ROLE OF MACROINVERTEBRATES IN NITROGEN DYNAMICS OF A DESERT STREAM[1]

Nancy B. Grimm

Department of Zoology, Arizona State University, Tempe, Arizona 85287 USA

Abstract. Organismal nitrogen budgets (nitrogen ingested, egested, excreted, and utilized in production) were constructed for collector-gatherer macroinvertebrates and grazing snails of a Sonoran Desert stream. Twenty-seven percent of ingested nitrogen was utilized in insect tissue production, 9–31% was excreted as ammonia, and the remainder (42–64%) was egested. Of nitrogen utilized in production, only 26% resulted in increased standing stock during a 20-d successional period. The remainder was lost to predation and nonpredatory mortality (70%) or as emergent adult insects (4%). Snail excretion was 9–13%, and egestion was 26–39% of ingestion. Of nitrogen ingested by snails 50–68% was used in tissue production.

As a percentage of nitrogen retained by the stream ecosystem, increased storage of N in insect biomass was 10%, insect emergence was 1%, and excretion recycled up to 70% of that amount back to the dissolved nitrogen compartment. Collector-gatherer macroinvertebrate influence on nitrogen dynamics, especially via recycling of excreted ammonia, increased over successional time.

Key words: collector-gatherers; consumer role; nitrogen budgets; nitrogen excretion; streams; succession.

INTRODUCTION

Patterns of energy flow are influenced to varying extents by types and abundances of consumer organisms in aquatic and terrestrial ecosystems. Herbivorous and detritivorous consumers may exert more influence on ecosystem dynamics through transformation and translocation of nutrients than by transformation of energy (Chew 1974, Kitchell et al. 1979). In forests, deserts, and grasslands, detritivores often are important to recycling of nutrients from decomposing litter (Gist and Sferra 1978, Woodmansee and Duncan 1980, Schaefer and Whitford 1981, Whitford et al. 1982). Herbivores have been thought to stimulate primary production through enhancement of nutrient cycling in grasslands (McNaughton 1976, 1984, Owen and Wiegert 1981; but see Belsky 1986), forests (Mattson and Addy 1975), and lakes (Cooper 1973, Flint and Goldman 1975, Cuker 1983). Comparable studies in streams have shown both stimulation (Gregory 1983, Lamberti and Resh 1983, Murphy 1984) and reduction (Sumner and McIntire 1982, Mulholland et al. 1983) of primary production per unit chlorophyll due to grazing. Several hypotheses have been suggested to explain stimulation of primary production by grazing (e.g., Lamberti and Moore 1984), but none has yet been tested experimentally in streams.

In hot desert stream ecosystems of the arid American Southwest, immature insects are important consumers. Ingestion by macroinvertebrate collector-gatherers exceeds gross primary production, supporting one of the

highest rates of secondary production yet reported for a stream macroinvertebrate community (Fisher and Gray 1983, Jackson and Fisher 1986). Adult insect emergence from a desert stream may exceed secondary production of most stream communities (Jackson and Fisher 1986). Because of their obvious importance to energy flow in this system, macroinvertebrates may also play an important role in nutrient dynamics. Nitrogen is the limiting nutrient in many southwestern desert streams (Grimm and Fisher 1986), and storage of nitrogen in macroinvertebrate biomass is a significant fraction of total ecosystem N storage (Grimm 1987).

The objectives of this paper are to describe organismal nitrogen budgets for common macroinvertebrates, to assess the role of macroinvertebrates in nitrogen dynamics of a N-limited desert stream ecosystem, and to examine how this role changes through successional time (following flood disturbance). Nitrogen budgets for chironomid and ephemeropteran collector-gatherers and grazing snails were constructed by quantifying nitrogen ingestion, egestion, excretion, and deposition in growth (utilization) and applying these values to community standing stocks. The potential role of the collector-gatherer macroinvertebrate community in nitrogen dynamics was evaluated by comparing nitrogen flux through the community with its flow through the ecosystem, as determined using 24-h nitrogen budgets constructed at different stages of postflood succession. These budgets are published in an earlier paper (Grimm 1987) and are used here as a frame of reference for evaluation of the consumer role, both at a single point in time and at

different times, representing a range of successional stages.

METHODS

Sycamore Creek is a midsized, spatially intermittent stream in the central Arizona Sonoran Desert. During late summer the stream is subject to severe flash flooding, which reduces standing stocks of algae and macroinvertebrates to near zero and initiates successional regrowth of biota. In the absence of further disturbance, recovery to preflood conditions occurs within a few weeks to months (Fisher et al. 1982, Grimm 1987), due to high rates of primary (Busch and Fisher 1981, Grimm and Fisher 1984) and secondary (Fisher and Gray 1983, Jackson and Fisher 1986) production. Comparisons of organismal and whole-ecosystem nitrogen budgets were made between 1980 and 1983 at different successional stages (2, 5, 7, 11, 27, 28, and >90 d postflood) at two sites on Sycamore Creek. A detailed description of the stream at those times and sites is provided in Grimm (1987). Collector-gatherer macroinvertebrates such as baetid and tricorythid mayflies and chironomid dipterans, which attain similar maximum sizes, dominate the fauna of Sycamore Creek (Gray 1981) and are the focus of this study. Standing stocks ranged from 4000 to nearly 110 000 individuals/m^2, and dry biomass (DM) ranged from 0.35 to 9.62 g/m^2 among eight diel nitrogen budget studies (Grimm 1985, 1987); collector-gatherers accounted for >70% of numbers and >80% of biomass in all cases except on day 2 following flooding, when they were less abundant.

