however, uptake length, the average downstream distance traveled by a dissolved molecule before removal from the water column, has been proposed as an estimator of retention efficiency of nutrients in the surface stream (Stream Solute Workshop 1990). Short-term nutrient additions have been used increasingly over the past 16 y to measure nutrient uptake length.

Most reports of uptake length are for small, temperate forest streams. In such systems, heterotrophic processes dominate nutrient cycling because the closed canopy causes light limitation of primary production (Mulholland et al. 1985). Further, because phosphorus is believed

to be the limiting nutrient in these streams, most studies to date have focused on phosphorus uptake length (Mulholland et al. 1985, Munn and Meyer 1990, D'Angelo and Webster 1991, Martí and Sabater 1996). In contrast, desert streams are limited by nitrogen, not light. The stream channel is wide as a result of floods, the riparian canopy does not cover the channel, and thus light is not limiting to primary producers. As a result, autotrophs play an important role in nutrient dynamics. In this paper we report nitrate uptake lengths for Sycamore Creek, a Sonoran Desert stream in central Arizona.

Nutrient uptake length varies as a function of channel morphology (Martí and Sabater 1996), organic matter standing stocks (D'Angelo and Webster 1991) and inputs (Mulholland et al. 1985), degree of nutrient limitation (Munn and Meyer 1990), season (Mulholland et al. 1985, D'Angelo and Webster 1991, Martí and Sabater 1996, Valett et al. 1996), and hydraulic conductivity of stream-bed sediments (Valett et al. 1996). Despite intense interest in disturbance as a force influencing stream communities and stream ecosystem structure and function (e.g., Resh et al. 1988), the influence of disturbance on nutrient uptake length has rarely been investigated (but see Aumen et al. 1990). Here we compare nitrate uptake length for a single reach of Sycamore Creek before and after a small summer flash flood in 1995. We also examine post-flood changes in nitrate uptake length calculated from data in Fisher et al. (1982), and compare these changes to the 1995 post-flood successional sequence.

Several assumptions are involved in the use of short-term nutrient additions to measure uptake length (Stream Solute Workshop 1990). First, characteristics of the channel and of flow are assumed to be uniform for the study reach. Second, assumptions associated with the nutrient uptake length calculations are: 1) additions of nutrient should elevate concentration only within the range where the nutrient uptake-concentration relationship is linear; and 2) release of nutrients to the stream water does not significantly affect nutrient concentration during the experiment. The latter assumption suggests that nutrient uptake rates calculated from uptake lengths based on solute additions are closer to gross uptake than to net uptake (i.e., uptake minus release); however, this has not been demonstrated conclusively (but see Mul-

holland et al. 1990). In Sycamore Creek and in many other Sonoran Desert streams, dramatic downstream declines in nitrate are common, particularly below in-channel springs (Grimm et al. 1981) or hyporheic discharge zones (i.e., points where subsurface water enters the surface stream; Valett et al. 1990, 1994). In this study, we also calculated nitrate uptake length from natural, longitudinal declines in nitrate concentration. This decline reflects the net result of uptake and release processes occurring in the surface stream. We compared these values with those from short-term nutrient addition experiments. We hope this comparison will provide a better understanding of the meaning of these concepts.

The objectives of this research were to answer three major questions. First, how does retention efficiency of nitrate in Sycamore Creek in particular and desert streams in general compare with other streams? To answer this question, we measured uptake length in Sycamore Creek using short-term nutrient addition experiments and calculated uptake length for a variety of streams using data from Grimm et al. (1981). Second, how do floods affect nitrate uptake length? We used data from nutrient addition experiments done before and after a flood and published data on post-flood nutrient retention to address this question. A secondary objective of this part of the study was to determine whether hydrologic or biotic factors were dominant in determining changes in uptake length over successional time. Third, we asked, what is measured by the short-term nutrient addition method? We hypothesized that nutrient additions reflect gross uptake, and predicted that uptake length calculated from natural declines in nutrient concentration would be longer than uptake length measured using nutrient additions.

Study Site

Sycamore Creek is a Sonoran Desert stream arising in the Mazatzal Mountains northeast of Phoenix, Arizona. Elevation ranges from 2164 m in the headwaters to 427 m at the confluence of Sycamore Creek with the Verde River. Catchment area is 505 km² and stream length is ~65 km. Annual precipitation means are 50 and 30 cm/y at higher and lower elevations, respectively (Thomsen and Schumann 1968). Peaks of pre-

precipitation mostly occur in winter and summer; however, rain events are irregularly distributed among different years. Heavy storms may cause the stream to flood. Flash floods during summer recede much faster than those in winter, and discharge can return to baseflow in <1 d. The intensity and frequency of floods greatly influence the morphology of the stream channel, the temporal variation in nutrient concentration, and the stream community's structure and function (Fisher et al. 1982). Evapotranspiration is high (>300 cm/y), especially in summer. High evapotranspiration and low precipitation (or intense and short rain events) during summer cause intermittency in surface stream flow along some reaches of this stream (Stanley et al. 1997).

The study site was a 240-m run located at an elevation of ~700 m in the middle reaches of Sycamore Creek. During this study, runs constituted 40 % of the mainstem (C. L. Dent, Arizona State University, personal communication); however, this percentage can vary among years (Fisher et al. 1997). Stream substrata in the study reach consisted primarily of sand and fine gravel, and depth of alluvial sediments averaged >1.5 m (Holmes et al. 1994). Surface flow occurs during most of the year; however, at baseflow the surface stream typically occupies <25% of the active channel with the remainder being dominated by extensive gravel bars. During the study period, the reach had a side channel that flowed parallel to the main channel from its origin 140 m downstream from the head of the reach to 200 m, where it joined the main channel. In late successional stages at baseflow, the surface stream in runs is usually covered by a well developed algal community. This community can be totally removed by floods because of the high mobility of the stream bed. However, recovery of the algal community after such floods occurs rapidly (Fisher et al. 1982). A small flash flood in which discharge increased from 22 L/s to 600 L/s at its peak, occurred on day 59 of the study (20 August 1995).

Methods

Field experiments

We conducted 8 short-term solute addition experiments in the 240-m reach from June to September 1995. Four experiments were conducted

before the 20 August flash flood and 4 after. The duration of each addition depended on discharge, but was usually <2 h (between 0830 and 1100 h). The solute solution, containing NaNO_3 as a nitrogen source and NaCl as a conservative tracer (Cl) source, was added at constant flow rate using a metering pump (Fluid Metering Systems®) placed at the head of the reach. We used the conservative tracer to correct changes in nitrate concentration for dilution within the reach; chloride concentration was increased an average of 6 mg/L above background. Nitrate concentration in the solution was adjusted for each experiment to result in a target stream concentration that was below levels of saturation for these algal communities (<55 $\mu\text{g/L}$; Grimm and Fisher 1986a) or within the natural concentration range. Nitrate concentration never exceeded $2.3 \times$ background concentration and the average increase was $1.8 \pm 0.1 \times$ background.

We collected water samples (3 replicates per station), in acid-cleaned polyethylene bottles, before and during the addition at 6 sampling stations located 20, 50, 90, 120, 190, and 240 m downstream from the injection site (0 m). During the addition, samples were collected when tracer concentration reached a plateau at the farthest downstream station, as determined by continuous measurement of conductivity at the 240-m station. This procedure ensured that added solutes were well mixed along the entire reach (Stream Solute Workshop 1990). Water samples were analyzed for nitrate and chloride. On each date, nitrate uptake lengths were calculated from a decline in background concentration along the reach, using samples collected before the addition, and also from concentrations in samples collected at plateau (corrected for background values). We also did an intensive sampling at stations 20 and 240 m. At the start of the addition, we collected water samples every 1–5 min depending on the location of the station, and continued this schedule for 1 h after the addition was terminated. These samples were analyzed for chloride and occasionally for nitrate. Chloride data over time from these 2 sampling stations were used to estimate the cross-sectional area of the transient storage zone (A_s) and the transient storage zone exchange coefficient (α) for the reach.

