

NITROGEN DYNAMICS DURING SUCCESSION IN A DESERT STREAM¹

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Abstract. Nitrogen dynamics of Sycamore Creek, Arizona, a lowland Sonoran Desert stream, are described by seven diel input–output budgets at different stages of postflood succession. Hydrologic inputs and outputs of nitrogen and N storage in periphyton, macroinvertebrates, and fish were measured over 24-h periods. Total nitrogen storage in this desert stream ($3\text{--}9\text{ g/m}^2$) was lower than that in forest streams of Oregon (12 g/m^2) and Quebec (22 g/m^2). While $>99\%$ of nitrogen in the latter systems is in allochthonous detritus, benthic algae and autochthonous detritus comprised $\approx 90\%$ of the total nitrogen pool in the desert stream. Up to 14% of nitrogen was in consumer organisms. Inputs of nitrogen to the stream ecosystem were dominated by dissolved nitrogen, of which 19–60% was inorganic, primarily nitrate. Particulate nitrogen in transport (4–15% of total input) was mostly autochthonous. Inputs of nitrogen exceeded outputs on most study dates. Rates of ecosystem nitrogen retention were as high as $400\text{ mg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and outputs exceeded inputs on only one study date. Retention was primarily of inorganic nitrogen and was presumed due to autotrophic assimilation. Nitrogen retention data from the seven budgets were used to evaluate the Vitousek and Reiners (1975) model that patterns of nitrogen retention during succession reflect patterns of net ecosystem production and biomass accumulation. Biomass and stored nitrogen increased asymptotically during a postflood successional sequence at a single site; nitrogen retention during this period accounted for increases in storage. Nitrogen retention among the seven study dates exhibited the predicted successional patterns of increases from early to middle successional stages, followed by late stage declines.

Key words: desert streams; flooding; nitrogen; nutrient budgets; nutrient retention; succession.

INTRODUCTION

The first objective of this study was to describe seven diel nitrogen (N) budgets in a Sonoran Desert stream. Budgets are not replicates, but 24-h snapshots of changing ecosystem N dynamics during succession (*sensu* Fisher et al. 1982), based on daily hydrologic inputs and outputs. Element budgets have been used widely to characterize inputs, outputs, and retention of nutrients by ecosystems. Budgets usually are calculated for an annual period and seldom are repeated because of logistical difficulties. The first annual mass balances for nitrogen and phosphorus in streams were constructed in forested watersheds of New England (Meyer and Likens 1979, Meyer et al. 1981), Quebec (Naiman and Melillo 1984), and the Pacific Northwest (Triska et al. 1984). Desert streams of the arid American Southwest are subject to severe flooding with peak flows often exceeding base flow by several orders of magnitude, which decimates their biotas. As a result, export often dominates annual mass balances to an even greater extent than in streams elsewhere. These rare events are important to watershed material budgets (Fisher and Grimm 1985) but reveal little about biologic fluxes in the stream between floods. Even for hydrologically

more stable streams, interpretation of annual budgets is difficult when year-to-year discharge variation is great (Meyer and Likens 1979, Cummins et al. 1983). In desert regions, differences in flooding regime among years would result in extreme variation in annual budgets. Therefore, diel budgets for between-flood successional periods were chosen to characterize N dynamics of this desert stream.

Vitousek and Reiners (1975) hypothesized that ecosystem N retention is predictable from net ecosystem production and biomass accrual during succession. Flash flooding in desert streams provides a disturbance that “resets” algal and macroinvertebrate standing crops to near zero (Fisher et al. 1982). The Vitousek and Reiners hypothesis predicts that ecosystem N retention (defined as the difference between N input and output) will increase as rates of net ecosystem production and standing stocks increase, then decline as biomass approaches a steady state. At steady state, nutrient input must equal output, although changes in form of the nutrient may occur (Vitousek and Reiners 1975). Grimm and Fisher (1986a) presented a modification of this hypothesis for streams, which incorporates transport and permits net ecosystem production to be positive at steady state. The second objective of this study was to evaluate Vitousek and Reiners’ (1975) model by analyzing diel budgets from a range of succes-

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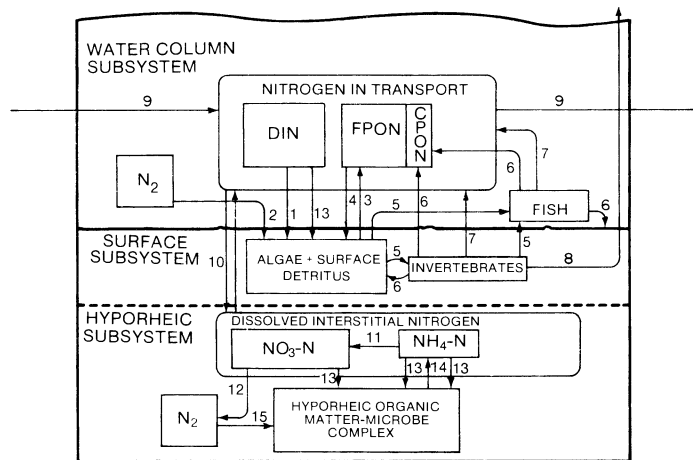


FIG. 1. A model of nitrogen dynamics in desert stream ecosystems. Numbered fluxes are: 1—algal assimilation, 2—nitrogen fixation (bluegreen algae), 3—entrainment of particulate nitrogen, 4—settling of particulate nitrogen, 5—ingestion, 6—egestion, 7—excretion, 8—emergence (insects), 9—import and export (dissolved and particulate nitrogen), 10—interstitial-surface water exchange, 11—nitrification, 12—denitrification, 13—microbial assimilation, 14—mineralization and leaching, 15—nitrogen fixation (bacteria).

sional stages, including three from a single postflood sequence.

Small desert streams of the Southwest provide unique opportunities to examine nitrogen dynamics. Pronounced longitudinal decline of N concentration in stream water is common; thus net ecosystem N retention by a defined stream segment is readily measured. Nitrogen transformations for the stream ecosystem (Fig. 1) are exaggerated in desert streams compared to other streams because of high temperature and insolation, high biotic standing crops, high turnover rates, and high system surface-area-to-volume ratio (Busch and Fisher 1981, Fisher et al. 1982, Fisher and Gray 1983). Fluxes and retention of N are therefore measurable on a daily basis. Finally, N is a critical element in desert streams because it can limit primary production (Grimm and Fisher 1986a). Ratios of N to phosphorus (P) are low, suggesting N limitation is widespread throughout the region (Grimm et al. 1981, Grimm and Fisher 1986b). These features of desert streams make it possible to study the dynamics of this important element on a short-term basis (24 h) using a mass balance approach. Furthermore, multiple diel N budgets constructed over a relatively short time allow examination of changes in N dynamics over the course of succession (recovery following flooding).

METHODS

Diel budget studies were conducted in Sycamore Creek, Maricopa County, Arizona. This stream has been described in detail by Fisher and Minckley (1978) and Fisher et al. (1982). Streamflow is usually continuous throughout much of the channel in winter when evapotranspiration is low and precipitation relatively high. During drier parts of the year Sycamore Creek is

composed of six major perennial segments segregated by long reaches of dry channel. Diel budget studies (hereafter referred to in chronological order as Diels I–VII) were conducted at two of these segments. These sites were dominated by uniform runs of coarse sand and fine gravel substrates. System dimensions and physical and chemical conditions were similar at all sites and times (Table 1).

Flash floods resulting from intense, localized summer thunderstorms occur during late summer and autumn in the Sonoran Desert. These floods scour and move substrates and obliterate much of the biota (especially algae and small macroinvertebrates) but recede within hours. During summer 1981 Sycamore Creek experienced two flash floods of 1- and 2- m^3/s peak discharges. One occurred 6 d prior to Diel I (3–4 August), and the second occurred 10 d prior to Diel II (18–19 August). Diel III was on 3–4 September 1981, 26–27 d after the flood of 8 August. This sequence of studies (I–III) therefore describes N dynamics for a single 90-m reach (site 1) 6, 10, and 26 d after disturbance. Chemical and biological data are also presented for days 2, 5, 20, and 38 of that same successional sequence. A 6- m^3/s flood ended the sequence after 38 d. Three diel studies during summer 1982 at site 2 included pre-flood Diel IV (6–7 July, >90 d since flood) and Diels V and VI, respectively 2 and 5 d after a 2- m^3/s flash flood on 24 August. The Diel VII study site was a short reach at site 2 upstream from the 1982 reach. This study was done 3–5 November 1983, 28 d after a 7- m^3/s flood.