Organismal nitrogen budgets may be described by the equations:

$$I = U + E + F, \tag{1}$$
$$A = U + E, \text{ and} \tag{2}$$
$$I = A + F, \tag{3}$$

where I = rate of ingestion, U = rate of utilization in formation of animal tissue, F = rate of egestion, E = rate of excretion, and A = rate of assimilation. These fluxes were either measured by a combination of laboratory and field studies, estimated from literature values, or calculated using Eqs. 1–3 for four invertebrate taxa: chironomids, tricorythid and baetid mayflies, *Cryptolabis* sp. (a small tipulid dipteran), and snails (*Physa virgata*).

Insect ingestion was estimated from Eq. 1. Utilization was calculated from the mean of four values of daily secondary dry mass production per unit area (Fisher and Gray 1983, Jackson and Fisher 1986) divided by dry biomass standing crop per unit area and the number of hours in a day to yield hourly rates of dry mass production per unit dry mass. This value was converted to nitrogen units by multiplying by the mean tissue N content of immature insects (8.78% of DM, SE = 0.093%, n = 45; Grimm 1985). Literature values for secondary production are for the entire macroin-

vertebrate community, which includes other taxa but is dominated by chironomids and mayflies (Fisher and Gray 1983). Utilization is the amount of nitrogen retained in animal tissue but does not reflect actual change in N standing stocks, since losses to mortality, predation, and emergence are included.

Detailed methods for excretion studies of insects followed those of Gardner et al. (1981) and Nalepa et al. (1983). Organisms were collected by gentle elutriation in the field, sorted by taxon in the laboratory, and maintained in aerated distilled water at 25°C with a food supply of dried and ground *Cladophora glomerata,* a common macroalga, and its epiphytes. Experiments were conducted within 48 h of collection. Five to 10 chironomid larvae (individual DM = 50–634 μg), Ephemeroptera nymphs (DM = 430–1530 μg), or *Cryptolabis* sp. larvae (DM = 139–162 μg) were rinsed five times by dipping in distilled water, then placed in an inverted polyethylene syringe containing 30 mL distilled water and a small piece of Nitex netting to serve as substrate. Contamination from sand substrates or natural stream water was thus avoided. Nalepa et al. (1983) showed that excretion rates of benthic chironomids and tubificids are not affected by presence or absence of a sand substrate or type of water medium. Control syringes containing 30 mL distilled water, Nitex, and no insects were incubated simultaneously. Syringes were continuously aerated through blunt syringe needles connected to an air supply. After a specified incubation period, 25 mL of each sample was removed for analysis of ammonia-N, then replaced with 25 mL distilled water. Initial ammonia-N concentration for subsequent incubations was calculated from dilution of the remaining 5-mL sample with 25 mL distilled water. Incubations on each group of animals were from 0–2, 2–4, 4–6, and 6–8 h, from 0–4 and 4–8 h, or from 0–8 h in a first set of experiments; from 0–3, 3–6, 6–9 h, or from 0–6 or 0–9 h in the second experiments; and from 0–3 and 3–15 h in the third experiments (*Cryptolabis* sp. only). After measurements were completed, lengths of larvae or nymphs were measured to the nearest millimetre. Dry masses were calculated from equations relating length to dry mass, developed for each taxon (L. Gray, *personal communication,* and P. Marsh, *personal communication*).

Egestion is difficult to measure in small collector-gatherers since fecal pellets are small or unconsolidated and often are indistinguishable from foods. I measured N egestion as total N released by immature insects incubated in the field, minus excretion determined as described previously. Measurements included four replicates each of 50 chironomid larvae (mean individual DM = 103–154 μg) and 50 baetid nymphs (DM = 209–334 μg), and one sample of 30 *Cryptolabis* sp. larvae (DM = 431 μg). Because egestion may be a function of gut fullness, organisms were taken directly from the stream, rapidly sorted, and placed in glass vials with 30 mL unfiltered stream water. Water tem-
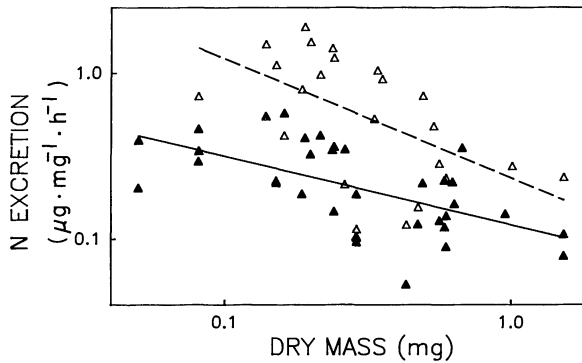
FIG. 1. Variation in mass-specific nitrogen excretion rate (E/DM) of common Sycamore Creek macroinvertebrates as a function of individual organism dry mass (DM). Fed animals (△): $\ln E/DM = -0.719 \ln DM - 1.460$ ($r^2 = 0.31$, $n = 23$, $P = .006$); unfed animals (▲): $\ln E/DM = -0.413 \ln DM - 2.107$ ($r^2 = 0.35$, $n = 35$, $P = .0002$).

perature was 17°. After a short (≤0.5 h) incubation time chosen to minimize problems of reingestion of fecal material, animals were removed with clean forceps and the vials were capped. Total N of vial contents was analyzed and N release (micrograms per hour) was corrected by data for control, then divided by mean DM to yield N release rate per milligram dry mass per hour. Egestion was obtained by subtracting excretion from this value.