On each nutrient addition date we estimated the morphometry of the surface stream and the areal coverage of different algal patch types in

the reach using a line intercept method (Lewis and Taylor 1967) applied at 13 cross-stream transects evenly distributed along the reach. Algal biomass (chlorophyll *a*) for the reach was calculated as the sum of the area-weighted chlorophyll *a* for each algal patch type. Patch-specific chlorophyll *a* for filamentous green algae (*Cladophora glomerata* and *Hydrodictyon reticulatum*) was the average of a long-term data set (~200 samples taken from 1985 to 1994) for this patch type in Sycamore Creek. Values of chlorophyll *a* for the other patch types were obtained by collecting 5 replicate cores of each patch type along the reach on each addition date. Cores were extracted in methanol followed by spectrophotometric determination of chlorophyll *a* (Tett et al. 1975).

Hydrologic linkages between the surface stream and adjacent subsystems can influence material retention of the whole stream-riparian ecosystem (Fisher et al. 1998); in particular, they may affect retention efficiency of nutrients in the surface stream. To characterize the reach in terms of vertical hydrologic interactions between the surface stream and the hyporheic zone, we measured vertical hydraulic gradient (VHG, Valett et al. 1994) every 10 m along the reach on a single date (4 September 1995). Measures of VHG show direction and magnitude of the potential for advective exchange between these 2 subsystems. Negative values indicate that the stream is losing water to the hyporheic zone (downwelling), whereas positive values indicate that hyporheic water is discharging to the surface stream (upwelling), accounting for significant dilution.

Laboratory analyses

Water samples were transported to the laboratory on ice, filtered (Whatman GF/F® fiber filters, 0.7 μm nominal pore size), and analyzed for nitrate-nitrogen and chloride. Samples for nitrate and chloride were analyzed on a Bran and Luebbe TRAACS® 800 autoanalyzer, using the cadmium reduction technique with a modified version of the Technicon Industrial Method # 818-87T for nitrate, and the Technicon Industrial Method # 783-86T for chloride. All nutrient analyses were completed within 24 h of collection.

Data analysis

Nitrate uptake length.—Nitrate uptake length from short-term solute additions was calculated as proposed in the Stream Solute Workshop (1990). Nitrate concentration at each sampling station at plateau was corrected by the background concentration and by the dilution factor (using chloride data). The natural logarithm of the ratio between corrected nitrate and corrected chloride at each station was plotted vs downstream distance. The slope of this regression is the downstream nutrient change coefficient (m⁻¹) and the inverse of this coefficient is the nutrient uptake length (m). A more detailed explanation of the actual calculation can be found in Martí and Sabater (1996). Nutrient uptake length is an index of the retention efficiency of nutrients in streams (Newbold 1992); shorter values indicate higher retention efficiency of nutrients than longer values.

To calculate uptake length from natural decline of nitrate concentration along the reach on each addition date, we used a similar approach to that for uptake length from short-term additions, but here we considered nitrate concentrations at ambient levels (i.e., from samples collected before the addition) and chloride concentrations at plateau to account for dilution. Nitrate and chloride concentrations at each station were corrected by their respective concentrations at station 1 (20 m). We assumed that if any net uptake occurred along the reach (i.e., a downstream decline in nitrate concentration compared to the concentration at station 1), the variation of nitrate concentration along the reach would be described by the following equation:

$$N_x = N_1 \cdot \left[\frac{Cl_x}{Cl_1} \right] \cdot e^{-bx}$$

where *N* is nitrate concentration and *Cl* is chloride concentration at station 1 and at the downstream points (*x*), and the slope of the curve (*b*) is the downstream nutrient change coefficient at ambient levels (/m). The inverse of the slope is the nitrate uptake length from natural decline, in m. We also calculated the nitrate uptake rates (mg m⁻² h⁻¹) from natural nitrate decline and from short-term addition on each date using the following equation:

$$U = \left(\frac{C \cdot Q}{S_w \cdot w} \right) \cdot 3600$$

TABLE 1. Uptake lengths of nitrate and soluble reactive phosphorus (SRP) calculated from the natural decline in nutrient concentration (uncorrected for dilution) for some streams of central and southern Arizona, USA. r^2 value indicates goodness-of-fit of line relating nutrient concentration to distance along a stream reach (see text for further explanation).

Site	NO ₃ Uptake length		SRP Uptake length	
	m	r^2	m	r^2
Cherry Creek	219	0.98	318	0.61
Bonita Creek ^a	3394	0.08	153	0.98
Sycamore Creek	56	0.47	-243	0.66
Picadilla Creek	4	0.85	1340	0.02
Mesquite Wash tributary 1 upstream	18	0.92	58	0.98
Mesquite Wash tributary 1 downstream	27	0.43	108	0.86
Mesquite Wash tributary 2 upstream	2	0.90	-636	0.10
Mesquite Wash tributary 2 downstream	10	0.96	-2223	0.22

^a Data collected after a flood

where S_w is the nutrient uptake length (m), C is the nitrate concentration at ambient levels at station 1 (mg/L), Q is the stream discharge (L/s), w is the average stream width in the reach (m), and 3600 is a constant for converting seconds to hours.

Hydrological parameters.—We used the variation in chloride concentration over time at the most upstream and downstream stations to calculate discharge (Gordon et al. 1992), nominal water velocity (Triska et al. 1989), and dilution in the reach. A 1-dimensional solute transport model (J. Webster, Virginia Polytechnical and State University, personal communication) was used to simulate chloride transport in surface stream waters. This model accounts for the influence of the transient storage zone, the zone where water is moving at a slower-than-average velocity, on tracer transport in the surface stream. Dispersion, cross-sectional area of the transient storage zone (A_s), and the transient storage exchange coefficient between surface and subsurface water (α) were estimated using this model. These parameters were iteratively adjusted in the model to achieve the best visual fit between data from the simulation and data collected during the addition experiment. The SYSTAT computer program (Wilkinson 1989) was used for all statistical analyses.

Results

Retention efficiency of nutrients in desert streams

Table 1 shows uptake lengths for nitrate and phosphate from various desert streams in Ari-

zona. These nutrient uptake lengths were calculated from downstream declines in ambient nutrient concentration using data collected during fall 1978, spring 1979, and fall 1992. Because calculation of these values did not account for the effect of nutrient dilution or enhancement along the reach as a result of inflows, they may slightly over- or underestimate the actual retention efficiency of nutrients. Many of these reaches were short, however, and inflows were therefore likely insignificant (personal observation). Overall, nitrate uptake lengths were much shorter than phosphate uptake lengths, suggesting that these streams retained nitrate more efficiently than phosphate. In fact, some phosphate uptake lengths were negative, indicating that there was a net increase of this nutrient along the reach. Additionally, nitrate uptake lengths in most of these streams were very short; on average, nitrate was removed from the water column over distances <50 m. The long nitrate uptake length in Bonita Creek was measured immediately after a flood when algae were absent and substrata were bare.

Flood effects

Hydrology and water chemistry.—The wetted surface stream accounted for an average of only 18% of the active channel width during the study period (Table 2); the rest of the channel was dominated by sand bars. Fifty per cent of VHG values measured along the reach on 4 September 1995 were negative and 33% were 0 (Fig. 1), indicating that the reach was slightly domi-

TABLE 2. Hydrologic and chemical parameters for the study reach on each nutrient-addition experiment date (1995). Wet active channel represents the % of the total active channel width occupied by surface water. A_s is the cross-sectional area of the transient storage zone (m^2), A is the cross-sectional area of the surface stream (m^2), and α is the transient storage zone exchange coefficient. NA = data not available.