Sampling and chemical analyses

Stream water (for nutrient analysis), dissolved oxygen (DO, Diel VII), and coarse particulate organic matter in transport (CPOM > 1 mm) were sampled at

TABLE 1. Physical and chemical characteristics of diel study sites, Sycamore Creek, 1981–1983.

Parameter	Diel study						
	I	II	III	IV	V	VI	VII
Date of study	Aug 1981	Aug 1981	Sep 1981	Jul 1982	Jul 1982	Jul 1982	Nov 1983
Study site	1	1	1	2	2	2	2
Days since flood	7	11	27	>90	2	5	28
Reach length (m)	110	90	90	120	120	120	60
Mean width (m)	3.5	3.4	3.1	1.9	2.7	2.7	3.5
Mean depth (cm)	5	6	7	7	6	6	7
Stream area (m ²)	382	303	276	232	328	326	210
Volume (m ³)	19.1	18.2	19.3	16.2	19.7	19.6	14.7
Discharge (m ³ /s)	0.022	0.017	0.019	0.016	0.017	0.012	0.063
Residence time (min)	14	18	17	17	19	27	4
Mean current velocity (cm/s)	13	8	9	12	10	7	26
Water temperature (°C)	23–36	25–34	26–32	21–25	23–29	23–27	19–23
Maximum PAR (μE/cm ²)	1900	1700	1920	1725	NA*	NA	900
pH range	7.4–7.9	7.3–7.9	7.4–7.9	7.5–7.9	6.0–7.3	6.3–6.7	NA
Conductivity (μS/cm)	470	NA	446	360	390	390	NA
Ammonium-N (μg/L)	9	NA	25	6	14	NA	0
Nitrate-N (μg/L)	146	27	63	30	28	15	49
TDN (μg/L)	253	167	189	178	180	128	135
SRP (μg/L)	45	47	42	45	77	78	47
iN:iP†	7.6	1.3	4.7	1.9	1.2	0.5	2.4
FPOM (mg/L)	0.35	0.64	0.61	0.51	0.41	0.35	0.40

* NA = not analyzed or measured.

† iN:iP = atomic ratio of inorganic N (nitrate + ammonium) to inorganic P (SRP), or nitrate-N to SRP where ammonium-N not measured.

4- or 6-h intervals beginning at 0800 on the first day and ending at 0400 on the second day at up- and downstream termini of each study reach. Light (photosynthetically active radiation, PAR) was measured hourly by Lambda Instruments quantum probe, and percentage shading of each reach (usually <30%) was estimated during sampling times. Discharge was estimated at up- and downstream termini of sites as the product of cross-sectional area and velocity, measured with a pygmy current meter. Discharge measurements were repeated 4–6 times and integrated over the 24-h period (Diels I–IV) or were made once at midmorning (Diels V–VII). Algal percentage cover and stream morphometry were mapped on transects at 10-m intervals along each reach (Fisher et al. 1982) and biological samples (algae and macroinvertebrates) were collected on the 2nd d.

Water samples, collected in triplicate in acid-rinsed polyethylene bottles, were stored at 4°C and filtered upon return to the laboratory (Whatman GF/F glass-fiber filters). Analyses for nutrients were completed within 4–24 h. Nitrate was determined after reduction to nitrite in cadmium–copper columns (Wood et al. 1967). Nitrite thus formed was measured by a diazotization technique (Strickland and Parsons 1972). Ammonium was measured with the phenolphthalein method of Solorzano (1969). Total dissolved N (TDN) was analyzed as nitrate + ammonium after 4 h of ultraviolet oxidation (Manny et al. 1971). Dissolved organic N (DON) was calculated by difference (TDN – [nitrate – N + ammonium – N]). Soluble reactive phosphorus (SRP) was measured colorimetrically (Murphy and Riley 1962). Dissolved oxygen meth-

odologies were modified Winkler and micro-Winkler (Busch and Fisher 1981) techniques. Fine particulate organic matter (FPOM, 0.7 μm–1 mm) was determined by dichromate oxidation of filters (Maciolek 1962).

Algae were sampled with 3–5 26-cm³ replicate cores (to 2 cm depth) per algal patch. Each sample was divided in the laboratory for determination of chlorophyll *a* and ash-free dry mass (AFDM). One subsample was filtered to remove water, frozen, and then extracted in methanol (Tett et al. 1977). AFDM was measured as mass loss of subsamples dried to constant mass (60°, 48 h) then combusted (550°, 2 h). Invertebrate standing crops were determined from 3–5 80-cm² cores to 10 cm depth. Animals were separated from substrate by elutriation through a 0.25-mm mesh and preserved in 70% ethanol. All individuals in each sample were sorted by taxon, enumerated, and their lengths (L) measured to the nearest 1.0 mm. Individual dry masses (DM) by species and size class were obtained from L. J. Gray (*personal communication*), P. C. Marsh (*personal communication*), and Smock (1980). N was determined in samples of fresh (unpreserved) immature and adult insects. Transported CPOM was sampled with 1.0-mm mesh drift nets, sorted into autochthonous, allochthonous, macrophyte, and invertebrate fractions, and dried to constant mass. AFDM and N were determined on subsamples of each fraction.

Total organic (Kjeldahl) N in biological materials was analyzed using a block digestion technique. Algae, invertebrates, CPOM, and fish were collected, sorted or washed clean of foreign material, and dried to constant mass. Dried material was ground to pass an 850-μm mesh screen and AFDM determined on five sub-

TABLE 2. Biological characteristics of diel study sites, Sycamore Creek, 1981–1983.

Parameter	Diel study						
	I	II	III	IV	V	VI	VII
Days since flood	7	11	27	>90	2	5	28
Chlorophyll <i>a</i> (mg/m ²)	82.5	228.2	295.0	342.6	7.1	17.5	99.0
AFDM (g/m ²)	79.1	121.1	144.7	115.5	61.5	66.4	140.6
Algal % coverage:							
Light diatoms	91	50	12	0	100	100	37
Heavy diatoms	0	28	40	37	0	0	41
Flocculent	0	0	0	11	0	0	19
<i>Cladophora glomerata</i> mat	9	20	35	0	0	0	0
Bluegreen mat	0	0	9	51	0	0	0
Macrophytes	0	2	4	1	0	0	3
Invertebrates:							
Thousands/m ²	32.0	109.8	107.9	65.0	4.1	4.0	40.9
Dry mass (g/m ²)	1.19	5.80	6.94	9.62	0.49	0.35	3.07

samples for estimation of percentage organic matter. Five 25–100 mg subsamples of each material were digested at 400° in a potassium sulfate–concentrated sulfuric acid solution with mercuric oxide as a catalyst. The resulting digest was diluted, pH-adjusted, and analyzed for ammonium using a modification of the phenolphthorite method. N as percentage DM and AFDM and atomic carbon to nitrogen (C:N) ratios were calculated, with C assumed to be 50% of organic mass (Whittaker and Likens 1973).

Metabolism

Chamber and whole-system oxygen techniques were used to estimate net ecosystem production (NEP) and ecosystem respiration (R). For Diels I–III, relationships of gross primary production (GPP) : chlorophyll *a* and R : chlorophyll *a* ratios to chlorophyll *a* standing crops were developed from chamber measurements on site ($n = 4, 4,$ and $6,$ respectively) and applied in a patch-weighted fashion to yield ecosystem metabolism estimates. These relationships were also used to calculate metabolism for days 2, 5, 20, and 38 of the postflood successional sequence at site 1. Metabolism for Diel IV was measured using chamber estimates ($n = 4$) for a single mixed bluegreen-diatom patch type, which accounted for 73% of areal coverage and had a mean chlorophyll *a* standing crop nearly equal to average standing crop of the total system. For Diel V, metabolism was based on measures ($n = 6$) of a single patch type (diatoms) accounting for 100% of coverage and standing crop. Metabolism was not measured for Diel VI. Finally, a method employing black plastic sheeting to measure diffusion and R (Grimm and Fisher 1984) was used in conjunction with the diel oxygen curve method for metabolism of Diel VII. Whole-system NEP was determined from diel oxygen change between up- and downstream termini of the study reach during daytime after correcting for diffusion (Odum 1956). This method differs from chamber estimates since hyporeic subsystem metabolism is included, provided in-

terstitial and surface waters exchange freely (Grimm and Fisher 1984).