Ingestion rate of algal nitrogen by snails was measured directly in the laboratory as change in total N in 50 mL water at 22° containing scrapings of algae grown in Sycamore Creek on unglazed clay tiles. Feeding dishes were prepared by swirling a suspension of algal scrapings and quickly pipetting two 25-mL aliquots into the dishes. Ten *Physa virgata* each (mean individual ash-free dry mass [AFDM] = 4.62–5.79 mg) that had been deprived of food for 4 h prior to experiments were allowed to feed for 1.5 h in five of the dishes. Three additional dishes were incubated with algal scrapings, but without snails, to provide corrections for leaching or uptake by algae. Material remaining after 1.5 h was filtered and analyzed for nitrogen.

Utilization was not measured directly for *Physa virgata,* nor was N content determined; rather utilization was calculated by difference (Eq. 1). Excretion by snails was estimated by analyzing the filtrate of each sample from the ingestion experiment for ammonia-N produced during the 1.5-h period. No fecal pellets were produced during this time because guts were initially empty and gut turnover time, determined by feeding snails a powdered charcoal marker mixed in food, is >1.5 h. A second estimate of excretion was obtained by allowing snails to feed overnight on algal scrapings, then transferring them to clean distilled water for 1.5 h. Feces were produced during this period (see below), but were removed immediately. Samples were filtered at the end of the period, and the filtrate was analyzed for ammonia N produced. These two measures prob-

ably encompass the limits of laboratory rates of excretion, since one measure represents the excretion rate of unfed snails and the second represents the excretion rate of animals fed for at least 12 h.

Snail egestion was determined in the laboratory during the second excretion experiment described previously. Fecal pellets were removed as they were produced so that snails were unable to reingest feces and so that loss of fecal mass by leaching could be minimized. Feces were dried, weighed, and combined for analysis of N content. Egestion was also measured in the field by collecting feces produced in two dishes by ≈100 snails each (mean individual AFDM = 5.30 and 6.36 mg). Water temperature was 21° at the time of this experiment. Snails were placed directly into dishes upon collection, and feces were removed continuously by fine-bore pipet. All feces produced during the first two 30-min intervals and four subsequent 60-min intervals were collected separately and later dried, weighed, and then combined for N analysis. Fecal dry mass production rates per unit AFDM for both egestion estimates were converted to N egestion rates by analysis of fecal N content.

Ammonia N produced in excretion experiments was measured using the phenolhypochlorite (indophenol blue) method of Solorzano (1969). Analysis of nitrogen content of feces (snail egestion), algal material (snail ingestion), and vial contents (insect egestion + excretion) was by a Kjeldahl block digestion technique. Liquid samples were boiled to near dryness, and dried material was ground to pass an 850-μm-mesh screen prior to digestion. Entire filters, vial contents, or 25–100 mg subsamples of dried 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 phenolhypochlorite method.

RESULTS

Dry-mass-specific nitrogen excretion rates of insect larvae varied from 0.053 to 1.90 $\mu g \cdot mg^{-1} \cdot h^{-1}$, and decreased with organism dry mass (Fig. 1). Small chironomid larvae (mean ± SE DM = 176 ± 56 μg; $n = 10$) and *Cryptolabis* larvae (199 ± 14 μg; $n = 8$) therefore exhibited highest dry-mass-specific N excretion rates ($\bar{X} = 0.526$ $\mu g \cdot mg \cdot h^{-1}$), while N excretion rates of Ephemeroptera (mean ± SE DM = 760 ± 98 μg; $n = 14$) were lower per unit dry mass ($\bar{X} = 0.291$ $\mu g \cdot mg^{-1} \cdot h^{-1}$). Rates varied depending on whether animals had been fed immediately prior to measurements. Regression equations predicting excretion from dry mass differed significantly between fed animals and animals that had been without food for >2 h ($F = 20.43$, df = 2,54; $P < .001$; Fig. 1). Rates for recently fed animals may have been high because of leaching from feces, whereas rates for unfed animals may have been low compared with natural rates of actively feed-
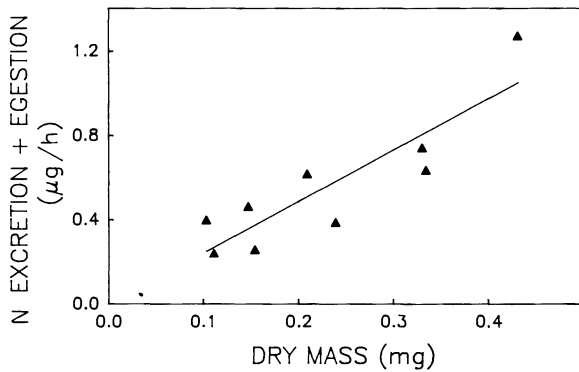
FIG. 2. Variation in field-measured total nitrogen release rates (E + F = excretion + egestion) of common Sycamore Creek macroinvertebrates as a function of organism dry mass (DM). Curve fitted by the equation E + F = 2.44 DM − 0.002 ($r^2 = 0.77$, $n = 9$, $P = .002$).

ing animals. These two equations therefore provided both high and low excretion estimates.

Insect N egestion (F) + excretion (E) measured in the field ranged from 0.24 to 1.27 $\mu g/h$, increasing with mean individual DM in a linear fashion (Fig. 2). There was no significant difference between dry-mass-specific N release rates ($F + E$) for mayflies (2.17 ± 0.248 $\mu g \cdot mg^{-1} \cdot h^{-1}$) and chironomids ($2.71 \pm 0.423$ $\mu g \cdot mg^{-1} \cdot h^{-1}$) ($T = 0.95$, df = 7). The single value for *Cryptolabis* sp. was 2.53 $\mu g \cdot mg^{-1} \cdot h^{-1}$. An overall mean dry-mass-specific N release rate of 2.45 $\mu g \cdot mg^{-1} \cdot h^{-1}$ therefore was used in budget estimates. Hourly egestion rates averaged 0.96 if the high excretion estimate was used, and 2.10 if the low excretion estimate was used.

