Research Article

Energy flow and elemental concentrations in the Steina River ecosystem (Black Forest, Germany)

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Abstract. Considering food web energetics and elemental cycling together allows the testing of hypotheses about the coevolution of biological systems and their physical environment. We investigated the energy flow and the distribution of 25 elements in the Steina River.

We constructed an annual energy flow network and estimated the emergy (“embodied energy” that includes all the energy involved in a process) contributions of resources sustaining the system. Furthermore, we measured the concentration of various macronutrients, essential elements, and heavy metals in the physical environment and trophic compartments. Finally, we examined the hypothesis of a positive relationship between the “rarity” of an element and its tendency to bioaccumulate. To do so, we used transformity, the relative energy input required to sustain a compartment’s net production or the concentration differential of an element between the living community and the physical environment.

Key words. Stream ecosystem; energy flow; elements; emergy synthesis; cycling.

Introduction

Two major aspects of ecosystem function are trophic web energetics and element cycling (Pomeroy, 1970; Odum, 1983; Williams and da Silva, 1996). They are tightly in-

The resulting energy flow network is one of the most complete available for streams. In the Steina, over 99% of the energy input is transported through the system without being processed. Dissolved inorganic matter and sunlight are the largest inputs, but uptake efficiency is much higher for dissolved and particulate organic matter. Transformities of trophic compartments and elements span 6 to 7 orders of magnitude.

The tendency to bioaccumulate was as predicted for most elements, with macronutrients showing no accumulation and heavy elements accumulating in high-transformity compartments. However, Na and K were found at highest concentrations in consumers, and Pb, Ga, and Cd in algae. Improved estimates may become possible as more knowledge is available on ecosystem flows. We suggest further ways of testing hypotheses about strategies of element processing.

terrelated: life systems use energy to maintain a concentration of elements different from concentrations in the non-living environment, through selective uptake, cycling, distribution, and biological use of the elements. In turn, the availability of the various elements regulates the rates of important ecological processes, such as succession (Pomeroy, 1970; Odum, 1983, 1991; J. L. Meyer et al., 1988; Williams and da Silva, 1996; Brett and Goldman, 1997).

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Investigating energetics and elemental cycling together should make it possible to address important questions on ecological function. For example, the energy involved in processing by a biological system may be expected to differ widely among elements. For simplicity, "processing" here means the exclusion, degradation, elimination, and immobilization (and thus bioaccumulation) of substances, and response to toxicity. The amount of metabolic energy needed for processing should be relatively low, per unit mass, for common elements, and relatively high for rare elements. Macronutrients (e.g., C, N, P) are common, used in large quantities, readily processed by organisms, and incorporated in biological support structures. Essential elements (metals such as Cu, Zn, Se, Mg, Mn) are rarer, have specific functions in metabolic processes as components of enzymes, chromoproteins and hormones, and are essential in small quantities. Rare elements such as heavy metals may not encounter any mechanism of processing and may be toxic even at low doses. They occur in variable concentrations and their availability is not reliable, so that biological systems have not evolved a use for them. They tend to be sequestered in tissues and organs specialized in storage and excretion; their elimination is more energy-consuming than the elimination of excess macronutrients (Knight, 1981; da Silva and Williams, 1991; Tessier and Turner, 1995; Williams and da Silva, 1996; Genoni, 1997).

In an ecosystem, the fate of elements will depend on differences in processing. If an element is rare, organisms of lower trophic levels may exclude it. Whatever they do take up, however, is more readily available, and thus less unusual, to organisms of higher trophic levels (biomagnification). Alternatively, a rare substance may be taken up directly from the physical environment by organisms of higher trophic levels (bioconcentration). Indeed, rare elements bioaccumulate more than common elements, through biomagnification or bioconcentration (Odum, 1990; Genoni and Montague, 1995).

Investigating these relationships at the level of an ecosystem, then, requires consideration of both trophic energetics and elemental cycling. Ecosystem studies, however, often emphasize either energetics (Odum, 1957; Teal, 1957; Tilly, 1968; Mann et al., 1972; Carrer and Opitz, 1999) or elemental concentrations and cycling (Ball and Hooper, 1963; Elwood and Nelson, 1972; Newbold et al., 1982a, 1982b). A few studies combined both perspectives, but dealt with only a few macronutrients (Hall, 1972; Fisher and Likens, 1973; Fisher, 1977; Cushing and Wolf, 1982; Edwards and J. L. Meyer, 1987; Dalsgaard, 1997) or heavy metals (Knight, 1981; Niederlehner and Cairns, 1992; Stewart et al., 1993). In a previous study covering various ecosystems and elements, a positive correlation was found between the "hierarchical position" of elements, from common to rare, and their tendency to bioaccumulate (Genoni and Montague,

1995). That, however, was a review of published studies not aimed at relating bioaccumulation to energy relationships, and hence differing in their data structure.

Here we investigate the energetics and elemental distribution of a stream ecosystem, the Steina River, Black Forest, Germany. We formulated a conceptual model of energy flow (sources, internal exchanges and sinks) and constructed an annual energy flow network with published and unpublished data. Furthermore, we measured the concentration of 25 elements of geological or anthropogenic origin differing in rarity (macronutrients, essential elements and toxic elements) in the physical environment (water, sediment) and trophic compartments.

Finally, we examined the hypothesis of a positive correlation between the "rarity" of an element and the energy required for processing it, and hence its tendency to bioaccumulate. To do so, we used the notion that the relative amount of energy input required to sustain a trophic compartment's net production (or, in similar fashion, the concentration differential of an element) quantifies its "hierarchical position". This relative "energy value" has been expressed in solar equivalent joules used per joule and has been called *transformity* (Odum, 1996). To measure transformities of parts of a system as different as trophic levels or elements, obviously the energy inputs and transfers in the process need to be known, as detailed in the Methods section and in the Appendices. We compared the transformity of elements with that of the trophic compartments in which their concentrations were highest.

Materials and methods

Study site

The Steina River is a third-order, gravel-bed, canopy-covered mountain stream in the Black Forest, Germany. The study site is a 400-m long, 3-m wide (1200 m²) reach located 13 km from the headwaters (47°47' N, 8°19' E, altitude 700 m). The average slope is 1.6%. The average discharge is 0.70 m³/s, and daily values vary over two to three orders of magnitude, with spates occurring several times a year. Mean cross-sectional area at a site where hydraulic measurements have been conducted was 0.52 m/s, and mean depth 0.13 m when discharge was 0.103 m³/s (Mutz, 1989). Current velocities in riffle areas varied from 0.2 to 2.5 m/s (Pusch, 1993). This system has been the subject of many investigations (Gessner, 1987; Bötsch, 1988; Semmler, 1988; Gädtgens, 1989; Kussmaul, 1990; Meyer et al., 1990; Ruhrmann, 1990; Deller, 1991; Meyer, 1992; Pusch and Schwoerbel, 1994; Meyer and Pöpperl, 2003; Meyer and Pöpperl, unpubl.).