Variable	22 Jun	3 Jul	21 Jul	14 Aug	24 Aug	30 Aug	12 Sep	24 Sep
Days post-flood	108	119	137	161	4	10	23	35
Wet active channel (%)	22	20	17	15	18	18	18	16
Discharge (L/s)	66	44	55	22	20	15	9	7
Water velocity (cm/s)	16.6	14.7	12.0	7.7	10.0	7.1	4.4	3.3
Width (m)	4.9	4.1	3.9	3.5	4.0	4.0	3.9	3.6
A (m^2)	NA	0.20	0.32	NA	0.19	0.16	0.17	0.14
$A_s:A$	NA	2.0	0.9	NA	3.0	7.5	7.4	17.8
α ($s^{-1} \times 10^{-4}$)	NA	4.0	0.6	NA	4.5	5.0	7.0	4.8
Dispersion (m^2/s)	NA	0.8	0.8	NA	0.5	1.0	0.5	0.5
Dilution (%)	3	6	9	6	32	25	30	32
N-NO ₃ ($\mu g/L$)	21	29	21	46	137	89	59	55
Cl (mg/L)	11.4	11.8	13.0	13.8	13.7	13.6	16.2	14.5

nated by downwelling zones at this time. This result is consistent with VHG measured in this reach on other dates under different discharge conditions. In fact, VHG tends to become more

negative as discharge decreases (Stanley and Valett 1992, Valett et al. 1994). Dilution, calculated from chloride concentrations at plateau, increased gradually along the reach on all dates,

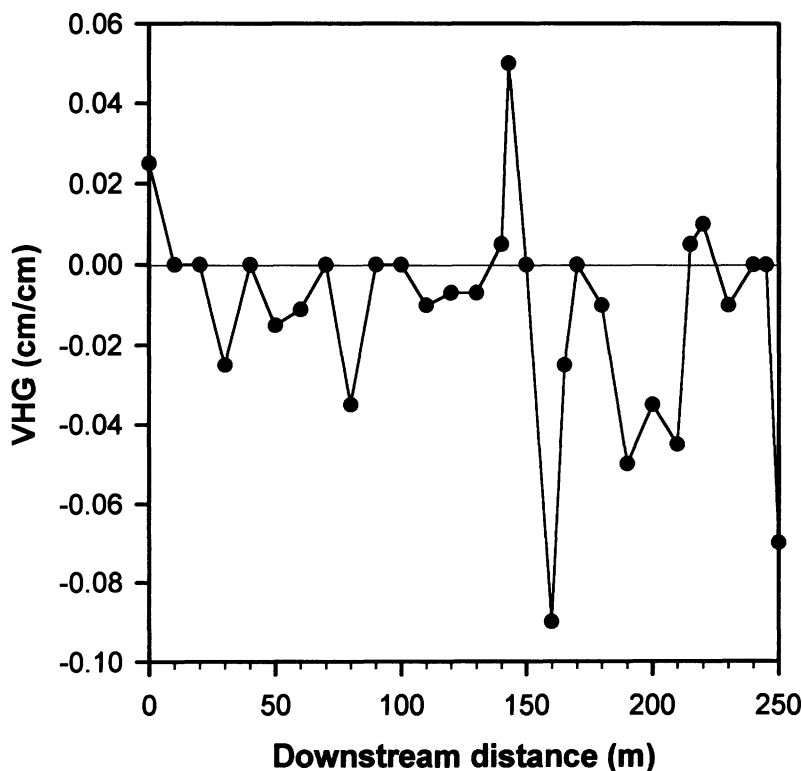


FIG. 1. Longitudinal variation in vertical hydrologic gradient (VHG) in the study reach of Sycamore Creek, Arizona, 4 September 1995.

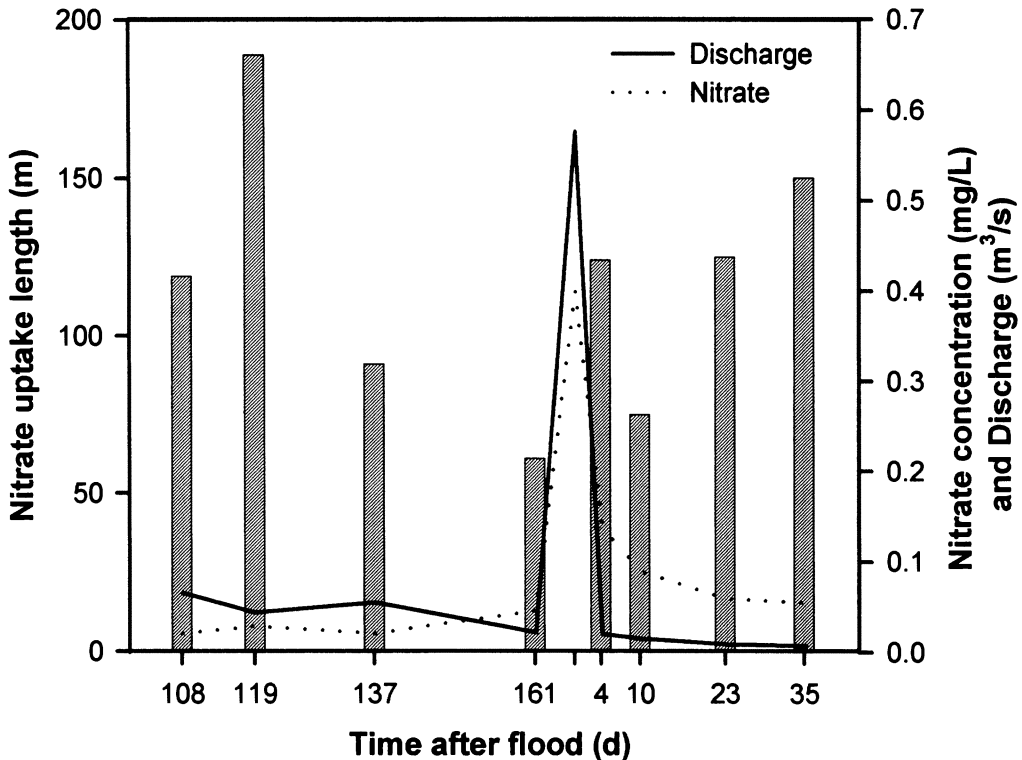


FIG. 2. Temporal variation in nitrate uptake length (bars), nitrate concentration (dotted line), and discharge (solid line) during the study period. Notations on the x axis represent days after flood for each nutrient addition experiment.

and was significantly greater after the flood (ANOVA: $F = 133.4$, $df = 1$, $p = 0.000$, Table 2). These results together with those from VHG measurements indicate that water inputs to the surface stream were mainly from lateral sources from either the side channel (surface water) or from adjacent sand bars (subsurface water). Discharge at peak flood ($0.6 \text{ m}^3/\text{s}$) was $27\times$ higher than pre-flood discharge (Fig. 2); however, discharge was similar to pre-flood conditions 4 d after the flood and it continued to decrease toward the end of the study period (Table 2). Cross-sectional area and width of the surface stream did not change significantly over the entire period; therefore, most of the changes in discharge were caused by changes in water velocity (Table 2).

The cross-sectional area of the transient storage zone normalized to the surface cross-sectional area (A_s/A) was close to or >1 on all dates (Table 2). Following \ln -transformation, A_s/A showed a negative relationship with dis-

charge ($\ln A_s/A = 5.08 - 1.24 \cdot \ln Q$; $r^2 = 0.92$, $p = 0.003$, $n = 6$). These results indicate that the magnitude of the transient storage zone was large compared with the surface stream and that hydrological transient storage decreased in importance as discharge increased. Values of the transient storage exchange coefficient (α) ranged from 0.6×10^{-4} to $7.0 \times 10^{-4} \text{ s}^{-1}$ (Table 2). This transient storage parameter also was negatively correlated with discharge ($\alpha = 6.57 - 0.09 \cdot Q$; $r^2 = 0.73$, $p = 0.031$, $n = 6$).