Hourly secondary dry mass production of collector-gatherer macroinvertebrates per unit dry mass was 8.81 $\mu g/mg$ (Fisher and Gray 1983). Jackson and Fisher (1986) obtained seasonally varying rates of 16.0, 12.0 and 4.56 $\mu g/mg$, respectively for autumn, spring, and summer periods. Corresponding values of N utilization per unit dry mass are 0.77, 1.40, 1.05, and 0.40

$\mu g \cdot mg^{-1} \cdot h^{-1}$ ($\bar{X} \pm$ SE = 0.91 $\pm$ 0.21). N ingestion, calculated as the sum of N egestion, excretion, and utilization per unit dry mass, was 3.36 $\mu g \cdot mg^{-1} \cdot h^{-1}$.

Mass-specific hourly flux rates were applied to DM standing crops on eight different dates, yielding N fluxes in milligrams per square metre per day (Table 1). Mass-specific excretion rates were first calculated from mean organism dry mass on each date (standing stock divided by numbers per square metre) using the equation in Fig. 2. Because egestion was calculated as nitrogen release ($F + E$) minus excretion (E), I present high and low estimates of egestion and excretion, but only single estimates of ingestion (calculated from Eq. 1) and utilization. Collector-gatherer macroinvertebrate community nitrogen-budget fluxes were generally highest in later stages of succession (Table 1).

Snail N ingestion per unit snail AFDM in the laboratory ranged from 0.93 to 3.96 $\mu g \cdot mg^{-1} \cdot h^{-1}$, with a mean value ($\pm$SE) of 2.46 $\pm$ 0.483 $\mu g \cdot mg^{-1} \cdot h^{-1}$ ($n = 5$). The average ($\pm$ SE) laboratory dry matter egestion per unit AFDM of snails fed on algae scrapings was 116.3 $\pm$ 13.6 $\mu g \cdot mg^{-1} \cdot h^{-1}$ ($n = 11$). Dry mass of feces averaged 0.811% N (SE = 0.102, $n = 6$); thus egestion of N per unit AFDM was 0.930 $\mu g \cdot mg^{-1} \cdot h^{-1}$. Fecal dry mass production rate per unit AFDM (F_t) in the field decreased exponentially with time since capture (t, hours) (Fig. 3) according to the equation:

$$\ln F_t = 4.50 - 0.409t \qquad (4)$$

($r^2 = 0.81$, $n = 12$). From this relationship, the extrapolated value of F_0 (egestion at time of capture) was 89.8 $\mu g \cdot mg^{-1} \cdot h^{-1}$. Fecal dry mass averaged 0.697% N (SE = 0.012, $n = 5$), thus N egestion per unit snail AFDM was 0.626 $\mu g \cdot mg^{-1} \cdot h^{-1}$. I used both field and laboratory estimates as estimates of N egestion by snails. N excretion was measured both during (unfed animals, $n = 5$) and after (fed animals, $n = 9$) the laboratory feeding period and the mean values ($\pm$SE) were 0.208 $\pm$ 0.005 and 0.306 $\pm$ 0.029 $\mu g \cdot mg^{-1} \cdot h^{-1}$, respectively.

TABLE 1. Nitrogen budgets for the collector-gatherer macroinvertebrate community at different successional stages and for grazing snails at average density (final row) in Sycamore Creek. Low and high estimates for excretion and egestion reflect differences between fed and unfed animals and are given to bracket natural rates.

Date	Days after flood	Invertebrate dry mass standing stock (g/m²)	Nitrogen fluxes (mg·m⁻²·d⁻¹)					
			Ingestion	Utilization	Excretion		Egestion	
					Low	High	Low	High
July 1980	>90	5.19[1]	418	113	36.0	131	174	269
August 1981	7	1.19[2]	96.0	26.0	13.6	71.0	0	56.6
August 1981	11	5.80[2]	468	127	56.9	267	74	284
September 1981	27	6.94[2]	560	152	63.3	280	128	345
July 1982	>90	9.62[2]	775	210	62.3	212	354	504
July 1982	2	0.49[2]	39.5	10.7	3.4	12.6	16.2	25.4
August 1982	5	0.35[2]	28.2	7.6	2.8	11.2	9.4	17.8
November 1983	28	3.07[2]	248	67.0	25.8	111	70	155
October 1983 (snails)	···	0.38[1]	22	11–15	1.9	2.8	5.7	8.5

[1] Standing stock data from Grimm (1985).
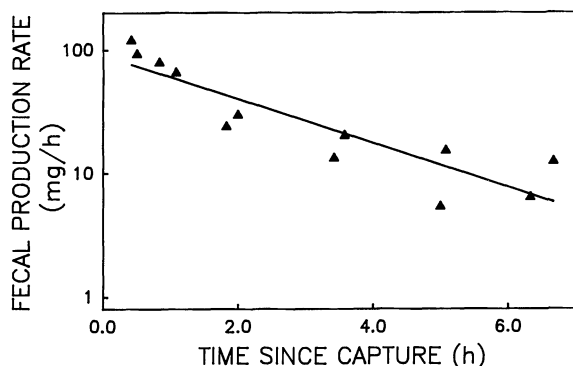[2] Standing stock data from Grimm (1987).