Energy flow network

To construct an annual energy flow network (inputs, transfers and exports), we formulated a moderately complex conceptual model of the ecosystem. The boundary of the system includes the 400-m by 3-m study site. Energy sources include sunlight, dissolved inorganic matter (DIM), coarse particulate organic matter (CPOM, i.e., organic particles > 1 mm), and dissolved organic matter (DOM). Non-living compartments include storages of DIM, CPOM, and FPOM & DOM (FPOM: fine particulate organic matter, < 1 mm) in the system. Living compartments (see Meyer and Pöpperl, 2003) include epilithic algae, scrapers (mostly Ephemeroptera larvae and molluscs), collectors (mostly larvae of Trichoptera, Ephemeroptera, Oligochaeta and Diptera), shredders (mostly Amphipoda, Isopoda, and larvae of Plecoptera, Trichoptera and Tipulidae), filter-feeders (mostly larvae of Hydropsychidae and Simuliidae), carnivorous invertebrates (mostly Turbellaria, Acari and larvae of Perlidae), carnivorous fish (trout, *Salmo trutta* spp., and sculpin or river bullhead, *Cottus gobio*), and microorganisms (bacteria, fungi, protozoans) and meiofauna (mostly nematodes). The latter two types of organisms are tightly asso-

ciated in the microbial loop. Sinks include respiration of the various organisms, export of DIM, CPOM, DOM and FPOM, emergence of insects, and capture of fish by aquatic birds (grey heron, *Ardea cinerea*) and fishermen. Energy flow between compartments include shredding of CPOM into FPOM, microbial mineralization, nutrient uptake, detritivory, herbivory, and carnivory.

Having defined 11 compartments and their relationships, we constructed an annual balance of the energy flows (Fig. 1). This was expressed in units of kilojoules per square meter per year. The estimates for flows were provided in good part by published data (Gessner, 1987; Bötsch, 1988; Semmler, 1988; Gädtgens, 1989; Deller, 1991; Meyer et al., 1990; Ruhrmann, 1990; Meyer, 1992; Pusch and Schwoerbel, 1994). Where expressed in units of carbon mass, estimates were converted to kilojoules with factors given by Cummins and Wuycheck (1971) and Meyer (1992). We completed the energy model by balancing the flows and through published information on similar ecosystems. These systems included the Necker River, a prealpine gravel bed stream in Switzerland (Naegeli and Uehlinger, 1997), and Bear Brook in the Hubbard Brook Forest, NH, U.S.A., also a small

Figure 1. Estimated energy inputs and flows in the Steina River (rounded-up values, in units of $\text{kJ}/(\text{m}^2 \cdot \text{yr})$), based on published and unpublished data. Ground symbols = heat of respiration.

canopy-covered, detritus-based river at about the same latitude, and similar in terms of discharge (Fisher and Likens, 1973; Gosz et al., 1978). The detail of the procedure is shown in Appendix 1.

Some assumptions and simplifications in the model were: (a) No net input/output of organisms occurs between up- and downstream boundaries; (b) Predation by birds on insects is negligible; (c) Aufwuchs consists only of algae; (d) FPOM and DOM were aggregated; and (e) Decomposers and the microbial loop were aggregated.

Transformity of the ecosystem's compartments

To calculate the transformities of each compartment, we used the guidelines given by Odum (1983, 1996). Generally, including the processes that contribute to sustaining a resource flow (the so-called "externalities") allows one to estimate its solar equivalent energy value (or *emergy*, a contraction of "embodied energy"; Scienceman, 1987; Odum, 1996; Brown, 2000). The *emergy* of a trophic compartment divided by the sum of its outflows (excluding respiration) is the transformity of this compartment's outflow, i.e., of its contribution to the ecosystem (Tennenbaum, 1988). The details of the procedure used here are shown in Appendix 2.

Concentrations of elements

We measured the concentration of 25 bulk elements and trace metals by sampling once seasonally each compartment of the trophic web, water, and sediment between April 1995 and February 1996. We averaged the concentrations in sediment and water (weighed by the mass of these two compartments) to obtain a concentration for the physical environment, and also with the living compartments to obtain a total for the living community. The annual average concentration of the 25 elements was calculated from the seasonal samples. For C, a DOC analysis was performed by high-temperature catalytic pyrolysis (680°C; 0.5% Pt on Al₂O₃; Shimadzu). For the analysis of N and P, samples were digested by K₂S₂O₈ in a closed glass flask at 120°C and 1 bar, for 2 h. The oxidation products nitrate and phosphate were determined by standard procedures with an air-segmented continuous flow analyzer (Technicon Auto-Analyzer II). For the remaining elements, freeze-dried samples were ground in an agate mortar and placed in teflon beakers. Extraction was done in 4 ml high purity HNO₃ 65% and 1 ml H₂O₂ 30% in a microwave oven for 20 min. Nanopure water was then added to achieve 25 ml. For bulk elements (Ca, Al, Mg, Na, Fe, K, and Mn), an analysis by inductively-coupled plasma optical emission spectrometry (ICP-OES) was done with a Spectroflame instrument (Spectro Analytical Instruments). Trace elements (Li, Zn, Ba, Sr, Cu, Ni, Cr, Pb, Co, Ga, Cd, In, Tl, Ag, and Bi) were measured by in-

ductively-coupled plasma mass spectrometry with an ELAN 5000A ICP-MS (Perkin Elmer/Sciex). We excluded from the analysis elements with concentrations below detection, requiring analytical techniques not available in our laboratory, or for which the ICP methods yielded only semi-quantitative data.

Transformities of elements

To calculate the transformity of each element, the *emergy* input to the ecosystem that drives the cycling of the elements was divided by the chemical energy actually cycling between the physico-chemical environment and the living community (Genoni and Montague, 1995). For the former, the entire *emergy* input to the system (i.e., the sum over all energy sources) was assumed to contribute to producing the final concentrations. For the latter (chemical energy), the energy in the concentration process was assumed to be at least equal to the change in Gibbs free energy associated with the concentration differential between physical environment and living community (Genoni and Montague, 1995). An example of this procedure is shown in Appendix 3.

Comparison of the transformities of elements and of compartments

Finally, to test the hypothesis of a positive correlation between the rarity of an element and its tendency to bioaccumulate, we compared the transformities of elements to the transformities of the corresponding trophic level of highest concentration. An example of this procedure is shown in Appendix 3.

Results

All results are rounded to three significant digits to avoid giving a false sense of accuracy, and to make comparisons easier.

Annual energy flow network

The estimated energy flow network of the study reach is shown in Figure 1. The total annual energy that sunlight, DIM, CPOM, and DOM make available to the ecosystem is $92400 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr})$ (sum of the terms of Table 1, I). DIM and sunlight are the largest energy inputs at $90900 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr})$ and $1470 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr})$, respectively. However, over 99% of these resources is transported through the system without being processed by the community, in particular DIM (0.000007% being taken up) and sunlight (0.002%). In contrast, the uptake efficiency is 20% for DOM and 46% for CPOM. Hence, of the *ca.* $30000 \text{ kJ}/(\text{m}^2 \cdot \text{yr})$ actually taken up (sum of the *sunlight*

Table 1. Energy contribution, emergy contribution and transformity of the sources and compartments of the Steina River ecosystem. See Appendices 1 and 2 for the calculation of these values.