Background nitrate concentration at station 1 ranged from 21 to $137 \text{ } \mu\text{g}/\text{L}$ (Table 2). Nitrate concentration during the flood was $20\times$ the pre-flood concentration, but it rapidly decreased after flood recession (Fig. 2). Overall, average nitrate concentration from all 4 pre-flood dates (mean $\pm 1 \text{ SE} = 29 \pm 6 \text{ } \mu\text{g}/\text{L}$) was significantly lower than the average concentration from all 4 post-flood dates (mean $\pm 1 \text{ SE} = 85 \pm 19 \text{ } \mu\text{g}/\text{L}$; ANOVA: $F = 7.914$, $df = 1$, $p = 0.031$). Background chloride concentration at station 1

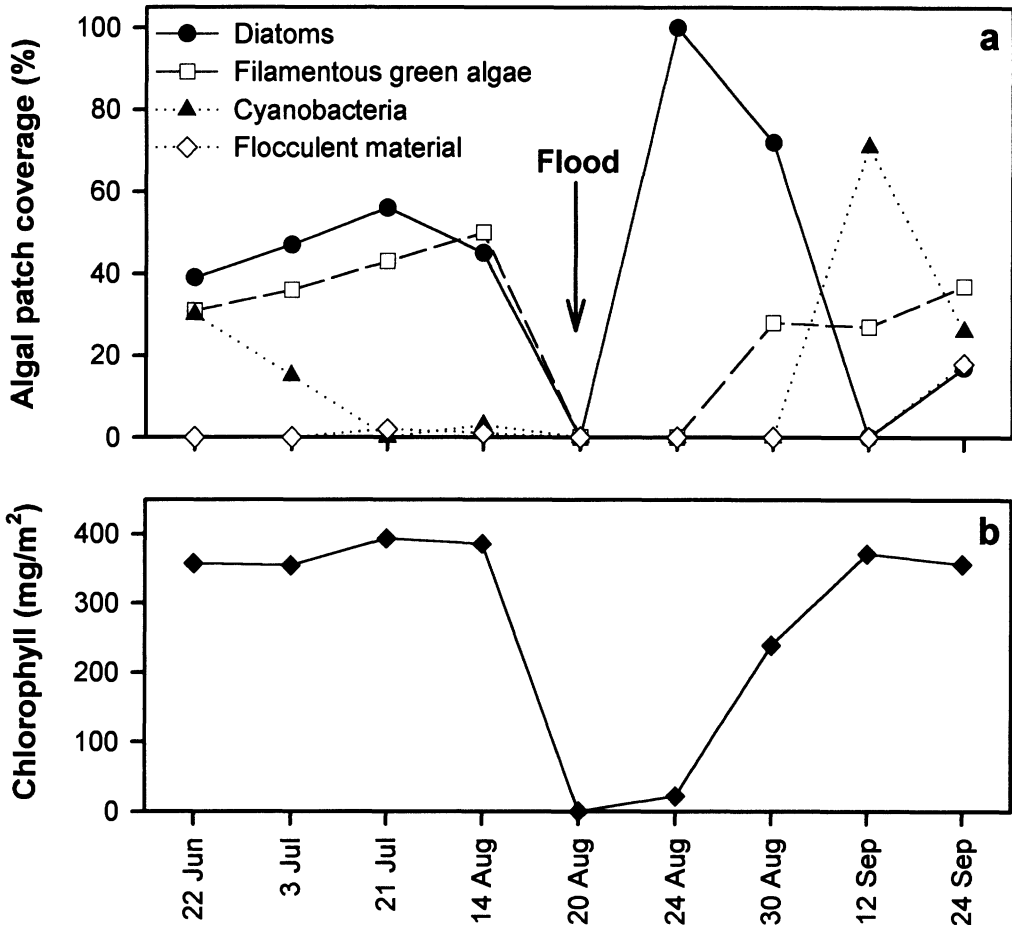


FIG. 3. Temporal variation in (a) % cover of algal patch types and (b) algal biomass (chlorophyll *a*) in the reach during the study period (1995).

ranged from 11.4 to 16.2 mg/L (Table 2). Chloride was significantly correlated with stream discharge ($r = -0.84$, $p = 0.009$, $n = 8$), but did not differ between pre- and post-flood sampling dates.

Algal composition.—Diatoms and filamentous green algae were the dominant patch types before the flood, covering >70 % of the stream bottom (Fig. 3a). The spatial arrangement of these 2 patches was consistent with previous observations. Filamentous green algae (*C. glomerata* and *H. reticulatum*) developed mainly on the edges and diatoms were found in the middle of the stream where water velocity was greater. The relative abundance of cyanobacteria, mainly a mat of *Anabaena* sp., progressively decreased from the 1st to the 4th pre-flood sampling date (Fig. 3a). After the flood, diatoms were domi-

nant on the 1st 2 dates, but were rapidly (within <20 d) replaced by filamentous green algae and cyanobacteria. Algal biomass was high before the flood (mean chlorophyll *a* ± 1 SE = 366 ± 9 mg/m², $n = 4$), but was reduced to 0 by the flood (Fig. 3b). Post-flood recovery of algal biomass in the reach was rapid, with pre-flood biomass levels reached within 23 d (Fig. 3b). In contrast to recovery of algal biomass, algal patch composition did not return to pre-flood conditions during the study period.

Nitrate uptake length.—Concentration of nitrate at plateau at the end of the reach (i.e., station at 240 m) was similar to or lower than the concentration before the addition in 7 of the 8 additions, although elevated chloride concentration indicated that the solute addition was transported to the end of the run. Consequently, ni-

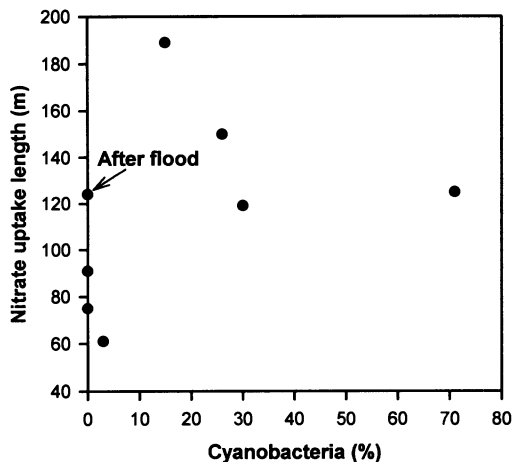


FIG. 4. Relationship between nitrate uptake length and % cover of cyanobacteria in the reach.

trate uptake lengths were calculated based on data from the 1st 5 sampling stations (reach length 190 m) on all dates.

Nitrate uptake length from solute additions ranged from 61 to 189 m during the study period. Uptake length doubled after the flood; however, this increase was within the range of variation for the pre-flood period (Fig. 2). During the post-flood successional period, uptake length initially decreased to a value close to the last pre-flood uptake length, but then increased

to 150 m by day 35. We did not find any significant correlation between nitrate uptake length and other physical, chemical, or biological parameters; however, some decreases in uptake length coincided with increases in the relative abundance of filamentous green algae. Longer values for nitrate uptake length coincided with dates when the abundance of cyanobacteria was relatively high (Fig. 4). In fact, average nitrate uptake length was significantly shorter when abundance of cyanobacteria was $<10\%$ (mean ± 1 SE = 88 ± 13 m, $n = 4$) than when it was $>10\%$ (mean ± 1 SE = 146 ± 16 m, $n = 4$; ANOVA: $F = 7.707$, $df = 1$, $p = 0.032$).