FIG. 3. Decline in fecal production rate (FPR) with time since capture (t) of *Physa virgata* from Sycamore Creek. Equation for curve is: ln FPR = $4.50 - 0.410t$ ($r^2 = 0.81$, $n = 12$, $P = .0001$).

These values are significantly different from one another ($T = 2.44$, $P = .04$, df = 12). As with the insects, both values were used as low and high estimates of snail excretion. N utilization per unit snail AFDM calculated as ingestion minus egestion and excretion (Eq. 1), was $1.22–1.63$ $\mu g \cdot mg^{-1} \cdot h^{-1}$.

Distribution of *Physa virgata* is temporally and spatially patchy. The snail often aggregates along shallow margins or in quiet, shallow waters at the termini of pools and is sparse or absent in other places. In October 1983, I censused snails in moderately dense aggregations by counting individuals enclosed within a 25-cm² area. Average density was 300 snails/m². Based on an estimate that 25% of the stream (the approximate area of shallow water along stream margins) supported such aggregations, density for the entire stream was 75 individuals/m². At AFDM of ≈5 mg/snail, standing stock was 0.38 g/m². Budget parameters at this standing stock were comparable to those for insects at low densities (Table 1).

DISCUSSION

Individual nitrogen budgets

Nitrogen excretion has not previously been measured for stream macroinvertebrates; however, some information is available for zooplankton and marine and lentic benthos. Mass-specific excretion rates of Sycamore Creek insects were well within the ranges reported for detritivores of similar sizes (Table 2). Both N and P excretion rates decline with time after removal of *Daphnia* from its food (Gardner and Scavia 1981, Scavia and Gardner 1982). Phosphorus release is similarly time-dependent in benthic oligochaetes and chironomids (Gardner et al. 1981). Benthic chironomids, however, excrete N at constant rates following removal from food (Gardner et al. 1983). Nitrogen excretion rates of Sycamore Creek macroinvertebrates were highest immediately following removal from food. Although high rates could reflect higher ammonia excretion of fed animals, they could also be the result of fecal leaching. Both values are used here to bracket probable natural rates of excretion.

Excretion rates are likely to be highly dependent on temperature. These laboratory studies were at 22°C, compared with stream temperatures of from 10° to 20° in winter and 20° to 30° in summer. Excretion thus may have been underestimated for summer and overestimated for winter. Although aquatic insects are ammonotelic (Campbell 1973), urea and other nitrogen compounds that may also be excreted were not measured, resulting in underestimation of excretion.

Egestion rates for mayflies and chironomids are difficult to compare with published values since N content of feces is unknown. Ward and Cummins (1979) and Shepard and Minshall (1981) reported N contents of lotic insect feces (as percentage DM) of 0.9–1.2% and 1.3–1.6%, respectively. Using an average value of 1.25% N, DM egestion rate per unit DM of a typical insect in Sycamore Creek would be $77–168$ $mg \cdot g^{-1} \cdot h^{-1}$ or $1840–4030$ $mg \cdot g^{-1} \cdot d^{-1}$. The hourly value is comparable to egestion reported for *Baetis quilleri* and the chironomid *Tribelos* sp., two species common in Sycamore Creek (Fisher and Gray 1983). The daily rate is higher than most reported by Shepard and Minshall (1984a) for macroinvertebrates of Mink Creek, Idaho, and elsewhere (range = $88–2800$ $mg \cdot g^{-1} \cdot d^{-1}$). Ladle and Griffiths (1980) reported respective rates of 2800, 5100, and 16 700 $mg \cdot g^{-1} \cdot d^{-1}$ for *Gammarus pulex,* oligochaetes, and *Simulium* in a chalk stream in England. The Sycamore Creek rate is also comparable to many listed by Hargrave (1972) for aquatic deposit-

TABLE 2. Nitrogen excretion rates of various aquatic invertebrates per unit tissue dry mass.

Organism	Habitat	Limits, individual mass (mg)	Limits, ammonia-N excretion ($\mu g \cdot mg^{-1} \cdot h^{-1}$)	Source
Daphnia magna	planktonic	⋯	0.304–1.12	Scavia and Gardner (1982)
Corophium volutator	marine benthos	0.1–1.9	0.009–0.342	Hawkins and Keizer (1982)
Chironomus sp.	lake benthos	1.3–6.5	0.983–1.675	Tatrai (1982)
Tubificidae	lake benthos	0.2–1.0	0.118–0.151	Gardner et al. (1983)
Chironomidae	lake benthos	0.1–1.5	0.163–0.206	Gardner et al. (1983)
Ephemeroptera	stream benthos	0.4–1.5	0.053–1.039	this study
Chironomidae	stream benthos	0.1–0.6	0.096–1.241	this study
Cryptolabis sp.	stream benthos	0.1–0.3	0.187–1.904	this study

feeding (=collector) invertebrates (range = 100–75 000 $mg \cdot g^{-1} \cdot d^{-1}$).

Ingestion calculated from Eq. 1 may be converted to AFDM units for comparison with data of Fisher and Gray (1983), assuming foods average 4.2% N (mean N content of particulate organic matter in drift from seven dates; Grimm 1985) and insect DM is 85% organic (Grimm 1985). Organic AFDM ingestion rate per unit AFDM then is 94 $\mu g \cdot mg^{-1} \cdot h^{-1}$, which is slightly below the range of ingestion values reported by Fisher and Gray*(105–251 $\mu g \cdot mg^{-1} \cdot h^{-1}$). Efficiencies of utilization of ingested N were much higher than organic matter efficiencies. Assimilation efficiency ($AE = A/I$, A calculated using Eqs. 1–3) for N was 37–71% (depending on which egestion estimate was used) compared with 7–14% for organic matter, while utilization efficiency ($UE = U/I$) for N was 27%, compared with growth efficiencies of 2–11% for organic matter. Macroinvertebrates in Sycamore Creek thus act as a sink for N to a substantially greater extent than for organic matter.