	Energy (kJ/(m ² · yr))	Emergy (S.E. kJ/(m ² · yr))	Transformity (S.E. J/J)
<i>I. Sources</i>			
Sunlight	1470 · 10 ³	1470 · 10 ³	1
DIM	90900 · 10 ³	815000 · 10 ³	9
CPOM	44 · 10 ³	815000 · 10 ³	19 · 10 ³
DOM	44 · 10 ³	815000 · 10 ³	19 · 10 ³
<i>II. Non-living resources</i>			
Sunlight	3 · 10 ³	3 · 10 ³	1
Allochthonous DIM	6	58	9
Allochthonous CPOM	20 · 10 ³	375000 · 10 ³	19 · 10 ³
Allochthonous DOM	9 · 10 ³	163000 · 10 ³	19 · 10 ³
CPOM (internal storage)	21 · 10 ³	382000 · 10 ³	18 · 10 ³
FPOM-DOM (internal storage)	30 · 10 ³	570000 · 10 ³	19 · 10 ³
<i>III. Living compartments</i>			
Algae	1 · 10 ³	3 · 10 ³	2
Shredders	3 · 10 ²	8440 · 10 ³	30 · 10 ³
Decomposers/microbial loop	3 · 10 ³	92300 · 10 ³	32 · 10 ³
Filter-feeders	3 · 10 ²	10900 · 10 ³	36 · 10 ³
Collectors	4 · 10 ³	12900 · 10 ³	42 · 10 ³
Scrapers	5 · 10 ³	20400 · 10 ³	44 · 10 ³
Fish	135	16900 · 10 ³	125 · 10 ³
Carnivorous invertebrates	55	8950 · 10 ³	163 · 10 ³
Adult insects	21	6200 · 10 ³	301 · 10 ³

and *allochthonous* terms in Table 1, II), CPOM and DOM constitute by far the highest input (over 98%). The detrital pathway contributes 2660 kJ/(m² · yr) to the food web (sum of the *CPOM*, *FPOM* & *DOM*, and *decomposers* flows to consumers in Fig. 1), whereas the algal pathway contributes only 543 kJ/(m² · yr) (sum of the *algae* flows to consumers in Fig. 1).

The estimated total emergy of the sources is $977 \cdot 10^9$ S.E. kJ/yr (eqs. 42–45, Appendix 2). DOM and CPOM have transformities that are higher by several orders of magnitude than DIM or sunlight ($19 \cdot 10^3$ S.E. J/J for DOM and CPOM each vs. 1 S.E. J/J for sunlight and 9 S.E. J/J for DIM; Table 1, I). They are more efficiently retained in the system (Fig. 1), and their actual emergy contribution to the community is significantly higher than that of sunlight or DIM: $375000 \cdot 10^3$ S.E. kJ/(m² · yr) for CPOM, $163000 \cdot 10^3$ S.E. kJ/(m² · yr) for DOM, 58 S.E. kJ/(m² · yr) for DIM, and $3 \cdot 10^3$ S.E. kJ/(m² · yr) for sunlight (Table 1, II).

The energy flow is further concentrated along the food web, with carnivore production being one order of magnitude smaller than the production of decomposers/microbial loop, and the transformity thereof 1 order of magnitude higher (Fig. 1, Table 1, III).

Total system respiration is 18200 kJ/(m² · yr) (eq. 18c, Appendix 1, and sum of the *respiration* terms in Table 3), i.e., 61% of total inputs.

Transformities of food web compartments

Estimated transformities span 6 orders of magnitude. There appear three clusters or trophic levels (Table 1): The algae (2 S.E. J/J), the detritivores/herbivores ($30\text{--}44 \cdot 10^3$ S.E. J/J) and the carnivores ($125\text{--}300 \cdot 10^3$ S.E. J/J).

Concentrations of elements

The 25 elements vary widely in their concentrations, which span 6 orders of magnitude in the physical environment (from 0.000015 µg/g for Bi to 10.5 µg/g for C) and in the community (from 0.0000003 µg/g for Bi to 0.06 µg/g for N) (Fig. 2 and Table 2).

Transformities of elements

Estimated transformities vary over 7 orders of magnitude, from $307 \cdot 10^3$ S.E. J/J for C to $461 \cdot 10^{10}$ S.E. J/J for Bi (Fig. 2 and Table 2). There is a general inverse relationship between the transformity of elements and their concentration in the community and environment (Fig. 2).

Comparison of the transformities of elements and compartments

Average annually, the elements of highest transformity (Bi, Tl, Ag and In) had highest concentrations at the level of detritivores/herbivores, and not of carnivores (Table 2). Most elements of lower transformity showed no accumu-

Table 2. Concentrations ($\mu\text{g/g}$) of 25 elements in trophic compartments, in the community (average of all compartments, weighted by the biomass of each), and in the physical environment (average of water and sediment, weighted by the mass of each) in the Steina River. Data are averages of 4 seasonal samples. Transformities (S.E. J/J) of the elements are also indicated (see Appendix 3 for their calculation).

	Algae	Shredders	Filter-feeders	Collectors	Scrapers	Carnivorous invertebrates	Fish	Community	Physical environment	Transformity of the element
C	341000.0	435000.0	440000.0	545842.4	548000.0	224000.0	170000.0	0.010	10.53	$307 \cdot 10^3$
N	31900.0	43000.0	49000.0	108000.0	77500.0	68900.0	91500.0	0.063	1.36	$1130 \cdot 10^3$
P	2980.0	4320.0	5750.0	11800.0	8550.0	8070.0	7760.0	0.0060	0.15	$27000 \cdot 10^3$
Al	12200.0	739.0	2330.0	1890.0	1310.0	592.0	254.0	0.0049	0.52	$33000 \cdot 10^3$
Ca	15800.0	7170.0	409.0	2760.0	435.0	376.0	651.0	0.0066	1.71	$40400 \cdot 10^3$
Fe	14600.0	299.0	1670.0	779.0	784.0	419.0	179.0	0.0056	0.79	$61900 \cdot 10^3$
Mg	5320.0	1310.0	1640.0	4710.0	1420.0	1400.0	511.0	0.0026	0.81	$62300 \cdot 10^3$
Na	804.0	3850.0	5360.0	10600.0	3480.0	3370.0	1380.0	0.0021	1.40	$80200 \cdot 10^3$
Mn	3030.0	33.7	355.0	47.5	82.0	90.1	12.5	0.0011	0.02	$246000 \cdot 10^3$
K	485.0	755.0	1440.0	4100.0	826.0	906.0	449.0	0.00073	0.26	$373000 \cdot 10^3$
Zn	324.0	150.0	186.0	320.0	205.0	219.0	81.4	0.00021	0.0056	$1670000 \cdot 10^3$
Ba	697.0	361.0	160.0	85.8	43.4	70.4	6.5	0.00030	0.025	$27200000 \cdot 10^3$
Li	27.8	15.7	19.4	22.4	11.4	5.4	0.9	0.000014	0.0027	$3070000 \cdot 10^3$
Cu	126.0	53.8	33.4	53.0	52.3	35.6	6.1	0.000061	0.0012	$5250000 \cdot 10^3$
Sr	188.0	142.0	21.0	42.6	29.8	13.9	10.6	0.000087	0.010	$6120000 \cdot 10^3$
Ni	51.1	4.2	6.6	12.5	4.0	6.9	1.5	0.000021	0.0014	$16100000 \cdot 10^3$
Cr	36.6	4.5	10.5	13.9	3.8	3.1	1.7	0.000016	0.0017	$19900000 \cdot 10^3$
Pb	77.9	6.3	15.2	20.0	9.3	5.6	2.0	0.000032	0.0016	$35900000 \cdot 10^3$
Co	12.8	1.8	3.3	6.5	2.3	1.6	0.6	0.0000056	0.00060	$62700000 \cdot 10^3$
Cd	12.1	2.9	2.4	10.0	12.0	3.9	0.8	0.0000066	0.00016	$87800000 \cdot 10^3$
Ga	7.7	1.5	2.4	4.0	0.9	1.5	0.5	0.0000035	0.00049	$124000000 \cdot 10^3$
In	0.6	1.5	1.6	4.9	0.5	1.6	0.4	0.00000084	0.00024	$916000000 \cdot 10^3$
Ag	0.7	0.3	0.6	2.8	0.3	0.3	0.2	0.00000053	0.000031	$1150000000 \cdot 10^3$
Tl	0.8	1.4	2.0	3.8	0.4	1.3	0.4	0.00000087	0.00025	$1570000000 \cdot 10^3$
Bi	0.2	0.4	1.1	0.7	0.2	0.2	0.1	0.00000026	0.000015	$4610000000 \cdot 10^3$

Figure 2. Concentrations in the living community and physical environment, and transformities of elements in the Steina River.

lation beyond the trophic level of algae. This included a few heavy elements that are not known to be essential (Pb, Ga and Cd). For the bulk elements C, N and P, the concentrations were highest at the detritivore/herbivore level, though with little difference with levels in other compartments (Table 2). Among low-transformity metals, Na and K also accumulated to the detritivore/herbivore level (Table 2).