Chambers for metabolism measurements of Diels I–V were circular Plexiglas chambers (90.8 cm²) inserted into sandy substrates to ≈ 15 cm, which enclosed algal-colonized substrates and 400–800 mL stream water depending on water depth. Chambers were fitted with lids equipped with motor-powered paddles that gently stirred the water column. Respiration was measured as oxygen change in darkened chambers, and NEP as oxygen change in open (lighted) chambers during 30–60 min incubation periods. Chamber measurements of R were made 4–5 times during the 24-h period and of NEP 3 times during the light period. NEP and R were integrated for the diel period and daytime NEP and R were summed to yield GPP.

N budgets

Nitrogen is present in the water column subsystem in dissolved compounds, particulates, and fish (Fig. 1). Instantaneous compartment size of dissolved and particulate N were calculated as the product of average concentration and water volume determined from transect data. To express these compartment sizes and fluxes on an areal basis, this total compartment size (or flux rate) was divided by stream surface area (Table 1). Wet mass standing crops (1978 and 1984) of *Agosia chrysogaster* (Cyprinidae), the most abundant fish in Sycamore Creek, varied from 7 to 17 g/m² and averaged 13 g/m² ($n = 4$; P. C. Marsh and S. G. Fisher, *personal communication*). These values were converted to dry mass (DM) assuming a DM : wet mass ratio of 0.2 (Grimm 1985). This mean standing crop was used in all diel budget calculations.

Surface subsystem compartments are algae + detritus and macroinvertebrates (Fig. 1). N as percentage AFDM was measured on algal samples collected at the site (bluegreens and *Cladophora glomerata*, Diels I–III), or a value determined for each algal type from a variety of samples (all other data) was used. An algal

patch-weighted percentage N was computed from percentage cover for each diel study. This value was used to calculate the algal N compartment from AFDM standing crop.

Since mass balances were constructed only for 24-h periods, meteorologic inputs (precipitation, throughfall, litterfall, lateral litter inputs) were zero or very small. Inputs of N via nitrogen fixation and losses due to denitrification were not measured in this study. Transport of all dissolved N forms was calculated from diel concentration curves by multiplying by hourly discharge. Hourly values were integrated over the 24-h period. FPON was estimated from FPOM flux rates by dividing by a weighted mean ratio of AFDM:N from algal, allochthonous, and macrophyte CPOM. CPON drift rates were calculated separately for each fraction by dividing total AFDM collected in drift nets over a timed interval by total water volume through the net. Net discharge was determined from velocity (pygmy current meter) and depth measurements in the net at the beginning and end of each interval, and was multiplied by time to obtain total water volume. Ash-free dry mass values were divided by the ratio of AFDM:N for each fraction, then multiplied by hourly stream discharge and integrated over the 24-h period.

Loss of N through emergence of aquatic insects was calculated from data of Jackson and Fisher (1986). Emergence-to-biomass ratios were calculated for each taxon as daily emergence rates divided by DM standing crops. Three estimates of emergence-to-biomass ratios from autumn, spring-early summer, and late summer 1982-1983 were averaged and multiplied by DM standing crop of each taxon for diel studies. Average N content of adult insects was used to convert DM rates to emergence loss of N.

RESULTS AND DISCUSSION

Mean concentrations of SRP were high on all study dates (42-79 $\mu\text{g/L}$), as is typical of many Southwestern streams (Sommerfeld et al. 1974, Grimm et al. 1981, Grimm and Fisher 1986b). Dissolved inorganic N (DIN = ammonium-N + nitrate-N) concentrations were more variable (36-154 $\mu\text{g/L}$), but often low. The atomic ratio of DIN to SRP (N:P) was therefore low (<8) on all study dates. FPOM was <1 mg/L on most dates (Table 1).

Standing crops of periphyton (as chlorophyll *a* or AFDM) generally were highest when flooding had not occurred for several months (Table 2) and at sites where *Cladophora glomerata* or other mat-forming algae occurred in abundance. *C. glomerata* coverage increased throughout the 38-d successional period at site 1 (including Diels I-III), as it gradually replaced early diatom colonizers. *C. glomerata* was not an important component of periphyton communities at site 2 during mid to late stages of recovery (Diels IV and VII); instead, bluegreen algal mats (*Anabaena* sp. and *Oscillatoria* sp.), diatoms, or flocculent material predomi-

TABLE 3. Metabolism estimates (measured as O_2) for Sycamore Creek, 1981-1983. Chamber methods used for all studies except Diel VII.

Study	Days since flood	O_2 flux ($\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$)			
		GPP	R	NEP	GPP/R
Diel I	7	4.24	3.58	0.66	1.2
Diel II	11	9.90	5.73	4.17	1.7
Diel III	27	12.25	6.51	5.75	1.9
Diel IV	>90	5.79	4.17	1.62	1.4
Diel V	2	2.74	4.04	-1.30	0.7
Diel VII	28	6.46	4.80	1.66	1.3

nated. Flocculent material consisted of accumulations of autochthonous detritus including fish, snail, and invertebrate feces and unrecognized detrital material. A diverse mixture of algae, including short filaments of *C. glomerata*, *Oedogonium* sp., and bluegreens, often grew from such flocculent detrital accumulations. Both chlorophyll *a* and AFDM standing crops of flocculent material were usually high (>200 mg/m^2 and >200 g/m^2 , respectively) in these thick accumulations.

Macroinvertebrate standing crops ranged from ≈ 4000 individuals/ m^2 and dry mass of 0.4 g/m^2 to >100 000 individuals/ m^2 and ≈ 7.5 g/m^2 (Table 2). On all dates >80% of numbers and biomass were collector-gatherer macroinvertebrates, although relative importance of the most common taxa (Ephemeroptera and Chironomidae) varied. In the site 1 succession (Diels I-III), Chironomidae dominated the fauna early on (day 7), while the mayfly *Leptohyphes packeri* became extremely abundant (82% of numbers and 90% of biomass) by day 27. At site 2 in 1982, ephemeropterans, hydropsychid caddisflies, chironomid dipterans, and stratiomyiid dipterans were principal pre-flood faunal components (Diel IV, >90 d since disturbance). After the 24 July flood (Diels V and VI), Stratiomyiidae and Tricorythidae accounted for most of the biomass and numbers. Stratiomyiids probably survived the low-intensity flood (2 m^3/s) at this site, whereas the increase in tricorythid numbers and biomass from day 2 (Diel V) to day 5 (Diel VI) is more likely due to recolonization.

Measured as O_2 , gross primary production ranged from 2.74 to 12.25 $\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and ecosystem respiration ranged from 3.58 to 6.51 $\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ among all studies (Table 3). Gross primary production exceeded ecosystem respiration on all dates except for Diel V. Respiration of the hyporheic zone was not measured in this study, but is important in Sycamore Creek (Grimm and Fisher 1984). Therefore, although surface sediments were autotrophic on most days, the whole system (including sediments to bedrock) may not have been. On the single occasion when whole-system (including hyporheic) metabolism was measured by upstream-downstream oxygen methods (Diel VII), however, the stream was autotrophic (Table 3).

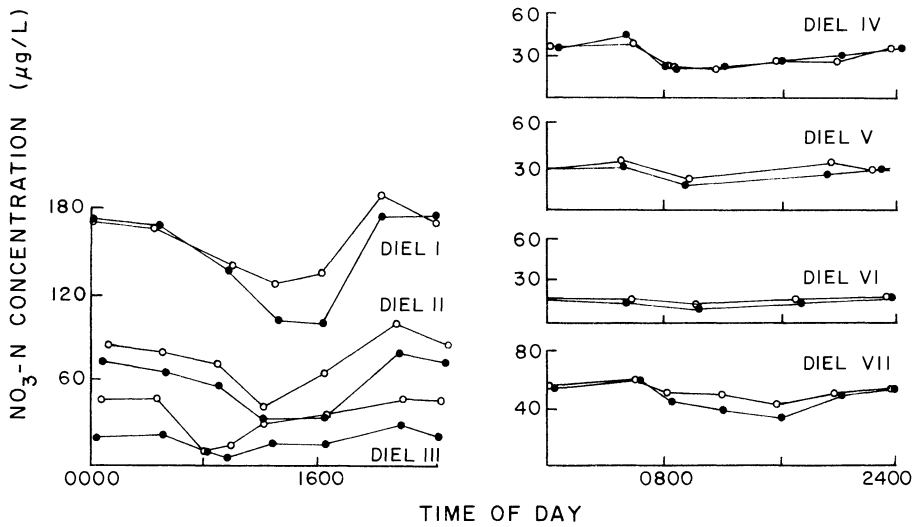


FIG. 2. Diel patterns of nitrate-nitrogen concentration at upstream (O) and downstream (●) termini of diel study reaches, Sycamore Creek.