Comparison between natural decline of nitrate and solute addition experiments

We found a decline in ambient nitrate concentration along the study reach on all dates. Nitrate uptake lengths calculated from ambient decline ranged from 151 to 799 m. These uptake lengths were between 2 and 6 \times longer than those from solute addition experiments. Nitrate uptake rates calculated from natural declines and from solute additions showed a similar temporal pattern (Fig. 5); overall, values ranged from 1.3 to 19.9 $\text{mg N m}^{-2} \text{h}^{-1}$. Uptake rates decreased dramatically at day 20 and day 35 post-flood and they gradually increased late in

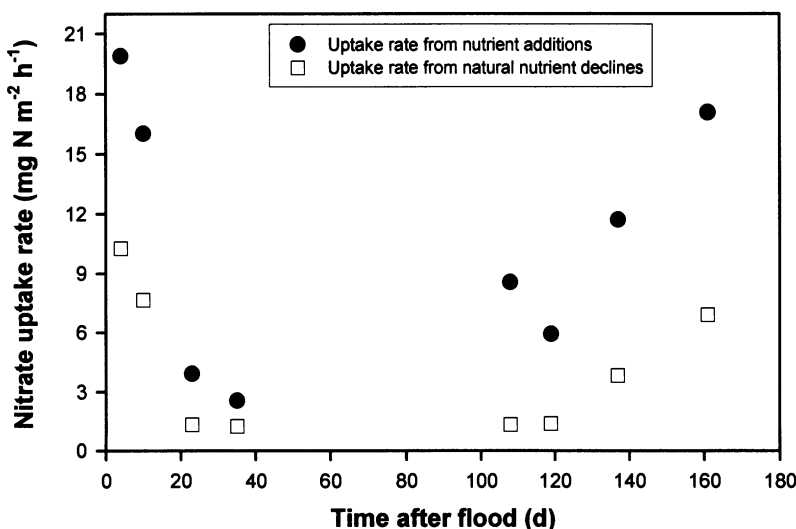


FIG. 5. Uptake rates of nitrate calculated from nutrient addition experiments and from natural declines of nitrate, where chloride concentration at plateau from a nutrient addition experiment done on the same day was used to correct for dilution.

succession. Although temporal pattern of the 2 rates was similar, the ratio between them became slightly greater in late successional stages (>100 d post-flood; ANOVA: $F = 4.13$, $df = 1$, $p = 0.088$). Uptake rates from solute additions were 2.2 ± 0.2 (mean ± 1 SE) \times greater than uptake rates from natural declines early in succession, but 4.0 ± 0.8 (mean ± 1 SE) \times greater in late successional stages.

Discussion

Intersite comparison of nutrient uptake length

Previous studies have shown that nitrogen is the limiting element to ecosystem productivity in Sycamore Creek (Grimm and Fisher 1986a) and probably in many other streams of southwestern USA (Grimm and Fisher 1986b, Grimm 1992). Nutrient uptake length has been used as an index of nutrient retention efficiency of the surface stream (Newbold et al. 1981). In contrast to uptake length from solute additions, uptake length calculated from natural declines can be positive (uptake > release) or negative (release > uptake). The negative phosphate uptake lengths indicate that phosphate concentration increased along the reach; this pattern clearly contrasts with that for nitrate. Grimm and Fisher (1986a) suggested that, in contrast to the biological control of nitrogen concentration, physicochemical mechanisms mainly control phosphorus concentration in southwestern streams. In this study, we found that nitrate retention efficiency was greater than phosphate retention efficiency (i.e., uptake lengths calculated from natural declines were shorter for nitrate than for phosphate). These results agree with previous studies (Munn and Meyer 1990, Martí and Sabater 1996) in that the limiting nutrient is usually retained more efficiently than other elements.

Nitrate uptake lengths from solute addition experiments reported in this study show that a molecule of nitrate travels an average of <120 m before it is removed from the water column. These data are at the low end of the range of published values (Valett et al. 1996, and see Martí and Sabater 1996 for a review), and illustrate the high nitrate retention efficiency of nitrogen-limited streams.

Hydrologic and biologic controls of nitrate retention efficiency

Many researches have shown that surface–subsurface hydrologic interactions can be a strong determinant of nutrient retention in lotic ecosystems (Triska et al. 1993, Valett et al. 1996). Transient storage zones increase water residence time and allow reactive solutes greater time for chemical and biological interactions (Bencala 1993). These zones can potentially contribute to increased nutrient retention. Values of A_s/A in Sycamore Creek are high compared to other streams (D'Angelo et al. 1993, Morrice et al. 1997), indicating that this stream has a large transient storage zone. The authors cited above have shown that the relative magnitude of the transient storage zone for a given stream is a function of the stream discharge (i.e., the A_s/A ratio decreases as discharge increases); our results are consistent with this finding. In fact, there is a significant relationship between discharge and A_s/A when we consider data from a variety of streams together (Fig. 6). Using this general relationship, the A_s/A ratio in Sycamore Creek is greater than that for other streams at any given discharge. This fact may account partly for the shorter nitrate uptake lengths measured in Sycamore Creek compared to other streams.

Two factors may explain the high A_s/A ratios measured in Sycamore Creek, especially at low flow. First, as discharge decreases, the water residence time in the reach increases, allowing surface water to interact more with sediments. The study reach was dominated mainly by downwelling zones. Stanley and Valett (1992) and Valett et al. (1994) reported that in Sycamore Creek the VHG became more negative as discharge decreased (i.e., the strength of downwelling increased). Under these conditions, there is a higher proportion of water moving from surface to subsurface zones, resulting in a relative increase in the subsurface transient storage zone. Second, the structure and distribution (mainly on the stream edges) of the filamentous algal patches increase the morphometric complexity of the surface stream, creating zones of slow water movement (i.e., surface transient storage zones). Mulholland et al. (1994) showed that thick patches of filamentous green algae that developed in artificial channels decreased the downstream transport of conservative solutes.

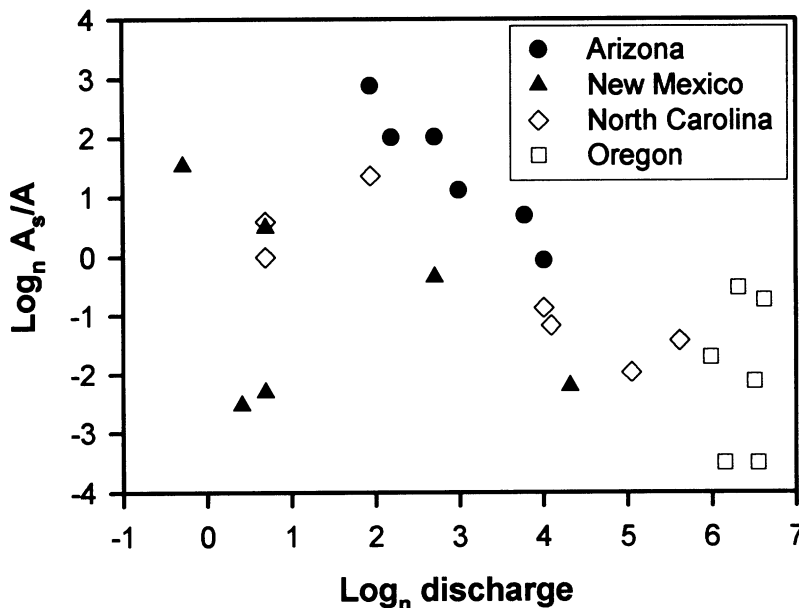


FIG. 6. Relationship between the natural logarithm of A_s/A (cross-sectional area of the transient storage zone normalized to the surface cross-sectional area) and the natural logarithm of discharge using data from a variety of streams from Arizona (this study), North Carolina (D'Angelo et al. 1993), Oregon (D'Angelo et al. 1993), and New Mexico (Morrice et al. 1997).

Although those results were obtained under laboratory conditions, they showed that filamentous green algae could act as zones of hydrological transient storage. In Sycamore Creek, the abundance of filamentous green algae may enlarge the overall transient storage zone especially as discharge decreases. Both factors would increase transient storage zone size, but their effect on nitrate retention in the surface stream will depend on whether hydrological transient storage is a result of surface–subsurface interaction or interception by algal mats. Algal mats may locally deplete nitrate and release dissolved organic nitrogen. In contrast, nitrate concentration generally increases along subsurface flow paths in Sycamore Creek (Holmes et al. 1994). These increases can potentially result in increases of nitrate concentration in the surface stream at up- or out-welling sites.