For most elements, the seasonal values for the level of highest concentration varied, but no particular pattern emerged (data not shown).

Discussion

Annual energy flow network

The estimated annual total energy inputs to the 1200-m² reach of the Steina River ecosystem is $92 \cdot 10^6$ kJ/(m² · yr). We know of no data for comparison with other rivers. Of this energy, only 30,000 kJ/(m² · yr) is taken up by the living community. This value is comparable to that for Bear Brook, NH, U.S.A., also a small canopy-covered detritus-based river, located at about the same latitude, and similar in terms of discharge (ca. 25000 kJ/(m² · yr); Fisher and Likens, 1973), and those of a few other mid-latitude rivers reviewed by Minshall (1978). Small temperate woodland streams are open systems with a high throughflow of energy (Cummins, 1974; Schwoerbel, 1994).

The estimated total emergy (solar embodied energy) that these sources represent is $4.5 \cdot 10^{15}$ S.E. kJ/(m² · yr). Retention is different between resources: DOM and CPOM, being more highly processed and concentrated forms of energy, have transformities that are several orders of magnitude higher than DIM or sunlight (Odum, 1996). Therefore, they can make higher emergy contributions (per unit mass) to the system, and indeed, they are more efficiently retained. The Steina River shares with Bear Brook (Fisher and Likens, 1973) a dominance of allochthonous detrital inputs (ca. 99% in both rivers), mostly in the form of leaf litter but with a significant contribution of DOM. This is indicative of a largely heterotrophic ecosystem, as noted previously on the basis of organic matter budgets (Ruhrmann, 1990; Gessner, 1987), and typical of mid-latitude streams that have a well-developed riparian vegetation (Cummins, 1974; Naegeli and Uehlinger, 1997). The abundance, solubility and lability of organic matter, and hence the availability of the microbial flora to shredders, collectors and decomposers, are likely the limiting step in stream metabolism (Cummins, 1974; Schwoerbel, 1994).

The autotrophic and detrital pathways converge partially at the level of the detritivorous/herbivorous insects, and completely at the level of carnivorous invertebrates and fish (Fig. 1). As a consequence of the dominance of allochthonous inputs, the detrital pathway strongly exceeds the autotrophic pathway in terms of energy, and even more strikingly so in terms of emergy (Table 1). The

Table 3. Conversion of annual flow values in units of dry mass from Meyer and Pöpperl (unpubl.; data grouped by feeding types) into energy units, as described in Appendix 1.

Uptake or respiration by ...	Uptake of ... or respiration	Dry mass g/(m ² · yr)	Energy kJ/(m ² · yr)
decomposers/ microbial loop	detritus	946.13	17475.02
	respiration	529.83	14549.13
shredders	CPOM	21.68	406.28
	algae	7.82	107.21
	decomposers	0.86	23.62
	collectors	0.20	5.49
	scrapers	0.07	1.92
	respiration	8.42	231.21
scrapers	FPOM & DOM	49.54	915.00
	algae	24.73	339.05
	decomposers	3.39	93.09
	respiration	32.13	882.29
collectors	FPOM & DOM	22.43	414.28
	algae	1.41	19.33
	decomposers	9.06	248.78
	scrapers	0.14	3.84
	respiration	10.10	277.35
filter-feeders	FPOM & DOM	15.20	417.39
	algae	4.05	55.53
	decomposers	1.27	34.87
	scrapers	1.27	34.87
	collectors	0.25	6.86
	carnivorous invertebrates	0.25	6.86
	respiration	9.37	257.30
carnivorous invertebrates	FPOM & DOM	4.52	84.70
	algae	1.58	21.66
	decomposers	0.79	21.69
	shredders	1.41	38.72
	scrapers	2.28	62.61
	collectors	1.40	38.44
	filter-feeders	1.24	34.05
	respiration	8.99	246.87
fish	algae	0.07	0.96
	scrapers	2.36	64.81
	shredders	1.80	49.43
	collectors	1.20	32.95
	filter-feeders	0.80	22.00
	carnivorous invertebrates	0.97	26.64
	respiration	3.82	82.57

dominance of the detrital pathway over the autotrophic pathway is also reflected by the much higher transformity of the decomposers/microbial loop than that of the algae ($32 \cdot 10^3$ vs. 2 S.E. J/J; Table 1).

System respiration was 61% of the energy input to the system. The respiration of the decomposers/microbial loop is in good part responsible for this high value. Present-day stream investigations account better for microconsumers other than bacteria and fungi (Schwoerbel, 1994), which may explain the difference with the value reported for Bear Brook (34%; Fisher and Likens, 1973).

Transformities of food web compartments

The energy needed to sustain a compartment is relatively low, per unit biomass, for lower trophic levels, and relatively high for upper levels (Colinvaux, 1978; Odum, 1983; Costanza and Neill, 1984). Differences between successive trophic levels in relative energy requirements often approach one order of magnitude, because at any level respiration accounts for most of the energy expenses and only a small part is transferred to the next trophic level (Odum, 1983). Here the precise gut content analyses of Gädtgens (1989), Deller (1991), and Meyer (1992) made it possible to develop a detailed model of energy relationships between functional groups of macroconsumers. There appear three trophic levels, spanning 6 orders of magnitude of transformities: The algae, the detritivores/herbivores and the carnivores (see Fig. 1).

Concentrations of elements

The set of elements investigated here is diverse in terms of concentrations and biological functions, although a few other biologically and ecotoxicologically important elements (such as Se, Hg, S and Cl) were not measured.

Transformities of elements

This diversity of elements is also reflected in the broad range of transformities, spanning 7 orders of magnitude, and representing vastly different concentrations of chemical energy. Here too, order-of-magnitude differences exist between relative energy requirements because the energy needed by life systems to maintain a concentration differential vs. its environment (by taking up or by excluding an element) depends on the kind of element. The low-transformity, bulk elements such as C, N and P are readily available in the physical environment and likely influence the ecosystem in a bottom-up fashion. At intermediate concentrations and transformities are alkali and alkaline earth metals, believed to be essential for organisms. The most concentrated forms of chemical energy are heavy metals, that occur at low concentrations in the physical environment and exert top-down control on the system. Some of them are essential elements for organisms; all of them can be toxic (Knight, 1981; Odum, 1983; Brett and Goldman, 1997; Genoni and Montague, 1995; Genoni, 1997).

Comparison of the transformities of elements and compartments

The comparison between the transformities of elements and trophic levels shows results that were partly predicted and partly surprising. The elements of highest transformity (Bi, Tl, Ag and In) bioaccumulated to high-transformity trophic compartments, but not to the highest. Most

elements of lower transformity showed no accumulation along trophic levels. For C, N and P there was no distinct bioaccumulation, and only a small concentration excess in consumers. A surprising result was that, among the heavy elements not known to be essential, Pb, Ga and Cd were found at higher concentrations in algae and, among the low-transformity metals, Na and K accumulated at the level of consumers.