Ingestion of nitrogen per unit snail AFDM by *Physa virgata* was 2.46 $\mu g \cdot mg^{-1} \cdot h^{-1}$ compared with organic matter ingestion of 73.5 $\mu g \cdot mg^{-1} \cdot h^{-1}$ (Fisher and Gray 1983). By dividing N ingestion rate by organic matter ingestion rate, the percentage N of the snail's food was calculated to be 3.3% of AFDM. Percentage N of algae, the principal food of these grazers, ranges from 3.2 to 7.0% ($n = 23$; Grimm 1985); the calculated value falls within, but at the lower end of, this range. Dry mass egestion rates per unit AFDM (90–116 $\mu g \cdot mg^{-1} \cdot h^{-1}$) were twice as high as the 51.5 $\mu g \cdot mg^{-1} \cdot h^{-1}$ reported by Fisher and Gray (1983) for *P. virgata*. Their value was in organic mass rather than DM units and therefore was lower. N egestion and excretion per unit AFDM together accounted for 32–51% of ingested N, and the remaining 49–65% was attributed by difference to utilization (1.17–1.57 $\mu g \cdot mg^{-1} \cdot h^{-1}$). Comparison with AFDM-specific growth rates of 6.2–7.3 $\mu g \cdot mg^{-1} \cdot h^{-1}$ obtained by Fisher and Gray (1983) suggests that snail organic mass is ≈20% N, which is obviously an overestimate; published values for molluscs range from 4 to 9% N (Bowen 1979). Unmeasured loss of N through nonfecal wastes may account for my overestimate of utilization using Eq. 1. Fisher and Gray (1983) found that ≈20% of wastes produced by *P. virgata* were mucus or dissolved organic materials. Nitrogen contents of these materials are unknown. Excretion also may have been slightly underestimated since only ammonia N was measured. The predominant form of N excreted by aquatic molluscs is ammonia (Campbell and Bishop 1970), but some urea is excreted as well (Friedl 1974).

Significance of consumers to nitrogen dynamics in the stream ecosystem

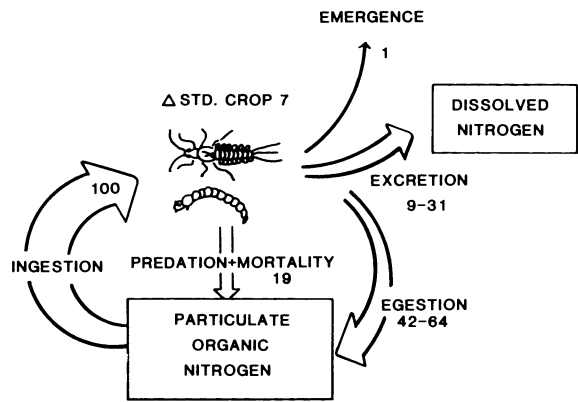To evaluate the significance of N budgets of collector-gatherer macroinvertebrates to ecosystem dynam-

FIG. 4. Fate of nitrogen ingested by the collector-gatherer macroinvertebrate community in Sycamore Creek during a 20-d postflood successional period. Predation plus mortality was calculated as utilization minus emergence plus measured change in standing stock (the latter from Grimm 1987).

ics, I compared N flow through the community with its utilization by the entire stream ecosystem. Data on rate of increase of invertebrate standing stock are available for a 20-d successional period that includes diel studies I–III (August–September 1981) of Grimm (1987); this postflood period was used as the basis for comparison of community with ecosystem nitrogen utilization. During this period, algal standing crops measured as chlorophyll *a* increased from 82.5 to 295.0 mg/m^2, and those measured as AFDM increased from 79.1 to 144.7 g/m^2; invertebrate standing stocks increased from 32 000 to 108 000 individuals/m^2, and the DM represented by those individuals from 1.19 to 6.94 g/m^2; total nitrogen retention increased from 100 to 400 $mg \cdot m^{-2} \cdot d^{-1}$. Chironomidae and the mayfly *Leptohyphes packeri* dominated the fauna during this period (>95% of numbers and biomass).