Diel patterns

Concentration of nitrate-N varied diurnally (Fig. 2). Overall patterns of concentration at upstream stations reflected processes of in-stream uptake and release occurring above the study sites. Marked daytime depression of nitrate-N suggests uptake by photosynthetic organisms. Similar diel patterns of elevated nighttime and lower daytime concentrations have been reported

by others (Manny and Wetzel 1973, Sebetich et al. 1984) and attributed to autotrophic uptake.

Transport of FPOM was highest at midday and lowest at night (Fig. 3). CPOM transport was much lower than FPOM, but when measurable, it showed the same diel pattern. This daytime peak in particulate transport is in contrast to the nighttime transport maxima reported by Manny and Wetzel (1973) and attributed to

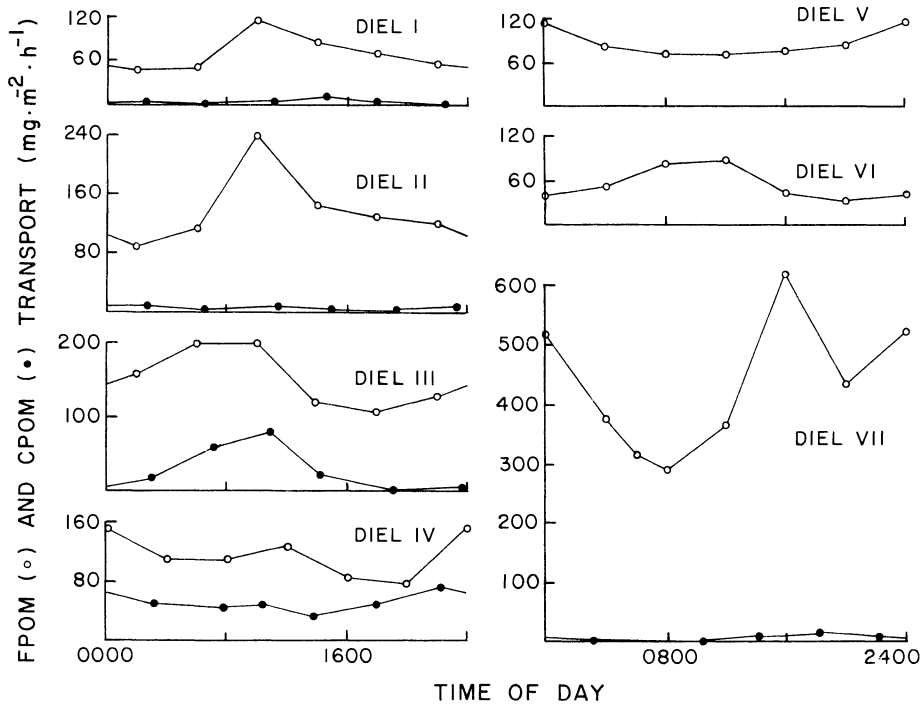


FIG. 3. Diel variation in transport of fine particulate organic matter (FPOM, O) and coarse particulate organic matter (CPOM, ●) in Sycamore Creek.

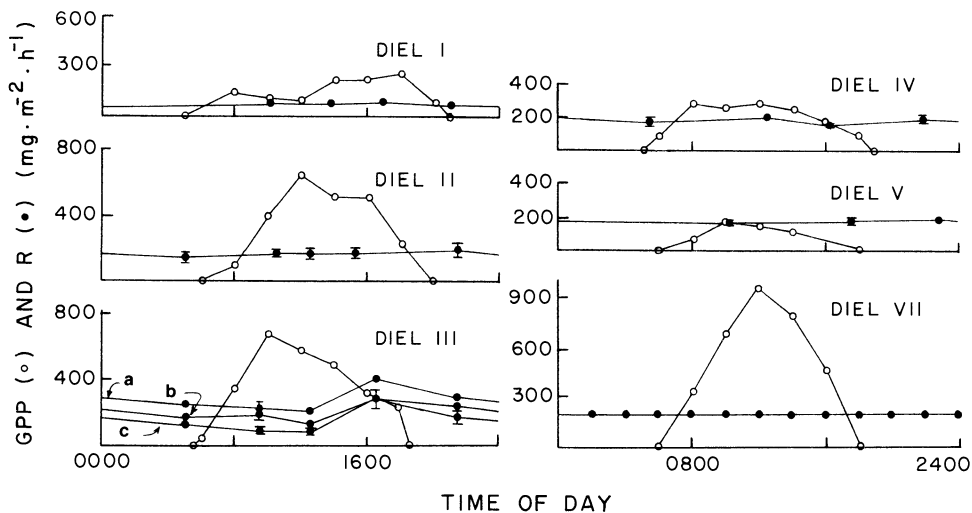


FIG. 4. Diel patterns of gross primary production (GPP) and ecosystem respiration (R) in Sycamore Creek. (a) *Cladophora glomerata* mat, (b) low density of *C. glomerata* filaments, (c) high density of diatoms. Error bars for Diels I-V represent ± 1 standard error (standard errors $< 15 \text{ mg} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ not plotted).

nocturnal feeding activities of invertebrates. In Sycamore Creek, many invertebrates feed constantly (Gray 1980) and *Agosia chrysoaster* feeds primarily at midday (Fisher et al. 1981). Other factors contributing to high daytime CPOM and FPOM transport are suspension of fine particulates by actively swimming fishes, disturbance by humans or cattle, and gas bubble formation resulting in flotation of highly productive algal mats (especially bluegreens). This last factor also contributed to high algal export and a diel pattern of daytime export maxima in a Washington thermal spring (Stockner 1968) and in a California thermal stream (Naiman 1976).

Diel patterns of GPP and R (Fig. 4) were similar to patterns observed earlier in Sycamore Creek (Busch and Fisher 1981) and elsewhere (McConnell and Sigler 1959, Marker 1976, Kaplan and Bott 1982). Daytime maxima in DO and GPP usually were between 1000–1300 when PAR was near its maximum. Diel variations in R were not significant (ANOVA, $P > .05$), except for Diel III *C. glomerata* mats ($F = 13.5$, $P < .01$), despite rather large fluctuations in temperature. This contrasts with findings of Busch and Fisher (1981), who found R strongly influenced by temperature.

Nitrogen budgets

Diel nutrient budgets have not heretofore been published for any ecosystem, but there are three annual N budgets for temperate forest streams with which Sycamore Creek budgets may be compared. Relative distributions of forms of N in transport and net changes in these distributions caused by biotic processing in stream segment ecosystems are amenable to comparison between different streams or stream segments; however, comparisons of percentage total input in

transport vs. other vectors (e.g., nitrogen fixation) are not conceptually meaningful. This is because areal inputs are independent of system size, while transport inputs expressed on an areal basis increase or decrease in inverse proportion to system size (Cummins et al. 1983, Meyer and Tate 1983). Transport inputs also are sensitive to discharge fluctuations within an annual period and among streams (Fisher and Likens 1973, Fisher 1977, Meyer and Likens 1979, Cummins et al. 1983). The watershed approach to stream mass balances eliminates many of these difficulties, but is seldom used because it is impractical for any but the smallest streams (but see Triska et al. 1984). Since the stream segments I examined were similar in total surface area (Table 1) comparisons among diel studies are reasonable.

Hydrologic inputs of N to Sycamore Creek stream segments were dominated by the dissolved fraction (Table 4). DIN ranged from 16–58% of total inputs and from 19–60% of dissolved inputs; most DIN was nitrate. Particulate inputs ranged from 4–15% of total, most of which was FPON. Between 80 and 95% of outputs were as dissolved N and 5–20% of outputs were as particulate N (Table 4). Both inputs and outputs of particulate N were lowest in early postflood stages (Diels I, V, and VI). At these times CPON transport included a substantial allochthonous fraction (24, 91, and 42%, respectively). In middle to late recovery stages CPON transport was higher and was dominated by autochthonous material (77, 90, and 81% in Diels II, III, and IV, respectively), except during autumn (Diel VII, 75% allochthonous).