There are several possible causes for these unexpected findings. First, a single sample per season of element concentrations does not allow us to account for successional changes that follow spates, and that affect elemental concentrations (Cummins, 1974; J. L. Meyer et al., 1988). Would In, Ag, Tl and Bi, for example, be found to concentrate in carnivores if sampled at a later successional stage? Second, aufwuchs provides a high surface area for adsorption (Stewart et al., 1993), an effect that may be stronger for Pb, Ga and Cd: these elements form low-spin complexes, whereas In, Ag, Tl and Bi form high-spin complexes (the spin state is the way the electrons are packed in $3d$ orbitals in the presence of different ligands, and this affects ion size; da Silva and Williams, 1991). Hence, the former are more stable and more likely to remain in aufwuchs during succession. In contrast, the latter are mobile and can be delocalized rapidly.

Third, present-day estimation of transformities in ecosystem science is still somewhat crude, and the representation of energy flow networks involves simplifying assumptions. For trophic compartments, the estimation of transformity does not account for some subsidies (water flow kinetic energy, bioturbation, cover, etc.). For elements, estimating transformity from the Gibbs free energy inherent in the concentration differential between the living community and environment accounts neither for the activation energy nor for the energy of reaction in the biochemical transformations involved (Genoni and Montague, 1995). For example, N occurs mostly as N_2 and NO_3^- in the physical environment and organic N in organisms. In our study, the underestimation of transformity for Na and K may be less than for the other metals: Na and K are present in the water as ions that can be used by biological systems, whereas other metals mostly occur as complexes (e.g., humic acids) and biological systems need to process them into the form of cell functional complexes and free ions, which requires additional energy (da Silva and Williams, 1991).

Refined estimates of transformity may be possible in the future as more knowledge becomes available on energy flows in ecosystems. Improved methods are needed especially to resolve the aufwuchs into algae and microconsumers, and the microbial loop into functional groups.

In stream ecosystems, there is a high temporal and spatial variability in energy flow, with fluctuations over seasons and years, in relation to spates and along the river

continuum. One can expect large fluctuations in the concentrations of elements in system compartments or in the sediments and water column over time and space, since these are related to energy flow. For example, in the Steina River, daily light input may vary by 3 orders of magnitude between shaded and unshaded sites, and by 2 orders of magnitude between seasons (Ruhmann, 1990). In this study, the concentrations of elements in system compartments varied by up to 3 orders of magnitude between seasonal samples, and the calculated transformity of the elements did as well (data not shown).

Conclusion

The estimated energy flow network of the Steina River ecosystem is one of the most complete available for any stream. This description of energy relationships and the carbon budget described by Meyer and Pöpperl (unpubl.) are views that should usefully complement each other (Odum, 1983; Elser et al., 1996). This whole-system approach is, in turn, complemented by detailed studies of various processes (Gessner, 1987; Bötsch, 1988; Semmler, 1988; Gädtgens, 1989; Kussmaul, 1990; Meyer et al., 1990; Ruhmann, 1990; Deller, 1991; Meyer, 1992; and Pusch and Schwoerbel, 1994). Some of the reported values await validation, but new results are unlikely to cause any significant change in estimated transformities, which span many orders of magnitude. Future studies should take into account the variability of energy flow over seasons and years as it is interrelated with elemental concentrations. Given enough time for processing by organisms, the transformity of elements should correlate with the transformity of trophic levels (Pomeroy, 1970; Genoni, 1997).

The use of systems analysis also made it possible to estimate the emergy contributions in the emergy flows sustaining the system and of the transformities of its ecological functional units and constitutive elements. This highlights the selective use of resources by the community. Similarly, it provides insight in the distribution, in a stream, of a set of elements very diverse in terms of transformity, and hence of their likelihood to bioaccumulate. Concentrations of emergy along trophic flows and in elemental cycling cover a broad spectrum, probably broader than shown here because of current limitations in the estimation of transformities. In stream ecosystems, the temporal and spatial scales of processes may vary over 16 orders of magnitude (Minshall et al., 1983; Minshall, 1988). Finally, estimates of transformity are generally of interest as a contribution to environmental policy analyses (Odum et al., 2000).

This study suggests ways of combining the interrelated perspectives of energetics and elemental cycling. It may open the way for testing hypotheses about the co-evolution of biological systems and the physical environ-

ment. Do thresholds exist below which an element may be so common that it is used wastefully, or above which an element may be too unusual to be processed by biological systems? How effective are plants at protecting the rest of the food web from toxic elements by trapping them, or at concentrating rare essential elements and passing them on to higher trophic levels? How does the growth and development of a biological system modify the palette of substances available? Reciprocally, how is growth and development limited by this palette? During succession a community increases in size and organization, which should result in a lower turnover rate for elements (E. P. Odum, 1969; Ulanowicz, 1985). The processing of “unusual” substances and their cycling should become more efficient because of the addition of processing pathways. The processing of “common” substances should be less strongly affected. The concentration differential should increase for rare elements. Reciprocally, regression would lead to an increase in resource turnover rate, as inferred from observations of Stewart et al. (1993).

In summary, energy flows and element cycles likely are quite dynamic. Detailed analyses of these combined processes would require more frequent sampling but would be rewarding, and so would comparisons between pristine and polluted streams, and between different kinds of ecosystems, which are likely to have different strategies of element cycling (Pomeroy, 1970).

Appendix 1: Estimation of annual energy flows

Energy inputs

Sunlight. The light input to the system was calculated from the data of Ruhrmann (1990; not shown):

$$\text{Sunlight input} = 1470 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (1)$$

DIM. The chemical potential energy in a stream can be calculated from the DIM concentration in the water (Odum, 1996):

$$\text{DIM input} = \text{Discharge} \cdot \text{Water density} \cdot G \quad (2a)$$

where G is the Gibbs free energy of river water relative to saltwater (Odum, 1996):

$$G = (8.33 \text{ J}/(\text{mol} \cdot \text{deg}))(300^\circ\text{C}) \cdot \ln((1 \cdot 10^6 - \text{DIM}) \text{ ppm}/965000 \text{ ppm}) \quad (2b)$$

Here the DIM concentration in water is 11.86 ppm (sum of the concentrations of all the elements investigated), thus G is 4.94 J/g. Average annual discharge is 0.70 m³/s (average of values in Meyer, 1990, and Pusch and Schwoerbel, 1994), or $22.08 \cdot 10^6$ m³/yr. Thus, for the 1200-m² area:

$$\begin{aligned} \text{DIM input} &= 22.08 \cdot 10^6 \text{ m}^3/\text{yr} \cdot 1 \cdot 10^6 \text{ g}/\text{m}^3 \\ &\cdot 4.94 \text{ J}/\text{g}/1200 \text{ m}^2/1000 \text{ J}/\text{kJ} \\ &= 90880 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (2c)$$

CPOM and DOM. The CPOM input was measured by Gessner (1987):

$$\text{CPOM input} = 44000.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (3)$$

The net DOM input is roughly equal to the CPOM input (Gessner, pers. comm.):

$$\text{DOM input} = 44000.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (4)$$

Internal transfers and exports

Where the available data were expressed in grams of dry mass (DM), they were converted to kilojoules with the following conversion factors (Meyer, 1992): 18.74 kJ/g for detritus, 13.71 kJ/g for algae, 27.46 kJ/g for decomposers and invertebrates, and 21.28 kJ/g for fish. These data are summarized in Table 3.