Possible fates of nitrogen ingested by consumers include transformation of particulate N to dissolved inorganic N (excretion), return of particulate N to the detritus pool via egestion, and production of animal tissue. Of nitrogen converted to macroinvertebrate biomass, only a fraction is seen as an increase in stream standing stock; the remainder emerges from the stream as adult insects, is transferred to higher trophic levels via predation, or is returned to the particulate N pool via nonpredatory mortality. During the 20-d successional period in Sycamore Creek, 27% of N ingested by the collector-gatherer macroinvertebrate community was converted to animal biomass, but only 26% of this (7% of ingested N) remained in the stream as increased macroinvertebrate community biomass and 1% emerged (Fig. 4). Nineteen percent of ingestion (70% of utilization) was lost to predatory and nonpredatory mortality. Finally, 9–31% of nitrogen ingested was released as ammonia N via excretion. This is potentially the most significant transformation caused by macroinvertebrate consumption, since excreted N is in a form readily used by autotrophs.
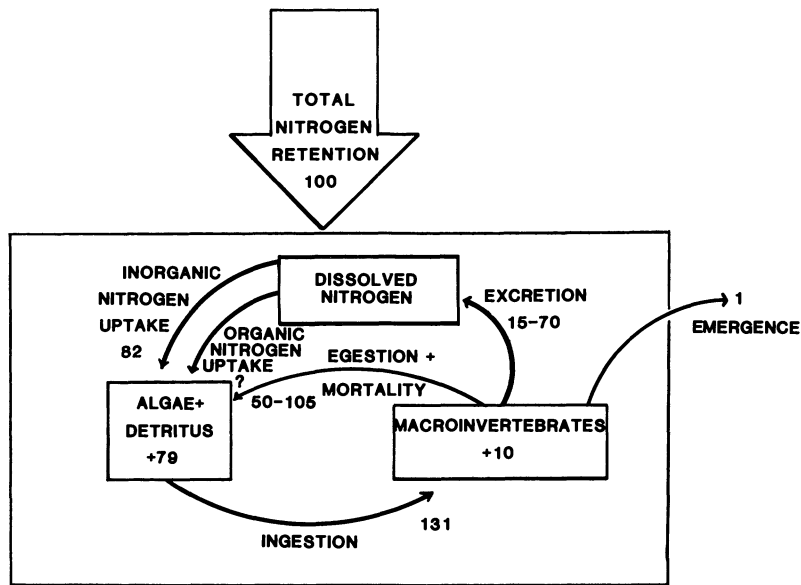
Fig. 5. Internal fluxes of nitrogen in the Sycamore Creek stream ecosystem during a 20-d postflood successional period. All fluxes related to mean rate of total nitrogen retention (Grimm 1987), which is set equal to 100%.

A major pathway of N transformation was egestion, which accounted for 42–64% of ingested N. Studies of nitrogen release during decomposition of insect feces would aid in understanding the importance of this recycling vector to ecosystem N dynamics. Several authors have pointed out that insect feces provide an abundant and reliable high-quality food resource for collector-gatherers and filter feeders (Grafius and Anderson 1979, Ward and Cummins 1979, Shepard and Minshall 1981, 1984a, b, Fisher and Gray 1983). Daily fecal production of three species studied by Ladle and Griffiths (1980) was equivalent to 1% of inorganic plus organic DM of sediments in the study stream. In Sycamore Creek, macroinvertebrates ingest more food each day than is produced by autotrophs and up to 30% of total organic matter in the stream; however, assimilation is low. Reingestion of feces is clearly necessary to support collector macroinvertebrate secondary production (Fisher and Gray 1983). Some nitrogen in feces is mineralized or leached and may become available to primary producers. On the other hand, remaining material may be colonized by bacterial decomposers and its quality (e.g., N content) improved through N immobilization (Fisher and Gray 1983). In laboratory studies, Grimm (1985) showed that nitrogen as a percentage of dry mass in feces of omnivorous fish and snails increased through 2 d of incubation in stream water, but later declined. Nitrogen enrichment or other improvements in food quality also have been reported for feces of the prosobranch snail, *Hydrobia* (Newell 1965), the amphipod *Hyalella* (Hargrave 1970, 1975), and ampharetid polychaetes (Taghon et al. 1984). Several species of lotic insects selected or associated to some degree with feces when offered a choice among similar-sized foods (Shepard and Minshall 1984b), and

the amphipod *Hyalella* preferred feces that had been "conditioned" by bacterial colonization (Hargrave 1970, 1975).

Substantial fractions of particulate transport in many streams may be derived from activities of macroinvertebrates. Experimental elimination of insects from a forested Appalachian stream resulted in significant declines in particulate transport compared with a reference, untreated stream (Wallace et al. 1982). Recovery of predisturbance particulate export rates paralleled shredder insect recolonization, suggesting that feeding activities of shredders, which reduce coarse particles to fine ones, generated much of the transported seston (Wallace et al. 1986). In Sycamore Creek, insects' feces are much the same size as their food and thus may not contribute substantially to export. On the other hand, rates of N egestion may be as high as 504 mg·m^{-2}·d^{-1} (Table 1), while net export of particulate N ranges only from 58–223 mg·m^{-2}·d^{-1} (Grimm 1987). In experimental streams, presence of grazing snails had no effect on seston transport rates, but did increase the proportion of benthic particulate organic matter and nutrients transported downstream (Mulholland et al. 1983). Similar studies in experimental heterotrophic streams indicated that leaf-shredding snails increased loss rates of organic matter through downstream export (Mulholland et al. 1985).

The mean rate of total nitrogen retention by the stream ecosystem over the 20-d period was used as a reference for assessing the contribution of macroinvertebrate community N fluxes to whole-ecosystem N utilization. Total N retention, measured at the beginning and end of the 20-d period as the difference between hydrologic inputs and outputs over 24 h, averaged 250 mg·m^{-2}·d^{-1} (Grimm 1987). If ecosystem N

retention is set at 100%, ingestion by macroinvertebrates was 131%; much of this was returned to the particulate N pool by egestion and mortality (Fig. 5). Thus a large fraction of N retained is "processed" by macroinvertebrates, supporting Fisher and Gray's (1983) contention that collectors reingest feces to support their high secondary production. Of total nitrogen retention, 10% appeared in increased macroinvertebrate standing stock, compared with 79% retained by algae + detritus. Losses of N from the stream via insect emergence represented a small fraction (1%) of nitrogen retention. Finally, an amount of nitrogen equivalent to at least 15%, but as much as 70%, of that retained by the stream is recycled back to primary producers as excreted ammonia. This ammonia is readily assimilated by autotrophs, which are often nitrogen-limited (Grimm and Fisher 1986). Rapid spinning of the cycle thus may result in increased primary production. The significance of this recycling vector depends on which estimate more accurately reflects natural excretion rates. Even if 15% is the better estimate, macroinvertebrates are clearly an important component of the nitrogen cycle in this desert stream.