In Sycamore Creek, DIN and DON each constituted on average approximately half the dissolved N in contrast to WS10, Oregon, and Beaver Creek, Quebec,

TABLE 4. Nitrogen budgets (as N) for Sycamore Creek stream segments, 1981–1983, rounded to two significant figures. Parenthetical values are percentage total inputs, outputs, or pools. * denotes percentages <1%.

Parameter†	Diel I		Diel II		Diel III		Diel IV		Diel V		Diel VI		Diel VII	
Inputs (mg·m ⁻² ·d ⁻¹)														
DIN	790	(58)	170	(17)	620	(40)	190	(16)	190	(22)	50	(11)	1300	(35)
DON	510	(37)	670	(69)	710	(47)	830	(69)	610	(69)	360	(78)	2200	(56)
FPON	58	(4)	130	(13)	160	(11)	170	(14)	73	(8)	51	(11)	360	(9)
CPON	4.4	(*)	7.1	(1)	36	(2)	17	(1)	2.4	(*)	0.23	(*)	8.9	(*)
Total	1400		980		1500		1200		880		460		3900	
Outputs (mg·m ⁻² ·d ⁻¹)														
DIN	750	(58)	91	(10)	440	(38)	240	(18)	170	(20)	44	(10)	1200	(31)
DON	470	(37)	699	(75)	490	(42)	860	(64)	630	(72)	370	(83)	2300	(59)
FPON	57	(4)	130	(14)	160	(14)	220	(16)	63	(7)	31	(7)	360	(9)
CPON	1.4	(*)	4.6	(*)	63	(6)	15	(1)	2.2	(*)	0.51	(*)	12	(*)
Emergence‡	1.6	(*)	6.9	(1)	3.3	(*)	8.2	(1)	1.2	(*)	0.31	(*)	4.8	(*)
Total	1300		930		1100		1300		870		440		3900	
Compartments (g/m ²)														
Water column														
Dissolved + particulate														
Fish§	0.014	(*)	0.012	(*)	0.016	(*)	0.015	(*)	0.012	(*)	0.009	(*)	0.010	(*)
	0.27	(6)	0.27	(4)	0.27	(3)	0.27	(3)	0.27	(8)	0.27	(7)	0.27	(3)
Surface sediments														
Algae	4.0	(91)	6.3	(89)	8.0	(90)	6.7	(86)	3.1	(91)	3.3	(91)	7.4	(93)
Inverts	0.10	(2)	0.51	(7)	0.61	(7)	0.84	(11)	0.043	(1)	0.031	(1)	0.27	(3)
Total pools	4.4		7.1		8.9		7.8		3.4		3.6		8.0	

† DIN = dissolved inorganic nitrogen; DON = dissolved organic nitrogen; FPON = fine particulate organic nitrogen; CPON = coarse particulate organic nitrogen.

‡ Dry mass (DM) emergence rates converted to N by applying a mean N:DM ratio for adult insects of 0.110 ($n = 30$, $SE = 0.0024$).

§ DM standing crop converted to N by applying a mean N:DM ratio for fish of 0.103 ($n = 41$, $SE = 0.0014$).

|| DM standing crop converted to N by applying a mean N:DM ratio for immature insects of 0.088 ($n = 45$, $SE = 0.0009$). Mean ratio determined from a combined sample including baetid and tricorythid mayflies, the caddisfly *Helicopsyche*, small chironomid dipterans, and large Chironomidae (*Chironomus* sp.). Taxa did not differ in N concentration (% DM) (ANOVA on transformed data, $F = 0.63$, $P = .64$).

where most dissolved N was organic (Table 5). Bear Brook had a large DIN fraction (mostly nitrate) presumably derived from high nitrate concentrations in precipitation (Junge 1958, Bormann and Likens 1979) and from high rates of terrestrial nitrification (Bormann and Likens 1979). Percentage PON in transport in Sycamore Creek was similar to other systems, although most was autochthonous in origin in contrast to the forest streams where energy and nutrient inputs are derived mostly from allochthonous sources.

Insect emergence percentages of total N outputs are not strictly comparable among studies because of system size differences. On an areal basis, however, emergence losses (as N) were quite high (0.3–8.2 mg·m⁻²·d⁻¹, Table 5) in Sycamore Creek compared with average daily losses (calculated from annual rates) of 0.05 mg·m⁻²·d⁻¹ in WS10 and 0.27 mg·m⁻²·d⁻¹ in Beaver Creek. Jackson and Fisher (1986) determined annual emergence rates (as DM) from Sycamore Creek of nearly equal magnitude as macroinvertebrate secondary production rates in many temperate forest streams. The present analysis supports their conclusion that insect emergence represents a significant energy and nutrient transfer from the aquatic to the terrestrial ecosystem, an interesting reversal of the terrestrial-to-aquatic en-

ergy transfer so common to temperate streams (e.g., Hynes 1963, Minshall 1967, Fisher and Likens 1973).

Although I measured only transport inputs, those from precipitation were known to be zero (N. B. Grimm, *personal observation*) and allochthonous inputs in the form of leaf litter and aeolian transfer of fine particulates were assumed low. In forest streams, litter may constitute 10–20% of annual N inputs (Meyer et al. 1981, Triska et al. 1984). Since leaf litter input to desert streams is typically low, especially in summer, an assumption of zero litter should not represent a significant error. Wind may on occasion transport substantial quantities of N into the stream. Summer convective storms are characteristic of the region from mid-July through mid-September, during which large volumes of dust are transported. Little storm activity occurred on days of the summer diel studies; wind transport was not measured but was probably minimal.

Nitrogen fixation in the stream by bluegreen algae was another unmeasured N source. Maximum seasonal nitrogen fixation rate of *Nostoc* sp. in a California stream was 1 mg·m⁻²·d⁻¹ (Horne and Carmiggelt 1975). If this value applies in Sycamore Creek, nitrogen fixation would account for <1% of total input but could represent a large fraction on N actually retained by the

TABLE 5. Comparison of N mass balances of four streams. Parenthetical values are percentage of transport inputs.

Parameter*	Sycamore Creek, Arizona	Watershed 10, Oregon†	Beaver Creek Riffle, Quebec‡	Bear Brook, New Hampshire§
Stream surface area	210–382	767	100	7095
Inputs (% of total)				
DIN	16–58 (16–58)	3 (5)	15 (15)	73 (85)
DON	37–69 (37–69)	69 (95)	67 (67)	11 (13)
PON	9–15 (9–15)	0 (0)	18 (18)	2 (2)
Precip + throughfall	0	2	0.02	3
Litter		19	0.12	11
Nitrogen fixation	?	5	0.004	?
Outputs (% of total)				
DIN	18–58	4	15	84
DON	37–72	74	67	12
PON	7–22	23	18	3.7
CPON	0.1–6	8	0.1	3
FPON	7–16	15	18	0.7
Emergence	0.1–1	0.2	0.1	?
Pools (% of total)				
FPON	0	40	19	
LPON	0	59	80	
Producers	86–93	0.6	? (0)	
Consumers	6–14	0.2	?	
Pools (g/m ²)				
FPON	0	4.8	4.3	
LPON	0	7.1	17.8	
Producers	3.1–8.0	0.07	...	
Consumers	0.3–1.1	0.02	...	

* DIN = dissolved inorganic nitrogen; DON = dissolved organic nitrogen; LPON, CPON and FPON, respectively, large, coarse, and fine particulate organic nitrogen.

† Triska et al. 1984.

‡ Naiman and Melillo 1984.

§ Meyer et al. 1981.

|| N in producers in Sycamore Creek includes that in associated autochthonous detritus.

ecosystem. Bluegreen algal mats were the dominant algal patch type during the Diel IV study (Table 2), and this was the only time hydrologic DIN outputs exceeded inputs (Table 4). Nitrogen fixation is inhibited by high concentrations of DIN, but concentrations during Diel IV were low (0.02–0.05 mg/L). Therefore, omission of nitrogen fixation may have been a significant error for this late-stage diel study. Bluegreen mat was present in only one other study (Diel III, 9% cover); concentrations of DIN at that time were higher (≈ 0.08 –0.12 mg/L).