CPOM and DOM retention and export. Of the available CPOM (eq. 3), 46% is available to consumers and the remainder drifts downstream (Gessner, 1987). Thus:

$$\begin{aligned} \text{CPOM retention} &= 44000.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.46 \\ &= 20240.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (5)$$

Of the available allochthonous DOM (eq. 4), only 10–30% is metabolized, the remainder consisting of refractory humic acids and being exported (Naegeli, pers. comm., Fiebig et al., 1990). Assume the average value of 20%. Thus:

$$\begin{aligned} \text{DOM retention} &= 44000.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.2 \\ &= 8800.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (6)$$

Calculate exports by difference between input and retention (eqs. 3–6):

$$\begin{aligned} \text{Allochthonous CPOM export} &= 44000.00 - 20240.00 \\ &= 23760.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (7)$$

$$\begin{aligned} \text{Allochthonous DOM export} &= 44000.00 - 8800.00 \\ &= 35200.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (8)$$

Uptake of CPOM by consumers. For shredders, see Table 3. The decomposers/microbial loop consume 6.5% (average of values in Gessner, 1987) of the CPOM input (eq. 3):

$$\begin{aligned} \text{Uptake of CPOM by decomposers/microbial loop} &= 44000.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.065 \\ &= 2860.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (9)$$

Uptake of FPOM & DOM by decomposers/microbial loop. Subtract from the uptake of detritus (Table 3) the uptake of CPOM (eq. 9):

$$\begin{aligned} \text{Uptake of FPOM \& DOM by decomposers/} \\ \text{microbial loop} &= 17475.02 - 2860.00 \\ &= 14615.02 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (10)$$

Mineralization. Assume that the production of DIM is 0.01% of the detritus processed by the decomposers/microbial loop (Odum, 1996; Table 3):

$$\begin{aligned} \text{Mineralization} &= 17475.02 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.001 \\ &= 17.48 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (11)$$

Other forms of uptake by consumers. See Table 3.

Emergence. Bötsch (1988) and Semmler (1988) captured emerged insects with rectangular traps. Their data were reorganized by larval trophic type and numbers of individuals were converted to milligrams. Calculate emergence, using the caloric conversion factor, by feeding type:

$$\begin{aligned} \text{Plecoptera biomass} &= 29.06 \text{ individuals}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 0.72 \text{ mg}/\text{individual} = 20.92 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (12a)$$

$$\begin{aligned} \text{Trichoptera biomass} &= 148.5 \text{ individuals}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 6.38 \text{ mg}/\text{individual} = 947.43 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (12b)$$

$$\begin{aligned} \text{Emergence of shredders} &= (20.92 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \\ &+ 947.43 \text{ mg}/(\text{m}^2 \cdot \text{yr}))/1000 \text{ g}/\text{mg} \cdot 27.46 \text{ kJ}/\text{g} \\ &= 26.59 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (12c)$$

$$\begin{aligned} \text{Ephemeroptera biomass} &= 159.77 \text{ individuals}/ \\ &(\text{m}^2 \cdot \text{yr}) \cdot 0.71 \text{ mg}/\text{individual} \\ &= 113.44 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (13a)$$

$$\begin{aligned} \text{Trichoptera biomass} &= 11.12 \text{ individuals}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 6.38 \text{ mg}/\text{individual} = 70.95 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (13b)$$

$$\begin{aligned} \text{Emergence of scrapers} &= (113.44 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \\ &+ 70.95 \text{ mg}/(\text{m}^2 \cdot \text{yr}))/1000 \text{ g}/\text{mg} \cdot 27.46 \text{ kJ}/\text{g} \\ &= 5.06 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (13c)$$

$$\begin{aligned} \text{Ephemeroptera biomass} &= 16.66 \text{ individuals}/ \\ &(\text{m}^2 \cdot \text{yr}) \cdot 0.71 \text{ mg}/\text{individual} = 11.83 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (14a)$$

$$\text{Chironomidae biomass} = 3642.67 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \quad (14b)$$

$$\begin{aligned} \text{Emergence of collectors} &= (11.83 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \\ &+ 3642.67 \text{ mg}/(\text{m}^2 \cdot \text{yr}))/1000 \text{ g}/\text{mg} \cdot 27.46 \text{ kJ}/\text{g} \\ &= 100.35 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (14c)$$

$$\begin{aligned} \text{Trichoptera biomass} &= 5.55 \text{ individuals}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 6.38 \text{ mg}/\text{individual} = 35.41 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (15a)$$

$$\text{Chironomidae biomass} = 187.40 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \quad (15b)$$

$$\begin{aligned} \text{Emergence of filter-feeders} &= (35.41 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \\ &+ 187.40 \text{ mg}/(\text{m}^2 \cdot \text{yr}))/1000 \text{ g}/\text{mg} \cdot 27.46 \text{ kJ}/\text{g} \\ &= 6.12 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (15c)$$

$$\text{Chironomidae biomass} = 74.18 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \quad (16a)$$

$$\begin{aligned} \text{Plecoptera biomass} &= 0.86 \text{ individuals}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 0.72 \text{ mg}/\text{individual} = 0.62 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (16b)$$

$$\begin{aligned} \text{Trichoptera biomass} &= 15.83 \text{ individuals}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 6.38 \text{ mg}/\text{individual} = 101.00 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (16c)$$

$$\begin{aligned} \text{Emergence of carnivorous invertebrates} &= (74.18 \text{ mg}/(\text{m}^2 \cdot \text{yr}) + 0.62 \text{ mg}/(\text{m}^2 \cdot \text{yr}) \\ &+ 101.00 \text{ mg}/(\text{m}^2 \cdot \text{yr}))/1000 \text{ g}/\text{mg} \cdot 27.46 \text{ kJ}/\text{g} \\ &= 4.83 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (16d)$$

Predation on adult insects by fish. Predation on invertebrates by trout (DW) is 4.25 g/(m² · yr), of which 16.8% consists of adult insects; For sculpin it is 3.67 g/(m² · yr), of which 1.0% consists of adult insects (Meyer and Pöpperl, unpubl.). Thus:

$$\begin{aligned} \text{Predation on adult insects by fish} &= (4.25 \text{ g}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 27.46 \text{ kJ}/\text{g} \cdot 0.168) + (3.67 \text{ g}/(\text{m}^2 \cdot \text{yr}) \cdot 27.46 \text{ kJ}/\text{g} \\ &\cdot 0.01) = 20.61 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (17)$$

Respiration of algae. The mean annual biomass of algae (DW) is 4.66 g/m² (Meyer, 1992); 1 g (ash-free dry mass, AFDW) of algae is equivalent to 4639 cal and 1 g (DW) of algae to 3277 cal (Cummins and Wuycheck, 1971). Thus:

$$\begin{aligned} \text{Algal biomass} &= 4.66 \text{ g}/\text{m}^2 \cdot 3277 \text{ cal}/4639 \text{ cal} \\ &= 3.29 \text{ g}/\text{m}^2 \text{ AFDW} \end{aligned} \quad (18a)$$

This corresponds to an O₂ consumption of 0.4 g/(m² · d) (see Fig. 3 in Naegeli and Uehlinger, 1997), or 146.00 g/(m² · yr). Convert this to energy lost in respiration, knowing that C makes up 46% of DW, using the stoichiometric ratios of C, CO₂ and O₂, and a conversion factor of 3277 cal/g DW (Cummins and Wuycheck, 1971):

$$\begin{aligned} 1 \text{ g O}_2 &= (44 \text{ g CO}_2/32 \text{ g O}_2) \cdot (12 \text{ g C}/44 \text{ g CO}_2)/ \\ &0.46 \text{ g C}/\text{g} \cdot 3277 \text{ cal}/\text{g} \cdot 4.185 \text{ J}/\text{cal}/1000 \text{ J}/\text{kJ} \\ &= 11.18 \text{ kJ} \end{aligned} \quad (18b)$$

Thus the energy given out in respiration is:

$$\begin{aligned} \text{Algal respiration} &= 146.00 \text{ g}/(\text{m}^2 \cdot \text{yr}) \cdot 11.18 \text{ kJ}/\text{g} \\ &= 1632.28 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (18c)$$

Respiration of consumers. See Table 3.