Geomorphic and hydrologic factors may largely determine differences in nutrient uptake lengths between streams (Munn and Meyer 1990, Martí and Sabater 1996, Valett et al. 1996); however, temporal variation in nutrient retention efficiency in a single stream cannot be explained solely by these factors. In Sycamore Creek, temporal variation in nitrate uptake

length during the study period was not correlated with transient storage zone size or any other physical or chemical parameters measured during the addition experiments. This finding contrasts with Valett et al. (1996), who showed a negative relationship between nitrate uptake length and transient storage zone size for a mountain stream in New Mexico. It is likely that the narrow range of conditions during this study precluded identification of important physicochemical parameters explaining temporal variation in nutrient retention efficiency. The most instructive result was that changes in nitrate uptake length appeared related to changes in the relative abundance of different algal patches. Although algal biomass varied little throughout the study period, except immediately after the flood, changes in patch structure were great. We know from previous studies that algal patches differ in their nitrate uptake rates or capacity (Grimm 1992), and cyanobacterial nitrogen fixers, like *Anabaena* sp. mats, can obtain nitrogen from dinitrogen (Grimm and Petrone 1997). In this study, nitrate retention efficiency was significantly lower when nitrogen fixers made up >10 % of the areal periphyton coverage. Thus biotic activity (i.e., algal uptake,

possibly N_2 fixation) controls temporal variation in nitrate retention efficiency of the surface stream subsystem during baseflow in Sycamore Creek, which lends further support to the conclusions of previous studies in this stream ecosystem (Grimm 1987, Grimm 1992) that baseflow nitrogen dynamics are largely controlled by algal activity in the surface stream. Biotic activity was also shown to strongly influence nutrient retention efficiency in a heterotrophic, woodland stream in Tennessee (Mulholland et al. 1985). These authors found that the shortest phosphate uptake lengths were associated with inputs of leaf litter during autumn. Results from both studies stress the fact that biotic factors can sometimes override physical factors in controlling nutrient retention in streams.

Effect of floods on nitrate uptake length

The strongest effect of a midsummer flash flood was a change in chemical and biological parameters. The flood caused an acute increase in nitrate concentration and complete removal of algal mats from the stream bottom. Nitrate uptake length 4 d after the flood showed a 2-fold increase. This result indicates that disturbances by floods not only affect physical, chemical, and biological stream attributes but also may affect ecosystem function (e.g., by decreasing stream nutrient retention efficiency); however, the post-flood increase in nitrate uptake length remained within the range of variation measured during the pre-flood period. Several factors may account for the apparent high resilience of stream nitrate retention efficiency, among them the rapid decrease in discharge from 0.6 to 0.02 m^3/s , a relatively large transient storage zone ($A_s/A = 3$), and a high algal recovery capacity. In fact, the stream was completely colonized by diatoms 4 d after the flood and chlorophyll reached pre-flood levels within 23 d.

The flood that occurred during the study period was of low magnitude (peak discharge = 0.6 m^3/s) compared with others reported for this stream over the last 35 y (Grimm 1993). Floods of this magnitude occur more than once per year. These floods usually do not cause major physical changes in morphology, but they wash out benthic algae. We expected the flood to increase nitrate uptake length much more than we observed. We used data from Fisher et al. (1982) to examine changes in uptake length

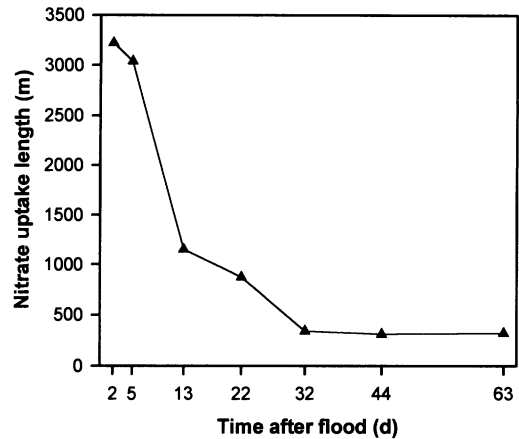


FIG. 7. Temporal variation in nitrate uptake length (calculated from natural decline in nitrate concentration uncorrected for dilution) during stream succession following a flood. Values calculated from data in Fisher et al. (1982).

after a larger flood. We calculated nitrate uptake lengths (without dilution correction) over a post-flood successional sequence, in summer–autumn 1979, at approximately the same site, using the natural decline in nitrate concentration (Fig. 7). Flood discharge on that occasion (7.0 m^3/s) was an order of magnitude greater than in summer 1995. The recurrence interval of these floods is >3 y. Accordingly, the range of uptake lengths was much broader than the range measured in this study. Nitrate uptake length varied from 3220 m immediately after the flood to 340 m 30 d after the flood (Fig. 7). Uptake lengths remained constant after day 30 and were within the range of uptake lengths from natural declines in nitrate concentration measured in the present study (from 151 to 799 m). Comparison of results from these 2 sequences (i.e., that in 1979 and the present study) suggests that larger floods have a greater impact on stream nutrient retention efficiency; however, post-flood recovery of nutrient retention efficiency is rapid in either case in this stream ecosystem.

Nitrate uptake length from natural declines and from nutrient additions

For the last 16 y, short-term nutrient additions of stable elements have been used to measure nutrient uptake length in stream ecosystems. This parameter measures the removal rate of a

nutrient from the water column relative to its downstream flux in the surface water. If nutrient additions are done for relatively short periods (<1–3 h) a very small fraction of the added nutrient that is taken up will be released to the stream during the experiment (Mulholland et al. 1990). Therefore, nutrient uptake lengths from nutrient additions may better reflect gross than net nutrient removal; however, this assumption has been tested on only 1 occasion by using ^{32}P (Mulholland et al. 1990).

Dramatic longitudinal declines in the concentration of nitrate in surface water along reaches are a common occurrence in many desert streams. The intensity of these declines can vary over time (e.g., on a diel basis, Grimm 1987; or over a successional period, Fisher et al. 1982) and in space (C. L. Dent, Arizona State University, personal communication). At the reach scale (i.e., tens to hundreds of m; Grimm and Fisher 1992), nitrate declines have been mainly attributed to biological uptake, especially by primary producers (Grimm 1987). These natural declines usually are evident below points where nitrate-rich subsurface water discharges to surface water (e.g., at springs or upwelling zones; Valett et al. 1994, Jones et al. 1995). These locations may be viewed as natural nutrient addition experiments; however, downstream changes in nutrient concentrations reflect the net result of uptake by adsorption or algal assimilation and release by algal excretion or mineralization. Variation in the relative rates of these processes determines whether the stream acts as source or as a sink of nutrients. Therefore, in streams where subsurface–surface hydrologic exchange results in significant nutrient inputs to the surface stream, and where there is a gradual decline in nutrient concentration along the surface stream, we can directly measure the nutrient retention efficiency of the surface stream subsystem. These conditions are found in Sycamore Creek, offering a good opportunity to compare uptake length from natural nutrient declines and from nutrient addition experiments.

Both nutrient uptake lengths showed similar temporal variation; however, uptake lengths from nutrient additions were always shorter than those from natural declines, and uptake rates calculated from nitrate additions were greater than those calculated from natural nitrate declines. These results supported our hy-

pothesis. Because natural decline in nutrient concentration reflects the net result of uptake and release processes (i.e., nutrient retention), we conclude that nutrient uptake lengths from solute addition experiments more closely reflect gross nutrient uptake. Comparing gross and net uptake rates over the period of this study we found that, despite similar temporal variation, the difference between these rates increased late in succession. This result suggests that, during late successional stages, processes such as mineralization that release nutrients to stream water occur at rates that approach a balance with nutrient uptake processes such as assimilation. This explanation is consistent with the hypothesis of successional change in nutrient retention (Vitousek and Reiners 1975), as modified by Grimm and Fisher (1986a).

Acknowledgements

We thank R. Gómez and W. M. Mallett for help in the field, and C. L. Dent for field assistance and comments on the manuscript. Thanks also to T. Colella for laboratory analyses. This manuscript benefitted from comments by Frank Triska and two anonymous reviewers. This research was supported by the National Science Foundation's Ecosystem Studies Program (grant no. DEB-9306909 to S.G.F. and N.B.G.) and Long-Term Studies Program (grant no. DEB-9615358 to N.B.G. and S.G.F.).