Denitrification was a potential N output not measured in my study. Differences between up- and downstream nitrate-N concentrations could be due to denitrification and gaseous loss from the system (Fig. 1). Others have found denitrification to account for a significant fraction of downstream nitrate-N decline (Kaushik and Robinson 1976, Van Kessel 1977, Chartarpaul and Robinson 1979) or budgetary N output (Hill 1979, 1983, Swank and Caskey 1982). Triska and Oremland (1981) found that denitrification can be associated with *Cladophora* mats, especially in high-nitrate systems. In general, denitrification is highest in areas of high nitrate-N concentration, high organic content, and relatively low oxygen concentration (Knowles 1982, Payne 1983). Local conditions favorable to de-

nitrification probably do exist at times in Sycamore Creek, but sediments are most commonly well oxygenated (Grimm and Fisher 1984) and nitrate-N is low (Table 1 and Grimm and Fisher 1986b), conditions which argue against high rates of denitrification in this stream. The importance of the process to N budgets is unknown, however, and deserves further attention.

N may be stored in the ecosystem in the water column; in primary producers, detritus, and consumers of surface sediments; and in the deep sediment organic matter-microbe complex (Fig. 1). Most N stored in surface and water column subsystems was in algae and associated detritus (86–93% of total N stored), but consumers (invertebrates, 1–11% and fish, 3–8%) represented significant storage compartments. N stored in the deep sediment (hyporheic) zone was not measured in this study. Although organic content of sediments below the surface (alga-colonized) layers is low (<0.5%), sediment depth is great, and storage in this subsystem is potentially significant. For example, assuming a 50-cm mean sediment depth, a sediment dry mass of 200 kg/m² per 10 cm depth, a 0.2% organic content, and a 0.7% N content (of organic matter) (Grimm 1985), N storage in deep sediments would be 14 g/m², about twice the amount stored in surface benthic organic material (algae plus detritus, Table 4). This value would

TABLE 6. Ratios of nitrogen outputs to inputs (O/I) for Sycamore Creek, 1981–1983.

Parameter	Diel study						
	I	II	III	IV	V	VI	VII
Dissolved	0.94	0.94	0.43	1.08	1.00	1.00	0.99
DIN	0.94	0.53*	0.71	1.25	0.90	0.88*	0.89
DON	0.93	1.04	0.69	1.04	1.04	1.03	1.05
Particulate	0.96	0.96	1.09	1.26	0.86	0.61	1.02
Total	0.94	0.95	0.75	1.11	0.99	0.96	0.99

* Nitrate-N only measured; DON = TDN – nitrate-N.

likely vary with time since disturbance, due to microbial utilization (Grimm and Fisher 1984).

Total N storage in Sycamore Creek, WS10, and Beaver Creek was similar, but percentage distributions of stored N were quite different (Table 5). Forest streams had large quantities of woody debris (59–80% of total stored N) and insignificant amounts of primary producers, while up to 93% of total N in Sycamore Creek was in algae and autochthonous detritus. Storage in consumer organisms (8–14%) was large in Sycamore Creek compared to other streams (Table 5), but high nutrient storage in consumers has been reported elsewhere. Pools of nutrients and biomass of higher trophic levels in forest ecosystems are dwarfed by large size of primary producers, whereas in most aquatic ecosystems consumers are large relative to primary producers (Wiegert and Owen 1971). Crayfish and salamanders are major sinks for Ca, Mg, and K in small South-eastern streams (Woodall and Wallace 1975). Newbold et al. (1983) found that only a small fraction of added ^{32}P spiralled through consumers, yet 25% of P standing stock was in consumer biomass. Fishes generally are large in size relative to their prey and to primary producers. Several workers have suggested that long-term storage may be the most significant impact of fishes on nutrient cycling in lakes (Kitchell et al. 1975, Nakashima and Leggett 1980). Hall (1972) suggested that in streams as well, annual flows of P associated with fish are minor in comparison to storage. In contrast, storage of nutrients in salamanders (Burton and Likens 1975) and birds (Sturges et al. 1974) was but a small (<1%) fraction of total nutrient storage in a northern hardwoods forest.

Nitrogen retention

Mass balances for streams can give only a minimum estimate of in-stream processing because internal recycling is not reflected in simple differences between inputs and outputs (Meyer and Likens 1979). Domination of budgets by transport, furthermore, obscures importance of areal inputs and outputs. Therefore, some expression reflecting actual transformation or uptake by stream biota is needed. Meyer and co-workers (Meyer and Likens 1979, Meyer et al. 1981, Meyer and Tate 1983), using the dimensionless output-to-input ratio

(O/I), showed that net transformation of P and N to progressively smaller particle size occurs in many forest streams. The opposite is true for desert streams: net uptake of dissolved inorganic N (transformation from dissolved to particulate) commonly occurs. In all diel studies except Diel IV, overall O/I < 1 (Table 6). The stream ecosystem on most study dates thus was not at steady state with respect to N.

Differences between inputs and outputs in Sycamore Creek were attributed to net uptake or release of dissolved N, except for Diels V and VI (postflood days 2 and 5) when dissolved inputs nearly balanced outputs, but FPON was retained (Table 6). Dissolved organic N export often exceeded import; however, inorganic N species were nearly always retained by the stream at a rate exceeding losses of other forms. Up to half of nitrate-N input was retained in the 60–120 m stream reaches (Table 6). Much of this retention was probably due to algal assimilation. Rates of nitrate-N uptake by isolated natural periphyton assemblages in Sycamore Creek ranged from -7.76 (negative uptake = release or mineralization) to 51.7 and averaged $7.77 \text{ mg} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (SE = 0.847, $n = 157$; Grimm 1985, Grimm and Fisher 1986a). Previously reported whole-ecosystem uptake rates for Sycamore Creek and other desert streams were as high as $38 \text{ mg} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (Grimm et al. 1981). Nitrate-N uptake in a productive, bluegreen-dominated Washington thermal spring was comparable to that of Sycamore Creek at $12.9 \text{ mg} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (Stockner 1968). These rates of algal nitrate-N assimilation are sufficient to account for the whole-system nitrate-N retention values of diel studies.

Outputs of DON exceeded inputs on most dates. When DON was released, mean diel DIN concentrations were low (15–49 $\mu\text{g/L}$), while when DON was retained, DIN concentrations were 155 and 89 $\mu\text{g/L}$ (Diels I and III, respectively; Table 6). This pattern may exist because of high rates of algal DON release under low N conditions (Fogg and Watt 1966, Nalewajko and Schindler 1976).

Small quantities of particulate N were retained in

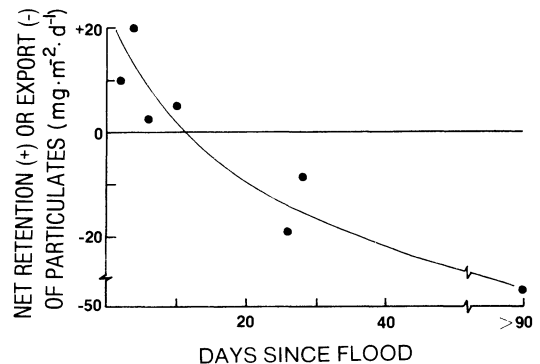


FIG. 5. Net diel flux of particulate nitrogen as a function of time since disturbance, Sycamore Creek, 1981–1983.

early postflood periods (Diels I, II, V, and VI), while later budgets showed a net loss of particulate N (Diels III, IV, and VII; Table 6). Rates of particulate N retention thus declined with time since disturbance (Fig. 5). Net export was primarily of algae, which achieved high standing crops and thus were susceptible to high rates of sloughing late in succession. Losses of particulates were not large relative to amounts of inorganic N retained by the stream segments (9 and 6% of DIN retention rates of Diels III and VII, respectively), but such losses may come to equal rates of DIN retention in late successional stages, thereby maintaining steady state biomass even when NEP is positive (Grimm and Fisher 1986a). In contrast to temperate forest streams that often show net retention of particulates or at least particle size reduction between inputs and outputs, export of photosynthate in the form of particulate material may represent a significant output of organic matter and nutrients in desert streams late in prolonged interflood periods (Fisher 1986).

Nitrogen retention and succession

Use of element mass balances to describe forest nutrient cycling has revealed much about capacities of forest ecosystems to retain and transform nutrients at different stages of succession and under different degrees of disturbance (Likens and Bormann 1977). The small watershed approach (Bormann and Likens 1979) to element budgets ascribes to forest processing changes in nutrients from precipitation inputs to streamflow outputs at the watershed base. Similarly, the stream mass balances presented here ascribe to in-stream processing of nutrients (especially algal uptake) changes from inputs to outputs between two points along the stream channel.