Capture of fish by birds and by recreational fishing. Calculate by difference of uptake and losses (see Table 3):

$$\begin{aligned} \text{Capture of fish} &= -82.57 + 64.81 + 49.43 + 32.95 \\ &+ 26.64 + 22.00 + 0.96 + 20.61 = 134.83 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (19)$$

Mortality of algae from other causes than predation, and exudation. Assume that this equals 2% of DOM export (Kaplan and Bott, 1982, for DOC; and see eq. 8). Thus:

$$\text{Algal mortality and exudation} = 35200.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.02 = 704.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (20)$$

DIM uptake by algae. Assume that mineral recycling by algae is 0.1% of the organic matter produced in the system (Odum, 1996). System production in the Steina is 399.7 g/(m² · yr) of DW (Meyer and Pöpperl, unpubl.), divided roughly into 50% of microorganisms (caloric value: 18.47 kJ/g) and 50% of algae (13.71 kJ/g). Use the average caloric value of 16.09 kJ/g:

$$\text{System production} = 399.7 \text{ g}/(\text{m}^2 \cdot \text{yr}) \cdot 16.09 \text{ kJ/g} = 6431.17 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (21a)$$

$$\text{DIM uptake by algae} = 6431.17 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.001 = 6.43 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (21b)$$

Sunlight uptake by algae. Calculate by balancing the outputs and inputs for algae (Table 3, and eqs. 49c, 20, 21b):

$$\begin{aligned} \text{Uptake of sunlight by algae} &= 107.21 + 339.05 \\ &+ 19.33 + 55.53 + 21.66 + 0.96 + 1632.28 \\ &+ 704.00 - 6.43 = 2873.59 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (22)$$

Export and uptake of autochthonous DIM. Since DIM is vastly in excess, the recycled part of DIM production (17.48 kJ/(m² · yr), eq. 11) is negligible and total DIM export is roughly equal to DIM input (eq. 2c):

$$\begin{aligned} \text{Uptake of autochthonous DIM by algae} \\ &= 0.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (23)$$

$$\begin{aligned} \text{Export of autochthonous DIM} \\ &= 17.48 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (24)$$

$$\text{Total DIM export} = 90880 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (25)$$

Retention of allochthonous DIM. This is equal to what algae take up (eqs. 21b and 23):

$$\begin{aligned} \text{Retention of allochthonous DIM} \\ &= 6.43 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (26)$$

Mortality of invertebrates from other causes than predation. Balance the flows for each compartment (see Table 3, and eqs. 12c, 13c, 14c, 15c, 16d). Assume that 80% of dead animal matter is CPOM and 20% FPOM & DOM (see size spectra of invertebrate fauna in Meyer, 1992; Pusch and Schwoerbel, 1994; Morin et al., 1995):

$$\begin{aligned} \text{Mortality of shredders} &= 406.28 + 107.21 + 23.62 \\ &+ 5.49 + 1.92 - 38.72 - 49.43 - 26.59 - 231.21 \\ &= 198.57 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (27a)$$

$$\begin{aligned} \text{CPOM from dead shredders} &= 198.57 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 0.8 = 158.86 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (27b)$$

$$\begin{aligned} \text{FPOM \& DOM from dead shredders} \\ &= 198.57 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.2 = 39.71 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (28)$$

$$\begin{aligned} \text{Mortality of scrapers} &= -1.92 + 915.00 + 339.05 \\ &+ 93.09 - 3.84 - 34.87 - 62.61 - 64.81 - 5.06 \\ &- 882.29 = 291.74 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (29a)$$

$$\begin{aligned} \text{CPOM from dead scrapers} &= 291.74 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.8 \\ &= 233.39 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (29b)$$

$$\begin{aligned} \text{FPOM \& DOM from dead scrapers} \\ &= 291.74 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.2 = 58.35 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (30)$$

$$\begin{aligned} \text{Mortality of collectors} &= -5.49 + 414.28 + 248.78 \\ &+ 19.33 + 3.84 - 6.86 - 38.44 - 32.95 - 100.35 \\ &- 277.35 = 224.79 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (31a)$$

$$\begin{aligned} \text{CPOM from dead collectors} &= 224.79 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 0.8 = 179.83 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (31b)$$

$$\begin{aligned} \text{FPOM \& DOM from dead collectors} \\ &= 224.79 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.2 = 44.96 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (32)$$

$$\begin{aligned} \text{Mortality of filter-feeders} &= 417.39 + 55.53 + 34.87 \\ &+ 34.87 + 6.86 + 6.86 - 34.05 - 22.00 - 6.12 \\ &- 257.30 = 236.61 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (33a)$$

$$\begin{aligned} \text{CPOM from dead filter-feeders} &= 236.61 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \\ &\cdot 0.8 = 189.29 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (33b)$$

$$\begin{aligned} \text{FPOM \& DOM from dead filter-feeders} \\ &= 236.61 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.2 = 47.32 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (34)$$

$$\begin{aligned} \text{Mortality of carnivorous invertebrates} \\ &= -6.86 + 38.72 + 62.61 + 38.44 + 34.05 + 84.70 \\ &+ 21.66 + 21.69 - 26.64 - 4.83 - 246.87 \\ &= 16.67 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (35a)$$

$$\begin{aligned} \text{CPOM from dead carnivorous invertebrates} \\ &= 16.67 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.8 = 13.34 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (35b)$$

$$\begin{aligned} \text{FPOM \& DOM from dead carnivorous invertebrates} \\ &= 16.67 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 0.2 = 3.33 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (36)$$

Mortality of fish from other causes than predation. This was assumed to be negligible:

$$\text{CPOM from dead fish} = 0.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (37)$$

$$\begin{aligned} \text{FPOM \& DOM from dead fish} &= 0.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \\ & \quad (38) \end{aligned}$$

Formation of FPOM & DOM from shredding and leaching of CPOM. Calculate by difference of CPOM input and uptake (see Table 3, and eqs. 5, 27b, 29b, 31b, 33b, 35b, 37):

$$\begin{aligned} \text{Formation of FPOM \& DOM from CPOM} \\ &= 20240.00 - 406.28 - 2860.00 + 158.86 + 233.39 \\ &+ 179.83 + 189.29 + 13.34 + 0.00 \\ &= 17748.43 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \end{aligned} \quad (39)$$

Mortality of decomposers/microbial loop from other causes than predation. Balance the flows for the decom-

posers/microbial loop compartment (see Table 3, and eqs. 10, 11):

$$\begin{aligned} \text{Mortality of decomposers/microbial loop} &= 2860.00 + \\ &14615.02 - 17.48 - 23.62 - 93.09 - 248.78 - 34.87 \\ &- 21.69 - 14549.13 = 2486.36 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (40) \end{aligned}$$

Export of autochthonous FPOM & DOM: Balance the flows for the FPOM & DOM compartment (see Table 3, and eqs. 6, 10, 20, 28, 30, 32, 34, 36, 39, 40):

$$\begin{aligned} \text{Export of autochthonous FPOM \& DOM} &= 8800.00 - 14615.02 - 915.00 - 414.28 - 417.39 \\ &- 84.70 + 704.00 + 39.71 + 58.35 + 44.96 + 47.32 \\ &+ 3.33 + 0.00 + 17748.43 + 2486.36 \\ &= 13486.07 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \quad (41) \end{aligned}$$

Appendix 2: Emergy and transformity of energy sources and ecosystem's compartments

Recalling that emergy is basically solar embodied energy, units of emergy (EM) are joules, but to avoid confusion with the actual energy flowing (also measured in joules), Odum (1996) has suggested using "solar embodied joules" (S.E. J). Transformity (TR), then, is expressed in solar equivalent joules used per joules produced (S.E. J/J).