Role of macroinvertebrates during succession

I considered how macroinvertebrate excretion changes as a percentage of total N input and algal N utilization to evaluate successional changes in the role of these organisms (Table 3). Total N inputs (Grimm 1987) include hydrologic inputs of all forms of nitrogen, and algal N utilization is calculated for each study from empirical relationships of algal uptake vs. nitrogen concentration and chlorophyll a standing crop (Grimm 1985). By both measures, the significance of macroinvertebrates to ecosystem nitrogen dynamics increases over successional time. Total N input and algal N utilization remain constant or even tend to increase with time since disturbance, thus the importance of collector-gatherers increases because their excretion rate rises over time. Insect excretion can potentially provide up to 20% of N inputs and all of the N utilized by algae at later stages of succession. The contention of others that influence of consumers on ecosystems is potentially greater than can be measured solely by their contributions to energy flow (Chew 1974, Kitchell et al. 1979, Merritt et al. 1984) is substantiated for this stream. In addition, by this measure the role of collector-gatherer macroinvertebrates increases over successional time. Few other studies have examined changes in consumer role during succession, although terrestrial ecologists have hypothesized that herbivorous terrestrial insects can accelerate plant succession through their effects on nutrient cycling (Schowalter 1981) and community structure (Brown 1984, 1985). This has been suggested (Lubchenko and Gaines 1981) and experimentally verified (Breitburg 1985) for marine intertidal systems as well. In laboratory streams, preferential grazing by snails on early successional algal

TABLE 3. Collector-gatherer macroinvertebrate excretion as a percentage of total nitrogen input and algal nitrogen utilization at several successional stages (days after flood) in Sycamore Creek. Low and high estimates of excretion are for unfed and fed animals and are expected to bracket natural rates.

Days after flood	Excretion as % of:			
	total N input		algal N utilization	
	Low	High	Low	High
2	0.4	1.4	11	41
5	0.6	2.4	8	34
7	1.0	5.1	8	40
11	5.8	27.2	42	198
27	4.2	14.1	27	120
28	0.7	2.9	31	132
>90	5.2	17.8	···	···
>90	1.6	19.3	···	···

species accelerated succession to later forms (Sumner and McIntire 1982).

Significance of collector-gatherers to desert stream nitrogen dynamics may also be evaluated using a measure of the linear stream distance required for 100% of nitrogen input to the stream to be converted to biomass (as N utilization) or emergent adults. This measure is similar to the nutrient spiralling parameter "uptake length" (Newbold et al. 1981), and may be termed an "equivalent uptake distance" for consumers. The shorter the distance, the more tightly nitrogen is cycled in the stream segment, rather than being transported downstream. Obviously the equivalent uptake distance must be longer than the true uptake length for nitrogen, since only a fraction of N taken up from the water column is used in production of insect biomass. Nitrogen input (grams per day) was divided by N utilization or emergence (grams per square metre per day), then divided by mean stream width (in metres) to obtain this distance. In early stages of postflood succession 10 km of stream were required for 100% of N input to be converted to macroinvertebrate biomass (Fig. 6), but <1 km was required in late stages. The length of stream required to convert total N input to emergence was much longer, but also declined through succession from 100 to 200 km to <20 km (Fig. 6). By 90 d postflood, 100% of N input was ingested by collector-gatherer macroinvertebrates in <200 m of stream, converted to growth in 700 m, and lost from the stream ecosystem in emergent adult insects in just 15 km.

The pattern of decline in equivalent uptake distances for consumers (Fig. 6) suggests that nitrogen spiralling length, or at least the component of spiralling length associated with consumer utilization, should decrease with time since disturbance. Stream ecosystem nitrogen retention increases from early to middle stages of succession but then declines in late stages (Grimm 1987), following predictions of a model of ecosystem nutrient retention during succession developed for for-
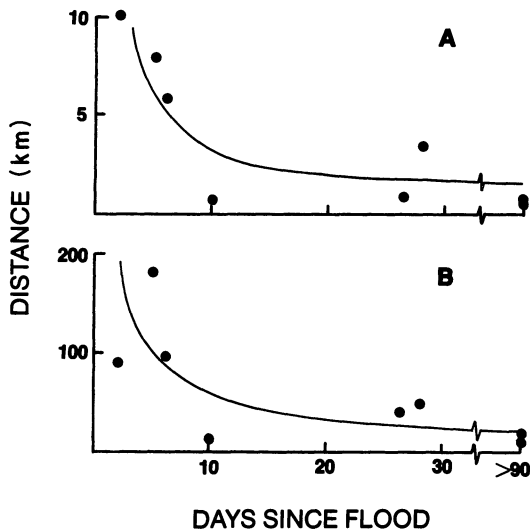
FIG. 6. Equivalent uptake distances for insect consumers in Sycamore Creek, defined as the distances required for 100% of nitrogen input to be converted to (A) immature and (B) adult insect biomass as a function of successional time.

est ecosystems (Vitousek and Reiners 1975). Spiralling length reflects the degree of intrasystem cycling of nutrients, whereas retention is a measure of differences between nutrient inputs and outputs. The two measures are not necessarily related. Desert streams are most retentive during middle stages of succession, while their spiralling length, if it is proportional to the equivalent uptake distance presented here, decreases monotonically with successional time. Significance of insect consumers to nitrogen dynamics of desert streams, based on the equivalent uptake distance, is highest in late stages of succession.

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