Nitrogen budgets presented in this paper represent a spectrum of conditions determined largely by time since last disturbance. Just as biomass and production are not predictable in desert streams unless time since flooding is known (Fisher 1983), these budgets vary primarily because they reflect nitrogen cycling at different stages of succession. Diel budget studies were used to test the Vitousek and Reiners (1975) hypothesis, which predicts that nutrient retention is highest in early to middle stages of succession, when NEP is maximal, and declines to zero late in succession. Patterns of successional change in nutrient retention are similar to those of net ecosystem production or net biomass accrual when uptake of the nutrient by autotrophs is the major retentive process.

The 38-d postflood sequence at site 2 provides data for a single site that may be used to evaluate the assumptions and predictions of the Vitousek and Reiners model. Algal standing stocks increased rapidly to 50% of maximum levels within 10 d (Fig. 6). Patterns of recovery were similar to those reported by Fisher et al. (1982) for a 1979 sequence at approximately the same site, but higher chlorophyll *a* and AFDM stand-

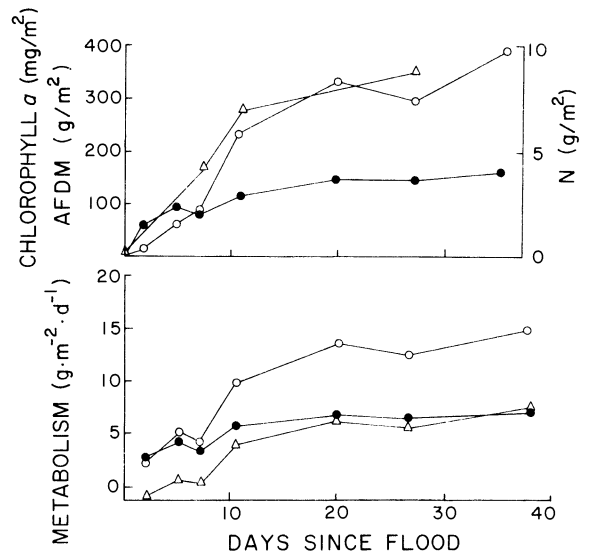


FIG. 6. Post-flood trajectories of (A) standing stocks of chlorophyll *a* (O), AFDM (●), and nitrogen (Δ) and (B) GPP (O), NEP (Δ), and R (●) in Sycamore Creek, site 2, 1981.

ing stocks were reached in 1981. Rates of metabolism increased asymptotically through the sequence (Fig. 6). Neither this sequence nor the 60-d period studied by Fisher et al. (1982) showed evidence of a late-stage decline in NEP as biomass approached a steady state (Fig. 6). Inorganic N retention also increased during the successional period, from 3% of N inputs on day 7, to 8% on day 11 and 12% on day 27, and showed no evidence of late successional decline. Longer successional sequences may exhibit the predicted decline; 1979 and 1981 successions were just 60 and 38 d in length.

Nitrogen stored in the surface sediment and water column subsystems increased from 4.4 to nearly 9.0 g/m² between day 7 and day 27 (Fig. 6). Assuming N was retained at a rate of 250 mg·m⁻²·d⁻¹ (average of N retention from Diels I and III), 79% of N retained over this 20-d period appeared in algal biomass, while 10% was accounted for by increased macroinvertebrate standing stocks. The increase in N was approximately linear from day 0 to day 11 at 605 mg·m⁻²·d⁻¹, followed by a slower increase of 110 mg·m⁻²·d⁻¹ from day 11 to day 27 (Fig. 6). Nitrogen retention, however, was lower on day 7 (100 mg·m⁻²·d⁻¹) than on day 27 (400 mg·m⁻²·d⁻¹). The discrepancy between estimates of N stored throughout the period and N retained by the stream on specific dates of the diel budget studies may result from variation in day-to-day rates of N retention during the early postflood period. By day 27, N retention rate suggests that N should be accumulating in the system at a faster rate than it actually is. This may also result from errors in estimation of retention rate, or N may indeed be accumulating in some unmeasured component of the system (e.g., the hyporheic zone). Nevertheless, over the 20-d period between Diel

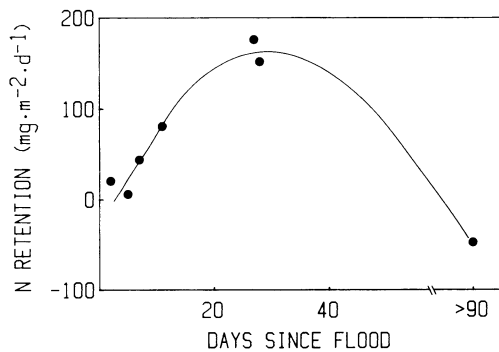


FIG. 7. Rates of ecosystem inorganic nitrogen retention as a function of time since disturbance in Sycamore Creek, 1981–1983.

I and Diel III, total N retention agrees well with total N accumulation in algal and animal tissue, supporting the assumption that autotrophic uptake is the major retentive process in this ecosystem.

The prediction of Vitousek and Reiners' model that ecosystem nutrient retention should increase from early to middle successional stages, then decline to zero in late succession was supported by analysis of the seven diel studies (Fig. 7). Since net biomass accrual is not known for all seven studies, I am unable to evaluate the prediction that it too declines in late stages. It is possible for steady state biomass to be maintained in streams while NEP remains positive, provided excess production is exported (Busch and Fisher 1981, Grimm and Fisher 1986a). The Diel IV study, which was done >90 d since disturbance, exhibited negative (but near zero) N retention and may have had zero or negative net biomass accrual. Additional studies of a longer successional sequence at a single site would be needed to determine whether NEP is reduced in late stages and under what conditions this occurs. In desert streams many opportunities arise in each year to examine effects of flooding and early recovery thereafter. Because of the paucity of rainfall in the region, occasional extended periods between floods also occur and provide a successional time frame akin to several hundreds of years in terrestrial ecosystems.