Literature Cited

- AUMEN, N. G., C. P. HAWKINS, AND S. V. GREGORY. 1990. The influence of woody debris on nutrient retention in catastrophically disturbed streams. *Hydrobiologia* 190:183–192.
- BENCALA, K. E. 1993. A perspective on stream-catchment connections. *Journal of the North American Benthological Society* 12:44–47.
- D'ANGELO, D. J., AND J. R. WEBSTER. 1991. Phosphorus retention in streams draining pine and hardwood catchments in the southern Appalachian mountains. *Freshwater Biology* 26:335–345.
- D'ANGELO, D. J., J. R. WEBSTER, S. V. GREGORY, AND J. L. MEYER. 1993. Transient storage zone in Appalachian and Cascade mountain streams as related to hydraulic characteristics. *Journal of the North American Benthological Society* 12:223–235.
- FISHER, S. G., L. J. GRAY, N. B. GRIMM, AND D. E. BUSCH. 1982. Temporal succession in a desert

- stream ecosystem following flash flooding. *Ecological Monographs* 52:92–110.
- FISHER, S. G., N. B. GRIMM, E. MARTÍ, AND R. GÓMEZ. 1997. Hierarchy, spatial configuration, and nutrient cycling in a desert stream. *Australian Journal of Ecology* (in press).
- FISHER, S. G., N. B. GRIMM, E. MARTÍ, R. M. HOLMES, AND J. B. JONES. 1998. Material spiraling in stream corridors: a telescoping ecosystem model. *Ecosystems* (in press).
- GORDON, N. D., T. A. MCMAHON, AND B. L. FINLAYSON. 1992. Stream hydrology: an introduction for ecologists. John Wiley and Sons, West Sussex, UK.
- GRIMM, N. B. 1987. Nitrogen dynamics during succession in a desert stream. *Ecology* 68:1157–1170.
- GRIMM, N. B. 1992. Biogeochemistry of nitrogen in arid-land stream ecosystems. *Journal of the Arizona-Nevada Academy of Science* 26:130–146.
- GRIMM, N. B. 1993. Implications of climate change for stream communities. Pages 293–314 in P. Kareiva, J. Kingsolver, and R. Huey (editors). *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts.
- GRIMM, N. B., AND S. G. FISHER. 1986a. Nitrogen limitation in a Sonoran desert stream. *Journal of the North American Benthological Society* 5:2–15.
- GRIMM, N. B., AND S. G. FISHER. 1986b. Nitrogen limitation potential of Arizona streams and rivers. *Journal of the Arizona-Nevada Academy of Science* 21:31–43.
- GRIMM, N. B., AND S. G. FISHER. 1992. Response of arid land streams to changing climate. Pages 211–233 in P. Firth and S. G. Fisher (editors). *Global climate change and freshwater ecosystems*. Springer-Verlag, New York.
- GRIMM, N. B., S. G. FISHER, AND W. L. MINCKLEY. 1981. Nitrogen and phosphorus dynamics in hot desert streams of southwestern USA. *Hydrobiologia* 83:303–312.
- GRIMM, N. B., AND K. C. PETRONE. 1997. Nitrogen fixation in a desert stream ecosystem. *Biogeochemistry* 37:33–61.
- HOLMES, R. M., S. G. FISHER, AND N. B. GRIMM. 1994. Parafluvial nitrogen dynamics in a desert stream ecosystem. *Journal of the North American Benthological Society* 13:468–478.
- JONES, J. B., S. G. FISHER, AND N. B. GRIMM. 1995. Vertical hydrologic exchange and ecosystem metabolism in a Sonoran desert stream. *Ecology* 76:942–952.
- LEWIS, T., AND L. R. TAYLOR. 1967. *Introduction to experimental ecology*. Academic Press, London, UK.
- MARTÍ, E., AND F. SABATER. 1996. High variability in temporal and spatial nutrient retention in Mediterranean streams. *Ecology* 77:854–869.
- MORRICE, J. A., H. M. VALETT, C. N. DAHM, AND M. E. CAMPANA. 1997. Alluvial characteristics, groundwater–surface water exchange and hydrologic retention in headwater streams. *Hydrological Processes* 11:253–267.
- MULHOLLAND, P. J., J. D. NEWBOLD, J. W. ELWOOD, L. A. FERREN, AND J. R. WEBSTER. 1985. Phosphorus spiraling in woodland streams: seasonal variations. *Ecology* 66:1012–1023.
- MULHOLLAND, P. J., A. D. STEINMAN, AND J. W. ELWOOD. 1990. Measurements of phosphorus uptake length in streams: comparison of radiotracer and stable PO₄ releases. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2351–2357.
- MULHOLLAND, P. J., A. D. STEINMAN, E. R. MARZLOF, D. R. HART, AND D. L. DEANGELIS. 1994. Effect of periphyton biomass on hydraulic characteristics and nutrient cycling in stream. *Oecologia* 98:40–47.
- MUNN, N. L., AND J. L. MEYER. 1990. Habitat-specific solute retention in two small streams: an intersite comparison. *Ecology* 71:2069–2082.
- NEWBOLD, J. D. 1992. Cycles and spirals of nutrients. Pages 379–408 in P. Calow and G. E. Petts (editors). *The rivers handbook*. Volume 1. Blackwell Scientific Publications, Oxford, UK.
- NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VANWINKLE. 1981. Measuring nutrient spiraling in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 38:860–863.
- RESH, V. H., A. V. BROWN, A. P. COVICH, M. E. GURTZ, H. W. LI, G. W. MINSHALL, S. R. REICE, A. L. SHELDON, J. B. WALLACE, AND R. C. WISSMAR. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:503–524.
- STANLEY, E. H., S. G. FISHER, AND N. B. GRIMM. 1997. Ecosystem expansion and contraction: a desert stream perspective. *BioScience* 47:427–435.
- STANLEY, E. H., AND H. M. VALETT. 1992. Interaction between drying and the hyporheic zone of a desert stream ecosystem. Pages 234–249 in P. Firth and S. G. Fisher (editors). *Climate change and freshwater ecosystems*. Springer-Verlag, New York.
- STREAM SOLUTE WORKSHOP. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *Journal of the North American Benthological Society* 9:95–119.
- TETT, P., M. G. KELLY, AND G. M. HORNBERGER. 1975. A method for the spectrophotometric measurement of chlorophyll *a* and pheophytin *a* in benthic microalgae. *Limnology and Oceanography* 20:887–896.
- THOMSEN, B. W., AND H. H. SCHUMANN. 1968. *Water resources of the Sycamore Creek watershed, Maricopa County, Arizona*. Water Supply Paper 1861, United States Geological Survey, Washington, DC.
- TRISKA, F. J., J. H. DUFF, AND R. J. AVANZINO. 1993. Patterns of hydrological exchange and nutrient

- transformations in the hyporheic zone of a gravel-bottom stream: examining terrestrial-aquatic linkages. *Freshwater Biology* 29:259-274.
- TRISKA, F. J., V. C. KENNEDY, R. J. AVANZINO, G. W. ZELLWEGER, AND K. E. BENCALA. 1989. Retention and transport of nutrients in a third-order stream: channel processes. *Ecology* 70:1877-1892.
- VALETT, H. M., S. G. FISHER, N. B. GRIMM, AND P. CAMILL. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* 75:548-560.
- VALETT, H. M., S. G. FISHER, AND E. H. STANLEY. 1990. Physical and chemical characteristics of the hyporheic zone of a Sonoran desert stream. *Journal of the North American Benthological Society* 9: 201-215.
- VALETT, H. M., J. A. MORRICE, C. N. DAHM, AND M. E. CAMPANA. 1996. Parent lithology, surface-groundwater exchange, and nitrate retention in headwater streams. *Limnology and Oceanography* 41:333-345.
- VITOUSEK, P. M., AND W. A. REINERS. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* 25:376-381.
- WILKINSON, L. 1989. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Illinois.