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LITERATURE CITED

- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.
- Burton, T. M., and G. E. Likens. 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* **56**: 1068–1080.
- Busch, D. E., and S. G. Fisher. 1981. Metabolism of a desert stream. *Freshwater Biology* **11**:301–307.
- Chatarpaul, W. L., and J. B. Robinson. 1979. Nitrogen transformations in stream sediments: ¹⁵N studies. Pages 119–127 in C. D. Litchfield and P. L. Seyfried, editors. Methodology for biomass determinations and microbial activities in sediments. ASTM STP 673, American Society for Testing and Materials, Philadelphia, Pennsylvania, USA.
- Cummins, K. W., J. R. Sedell, F. J. Swanson, G. W. Minshall, S. G. Fisher, C. E. Cushing, R. C. Peterson, and R. L. Vannote. 1983. Organic matter budgets for stream ecosystems: problems in their evaluation. Pages 299–353 in J. R. Barnes and G. W. Minshall, editors. Stream ecology: application and testing of general ecological theory. Plenum, New York, New York, USA.
- Fisher, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, USA. *Internationale Revue der Gesamten Hydrobiologie* **62**:701–727.
- . 1983. Succession in streams. Pages 7–27 in J. R. Barnes and G. W. Marshall, editors. Stream ecology: application and testing of general ecological theory. Plenum, New York, New York, USA.
- . 1986. Structure and dynamics of desert streams. Pages 119–139 in W. G. Whitford, editor. Pattern and process in desert ecosystems. University of New Mexico Press, Albuquerque, New Mexico, USA.
- Fisher, S. G., D. E. Busch, and N. B. Grimm. 1981. Diel feeding chronologies in two Sonoran Desert stream fishes, *Agosia chrysoaster* (Cyprinidae) and *Pantosteus clarki* (Catostomidae). *Southwestern Naturalist* **26**:31–36.
- Fisher, S. G., and L. J. Gray. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* **64**:1217–1224.
- 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**:93–110.
- Fisher, S. G., and N. B. Grimm. 1985. Hydrologic and material budgets for a small Sonoran Desert watershed during three successive cloudburst storms. *Journal of Arid Environments* **9**:105–118.
- Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* **43**:421–439.
- Fisher, S. G., and W. L. Minckley. 1978. Chemical characteristics of a desert stream in flash flood. *Journal of Arid Environments* **1**:25–33.
- Fogg, G. E., and W. D. Watt. 1966. The kinetics of release of extracellular products of photosynthesis by phytoplankton. Pages 165–174 in C. R. Goldman, editor. Primary productivity in aquatic environments. University of California Press, Berkeley, California, USA.
- Gray, L. J. 1980. Recolonization pathways and community development of desert stream macroinvertebrates. Dissertation. Arizona State University, Tempe, Arizona, USA.
- Grimm, N. B. 1985. Roles of primary producers and consumers in nitrogen dynamics of a desert stream ecosystem. Dissertation. Arizona State University, Tempe, Arizona, USA.
- Grimm, N. B., and S. G. Fisher. 1984. Exchange between interstitial and surface water: implications for stream metabolism and nutrient cycling. *Hydrobiologia* **111**:219–228.
- 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., S. G. Fisher, and W. L. Minckley. 1981. Nitrogen and phosphorus dynamics in hot desert streams of Southwestern USA. *Hydrobiologia* **83**:303-312.
- Hall, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. *Ecology* **53**:585-604.
- Hill, A. R. 1979. Denitrification in the nitrogen budget of a river ecosystem. *Nature* **281**:291-292.
- . 1983. Nitrate-nitrogen mass balances for two Ontario rivers. Pages 457-477 in T. D. Fontaine and S. M. Bartell, editors. *Dynamics of lotic ecosystems*. Ann Arbor Science, Ann Arbor, Michigan, USA.
- Horne, A. J., and W. W. Carmiggelt. 1975. Algal nitrogen fixation in California streams: seasonal cycles. *Freshwater Biology* **5**:461-470.
- Hynes, H. B. N. 1963. Imported organic matter and secondary productivity in streams. *Proceedings of the International Congress of Zoology* **16**:324-329.
- Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology* **67**:629-638.
- Junge, C. E. 1958. The distribution of ammonia and nitrate in rainwater over the United States. *Transactions of the American Geophysical Union* **39**:241-248.
- Kaplan, L. A., and T. L. Bott. 1982. Diel fluctuations of DOC generated by algae in a piedmont stream. *Limnology and Oceanography* **27**:1091-1100.
- Kaushik, N. K., and J. B. Robinson. 1976. Preliminary observations on nitrogen transport during summer in a small spring-fed Ontario stream. *Hydrobiologia* **49**:59-63.
- Kitchell, J. F., J. F. Koonce, and P. S. Tennis. 1975. Phosphorus flux through fishes. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **19**:2478-2484.
- Knowles, R. 1982. Denitrification. *Microbiological Reviews* **46**:43-70.
- Likens, G. E., and F. H. Bormann. 1977. *Biogeochemistry of a forested ecosystem*. Springer-Verlag, New York, New York, USA.
- Maciulek, J. A. 1962. *Limnological organic analysis by quantitative dichromate oxidation*. United States Fish and Wildlife Service Research Report **60**.
- Manny, B. A., M. C. Miller, and R. G. Wetzel. 1971. Ultraviolet combustion of dissolved organic nitrogen compounds in lake waters. *Limnology and Oceanography* **16**:71-85.
- Manny, B. A., and R. G. Wetzel. 1973. Diurnal changes in dissolved organic and inorganic carbon and nitrogen in a hardwater stream. *Freshwater Biology* **3**:31-43.
- Marker, A. F. 1976. The benthic algae of some streams in southern England II. Primary production of the epilithon in a chalk stream. *Journal of Ecology* **64**:359-375.
- McConnell, W. J., and W. F. Sigler. 1959. Chlorophyll and productivity in a mountain river. *Limnology and Oceanography* **4**:335-351.
- Meyer, J. L., and G. E. Likens. 1979. Transport and transformation of phosphorus in a forest stream ecosystem. *Ecology* **60**:1255-1269.
- Meyer, J. L., G. E. Likens, and J. Sloane. 1981. Phosphorus, nitrogen, and organic carbon flux in a headwater stream. *Archiv für Hydrobiologie* **91**:28-44.
- Meyer, J. L., and C. M. Tate. 1983. The effects of watershed disturbance on dissolved organic carbon dynamics of a stream. *Ecology* **64**:33-44.
- Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology* **48**:139-149.
- Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* **27**:31-36.
- Naiman, R. J. 1976. Primary production, standing stock, and export of organic matter in a Mohave Desert thermal stream. *Limnology and Oceanography* **21**:60-73.
- Naiman, R. J., and J. M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia (Berlin)* **62**:150-155.
- Nakashima, B. S., and W. C. Leggett. 1980. The role of fishes in the regulation of phosphorus availability in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:1540-1549.
- Nalewajko, C., and D. W. Schindler. 1976. Primary production, extracellular release and heterotrophy in two lakes in the ELA, Northwestern Ontario. *Journal of the Fisheries Research Board of Canada* **33**:219-226.
- Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: a study of nutrient spiralling. *Ecology* **64**:1249-1265.
- Odum, H. T. 1956. Primary production in flowing waters. *Limnology and Oceanography* **1**:102-117.
- Payne, W. J. 1983. Bacterial denitrification: asset or defect? *BioScience* **33**:319-325.
- Sebetich, M. J., V. C. Kennedy, S. M. Zand, R. J. Avanzino, and G. W. Zellweger. 1984. Dynamics of added nitrate and phosphate compared in a northern California woodland stream. *Water Resources Bulletin* **20**:93-101.
- Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biology* **10**:375-383.
- Solorzosa, L. 1969. Determination of ammonia in natural waters by the phenylhypochlorite method. *Limnology and Oceanography* **14**:799-801.
- Sommerfeld, M. R., R. D. Olsen, and T. D. Love. 1974. Some chemical observations on the upper Salt River and its tributaries. *Journal of the Arizona Academy of Science* **9**:78-81.
- Stockner, J. G. 1968. Algal growth and primary productivity in a thermal stream. *Journal of the Fisheries Research Board of Canada* **25**:2037-2058.
- Strickland, J. D. H., and T. R. Parsons. 1972. *A practical handbook of seawater analysis*. Fisheries Research Board of Canada Bulletin Number **167**.
- Sturges, F. W., R. T. Holmes, and G. E. Likens. 1974. The role of birds in nutrient cycling in a northern hardwoods ecosystem. *Ecology* **55**:149-155.
- Swank, W. T., and W. H. Caskey. 1982. Nitrate depletion in a second-order mountain stream. *Journal of Environmental Quality* **11**:581-584.
- Tett, P., M. G. Kelly, and G. M. Hornberger. 1977. Estimation of chlorophyll *a* and pheophytin *a* in methanol. *Limnology and Oceanography* **22**:579-580.
- Triska, F. J., and R. S. Oremland. 1981. Denitrification associated with periphyton communities. *Applied and Environmental Microbiology* **42**:745-748.
- Triska, F. J., J. R. Sedell, K. Cromack, Jr., S. V. Gregory, and F. M. McCorison. 1984. Nitrogen budget for a small coniferous forest stream. *Ecological Monographs* **54**:119-140.
- Van Kessel, J. F. 1977. Factors affecting the denitrification rate in two sediment-water systems. *Water Research* **11**:259-267.
- Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* **25**:376-381.
- Whittaker, R. H., and G. E. Likens. 1973. Carbon in the biota. Pages 281-302 in G. M. Woodwell and E. V. Pecan, editors. *Carbon and the biosphere*. CONF-720-510. United States Atomic Energy Commission, Springfield, Virginia, USA.
- Wiegert, R. G., and D. F. Owen. 1971. Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. *Journal of Theoretical Biology* **30**:69-81.

- Wood, E. D., F. A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in seawater by cadmium-copper reduction to nitrite. *Journal of the Marine Biology Association of the United Kingdom* 47:23-31.
- Woodall, W. R., and J. B. Wallace. 1975. Mineral pathways in small Appalachian streams. Pages 408-422 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. *Mineral cycling in southeastern ecosystems*. United States Energy Research and Development Administration, Washington, D.C., USA.

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- Page 2 of 4 -



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LINKED CITATIONS

- Page 3 of 4 -



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Stable URL:

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Limnology and Oceanography, Vol. 21, No. 1. (Jan., 1976), pp. 60-73.

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J. D. Newbold; J. W. Elwood; R. V. O'Neill; A. L. Sheldon

Ecology, Vol. 64, No. 5. (Oct., 1983), pp. 1249-1265.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28198310%2964%3A5%3C1249%3APDIAWS%3E2.0.CO%3B2-7>

LINKED CITATIONS

- Page 4 of 4 -



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Limnology and Oceanography, Vol. 1, No. 2. (Apr., 1956), pp. 102-117.

Stable URL:

<http://links.jstor.org/sici?sici=0024-3590%28195604%291%3A2%3C102%3APPIFW%3E2.0.CO%3B2-T>

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F. W. Sturges; R. T. Holmes; G. E. Likens

Ecology, Vol. 55, No. 1. (Jan., 1974), pp. 149-155.

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