Received: 18 April 1997

Accepted: 4 July 1997

LINKED CITATIONS

- Page 1 of 4 -



You have printed the following article:

Pre- and Post-Flood Retention Efficiency of Nitrogen in a Sonoran Desert Stream

Eugènia Martí; Nancy B. Grimm; Stuart G. Fisher

Journal of the North American Benthological Society, Vol. 16, No. 4. (Dec., 1997), pp. 805-819.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28199712%2916%3A4%3C805%3APAPREO%3E2.0.CO%3B2-1>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

Literature Cited

A Perspective on Stream-Catchment Connections

Kenneth E. Bencala

Journal of the North American Benthological Society, Vol. 12, No. 1. (Mar., 1993), pp. 44-47.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28199303%2912%3A1%3C44%3AAPOSC%3E2.0.CO%3B2-W>

Transient Storage in Appalachian and Cascade Mountain Streams as Related to Hydraulic Characteristics

D. J. D'Angelo; J. R. Webster; S. V. Gregory; J. L. Meyer

Journal of the North American Benthological Society, Vol. 12, No. 3. (Sep., 1993), pp. 223-235.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28199309%2912%3A3%3C223%3ATSIAAC%3E2.0.CO%3B2-3>

Temporal Succession in a Desert Stream Ecosystem Following Flash Flooding

Stuart G. Fisher; Lawrence J. Gray; Nancy B. Grimm; David E. Busch

Ecological Monographs, Vol. 52, No. 1. (Mar., 1982), pp. 93-110.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9615%28198203%2952%3A1%3C93%3ATSIADS%3E2.0.CO%3B2-6>

Nitrogen Dynamics During Succession in a Desert Stream

Nancy B. Grimm

Ecology, Vol. 68, No. 5. (Oct., 1987), pp. 1157-1170.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198710%2968%3A5%3C1157%3ANDDSIA%3E2.0.CO%3B2-C>

LINKED CITATIONS

- Page 2 of 4 -



Nitrogen Limitation in a Sonoran Desert Stream

Nancy B. Grimm; Stuart G. Fisher

Journal of the North American Benthological Society, Vol. 5, No. 1. (Mar., 1986), pp. 2-15.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28198603%295%3A1%3C2%3ANLIASD%3E2.0.CO%3B2-Z>

Nitrogen Fixation in a Desert Stream Ecosystem

Nancy B. Grimm; Kevin C. Petrone

Biogeochemistry, Vol. 37, No. 1. (Apr., 1997), pp. 33-61.

Stable URL:

<http://links.jstor.org/sici?sici=0168-2563%28199704%2937%3A1%3C33%3ANFIADS%3E2.0.CO%3B2-%23>

Parafluvial Nitrogen Dynamics in a Desert Stream Ecosystem

Robert M. Holmes; Stuart G. Fisher; Nancy B. Grimm

Journal of the North American Benthological Society, Vol. 13, No. 4. (Dec., 1994), pp. 468-478.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28199412%2913%3A4%3C468%3APNDIAD%3E2.0.CO%3B2-X>

Vertical Hydrologic Exchange and Ecosystem Metabolism in a Sonoran Desert Stream

Jeremy B. Jones, Jr.; Stuart G. Fisher; Nancy B. Grimm

Ecology, Vol. 76, No. 3. (Apr., 1995), pp. 942-952.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199504%2976%3A3%3C942%3AVHEAEM%3E2.0.CO%3B2-D>

Phosphorus Spiralling in a Woodland Stream: Seasonal Variations

Patrick J. Mulholland; J. Denis Newbold; Jerry W. Elwood; Leigh Ann Ferren; Jackson R. Webster

Ecology, Vol. 66, No. 3. (Jun., 1985), pp. 1012-1023.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198506%2966%3A3%3C1012%3APSIAWS%3E2.0.CO%3B2-C>

Habitat-Specific Solute Retention in Two Small Streams: An Intersite Comparison

Nancy L. Munn; Judy L. Meyer

Ecology, Vol. 71, No. 6. (Dec., 1990), pp. 2069-2082.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199012%2971%3A6%3C2069%3AHSRITS%3E2.0.CO%3B2-A>

LINKED CITATIONS

- Page 3 of 4 -



The Role of Disturbance in Stream Ecology

Vincent H. Resh; Arthur V. Brown; Alan P. Covich; Martin E. Gurtz; Hiram W. Li; G. Wayne Minshall; Seth R. Reice; Andrew L. Sheldon; J. Bruce Wallace; Robert C. Wissmar

Journal of the North American Benthological Society, Vol. 7, No. 4, Community Structure and Function in Temperate and Tropical Streams: Proceedings of a Symposium. (Dec., 1988), pp. 433-455.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28198812%297%3A4%3C433%3ATRODIS%3E2.0.CO%3B2-C>

Ecosystem Expansion and Contraction in Streams

Emily H. Stanley; Stuart G. Fisher; Nancy B. Grimm

BioScience, Vol. 47, No. 7. (Jul. - Aug., 1997), pp. 427-435.

Stable URL:

<http://links.jstor.org/sici?sici=0006-3568%28199707%2F08%2947%3A7%3C427%3AEEACIS%3E2.0.CO%3B2-O>

Concepts and Methods for Assessing Solute Dynamics in Stream Ecosystems

Stream Solute Workshop

Journal of the North American Benthological Society, Vol. 9, No. 2. (Jun., 1990), pp. 95-119.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28199006%299%3A2%3C95%3ACAMFAS%3E2.0.CO%3B2-C>

A Method for the Spectrophotometric Measurement of Chlorophyll a and Pheophytin a in Benthic Microalgae

Paul Tett; Mahlon G. Kelly; George M. Hornberger

Limnology and Oceanography, Vol. 20, No. 5. (Sep., 1975), pp. 887-896.

Stable URL:

<http://links.jstor.org/sici?sici=0024-3590%28197509%2920%3A5%3C887%3AAMFTSM%3E2.0.CO%3B2-J>

Retention and Transport of Nutrients in a Third-Order Stream: Channel Processes

Frank J. Triska; Vance C. Kennedy; Ronald J. Avanzino; Gary W. Zellweger; Kenneth E. Bencala
Ecology, Vol. 70, No. 6. (Dec., 1989), pp. 1877-1892.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198912%2970%3A6%3C1877%3ARATONI%3E2.0.CO%3B2-O>

LINKED CITATIONS

- Page 4 of 4 -



Vertical Hydrologic Exchange and Ecological Stability of a Desert Stream Ecosystem

H. Maurice Valett; Stuart G. Fisher; Nancy B. Grimm; Philip Camill

Ecology, Vol. 75, No. 2. (Mar., 1994), pp. 548-560.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199403%2975%3A2%3C548%3AVHEAES%3E2.0.CO%3B2-1>

Physical and Chemical Characteristics of the Hyporheic Zone of a Sonoran Desert Stream

H. Maurice Valett; Stuart G. Fisher; Emily H. Stanley

Journal of the North American Benthological Society, Vol. 9, No. 3. (Sep., 1990), pp. 201-215.

Stable URL:

<http://links.jstor.org/sici?sici=0887-3593%28199009%299%3A3%3C201%3APACCOT%3E2.0.CO%3B2-C>

Parent Lithology, Surface-Groundwater Exchange, and Nitrate Retention in Headwater Streams

H. Maurice Valett; John A. Morrice; Clifford N. Dahm; Michael E. Campana

Limnology and Oceanography, Vol. 41, No. 2. (Mar., 1996), pp. 333-345.

Stable URL:

<http://links.jstor.org/sici?sici=0024-3590%28199603%2941%3A2%3C333%3APLSEAN%3E2.0.CO%3B2-D>

Ecosystem Succession and Nutrient Retention: A Hypothesis

Peter M. Vitousek; William A. Reiners

BioScience, Vol. 25, No. 6. (Jun., 1975), pp. 376-381.

Stable URL:

<http://links.jstor.org/sici?sici=0006-3568%28197506%2925%3A6%3C376%3AESANRA%3E2.0.CO%3B2-T>