Watershed energy sources

The flow of DIM, DOM and POM to the river is sustained by ecosystem processes at the watershed scale. The watershed's surface area is $19.42 \cdot 10^6 \text{ m}^2$ for a 13850-m reach (Gessner, 1987), or, for this 400-m reach, $560.87 \cdot 10^3 \text{ m}^2$. This emergy comes mainly in the forms of direct sunlight, earth cycle energy (balance of uplift and erosion), and the chemical and physical energies in rain and snow (Odum, 1996).

For sunlight, knowing the energy flow (eq. 1) and correcting for the 15% of light which is reflected by the canopy (Gosz et al., 1978):

$$\begin{aligned} \text{Energy}_{\text{sunlight}} &= (1470 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) / (1 - 0.15)) \\ &\cdot 560.87 \cdot 10^3 \text{ m}^2 = 969.98 \cdot 10^9 \text{ kJ}/\text{yr} \quad (42) \end{aligned}$$

For the earth cycle, multiply the heat flow by the surface area. For heat flow, an average value of $2 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr})$ was assumed, this region being neither very young nor very old (see Odum, 1996):

$$\begin{aligned} \text{Energy}_{\text{earth cycle}} &= 2 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \cdot 560.87 \cdot 10^3 \text{ m}^2 \\ &= 1.12 \cdot 10^9 \text{ kJ}/\text{yr} \quad (43) \end{aligned}$$

For the chemical potential of rain and snow, knowing precipitation (0.96 m/yr; Gessner, pers. comm.) and the Gibbs free energy of rainwater relative to saltwater (4.94 J/g), calculate as follows (see Odum, 1996):

$$\begin{aligned} \text{Energy}_{\text{rain, chemical}} &= 0.96 \text{ m}/\text{yr} \cdot 1 \cdot 10^6 \text{ g}/\text{m}^3 \cdot 4.94 \text{ J}/\text{g} \\ &\cdot 560.87 \cdot 10^3 \text{ m}^2 / 1000 \text{ J}/\text{kJ} = 2.66 \cdot 10^9 \text{ kJ}/\text{yr} \quad (44) \end{aligned}$$

The physical potential of rain depends on rainfall and elevation (Odum, 1996):

$$\begin{aligned} \text{Energy}_{\text{rain, physical}} &= 0.96 \text{ m}/\text{yr} \cdot 560.87 \cdot 10^3 \text{ m}^2 \cdot 1 \\ &\cdot 10^3 \text{ kg}/\text{m}^3 \cdot 9.8 \text{ m}/\text{s}^2 \cdot 700 \text{ m} / 1000 \text{ J}/\text{kJ} \\ &= 3.69 \cdot 10^9 \text{ kJ}/\text{yr} \quad (45) \end{aligned}$$

Transformity of energy resources

Sunlight. The transformity of sunlight is by definition (Odum, 1996):

$$\text{TR}_{\text{sunlight}} = 1.00 \text{ S.E. J}/\text{J} \quad (46)$$

DIM, CPOM and DOM. The sum of energy inputs (eqs. 42–45) is needed to drive each of these flows (eqs. 2c, 3, 4). In other words, this energy is embodied in these flows. Thus, divide the sum ($977.46 \cdot 10^9 \text{ S.E. kJ}/\text{yr}$) by each energy flow. For the 1200-m² reach:

$$\begin{aligned} \text{TR}_{\text{DIM}} &= 977.46 \cdot 10^9 \text{ S.E. kJ}/\text{yr} / (90880 \cdot 10^3 \text{ kJ}/ \\ &(\text{m}^2 \cdot \text{yr}) \cdot 1200 \text{ m}^2) = 8.96 \text{ S.E. J}/\text{J} \quad (47) \end{aligned}$$

$$\begin{aligned} \text{TR}_{\text{CPOM}} &= 977.46 \cdot 10^9 \text{ S.E. kJ}/\text{yr} / (44000.00 \text{ kJ}/ \\ &(\text{m}^2 \cdot \text{yr}) \cdot 1200 \text{ m}^2) = 18512.50 \text{ S.E. J}/\text{J} \quad (48) \end{aligned}$$

$$\begin{aligned} \text{TR}_{\text{DOM}} &= 977.46 \cdot 10^9 \text{ S.E. kJ}/\text{yr} / (44000.00 \text{ kJ}/ \\ &(\text{m}^2 \cdot \text{yr}) \cdot 1200 \text{ m}^2) = 18512.50 \text{ S.E. J}/\text{J} \quad (49) \end{aligned}$$

To calculate the emergy contributions of these sources to the ecosystem, multiply their transformity by the energy flowing to the system:

$$\begin{aligned} \text{EM}_{\text{DIM}} &= 8.96 \text{ S.E. J}/\text{J} \cdot 90880 \cdot 10^3 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \\ &= 814285 \cdot 10^3 \text{ S.E. kJ}/(\text{m}^2 \cdot \text{yr}) \quad (50) \end{aligned}$$

$$\begin{aligned} \text{EM}_{\text{CPOM}} &= 18512.50 \text{ S.E. J}/\text{J} \cdot 44000.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \\ &= 814550 \cdot 10^3 \text{ S.E. kJ}/(\text{m}^2 \cdot \text{yr}) \quad (51) \end{aligned}$$

$$\begin{aligned} \text{EM}_{\text{DOM}} &= 18512.50 \text{ S.E. J}/\text{J} \cdot 44000.00 \text{ kJ}/(\text{m}^2 \cdot \text{yr}) \\ &= 814550 \cdot 10^3 \text{ S.E. kJ}/(\text{m}^2 \cdot \text{yr}) \quad (52) \end{aligned}$$

Internal compartments

Algae. Emergy inputs are sunlight and DIM (eqs. 46, 47);

$$\begin{aligned} \text{EM}_{\text{algae}} &= [(1.00 \cdot 2873.59) + (8.96 \cdot 6.43)] \\ &= 2931.2 \text{ S.E. kJ}/(\text{m}^2 \cdot \text{yr}) \quad (53) \end{aligned}$$

The sum of outputs for algae is $1247.74 \text{ kJ}/(\text{m}^2 \cdot \text{yr})$ (Table 3, eq. 20). Thus:

$$\text{TR}_{\text{algae}} = 2931.2 / 1247.74 = 2.35 \text{ S.E. J}/\text{J} \quad (54)$$

Retained resource flows and other compartments. In similar fashion, derive the values for the retained sunlight, DIM, CPOM and DOM, and for autochthonous CPOM, decomposers/microbial loop, FPOM & DOM, and consumers (Table 1).

Appendix 3: Example of calculation of elemental transformities

The cycling of an element such as copper (Cu) is driven by ecosystem processes at the watershed scale. To relate the distribution of Cu to its energy value, first calculate the transformity of Cu: In the numerator, report the annual emery input to the watershed divided by the surface area (eqs. 42–45).

$$\text{Annual emery input} = 977.46 \cdot 10^9 \text{ S.E. kJ/yr} / 560.87 \cdot 10^3 \text{ m}^2 = 1.74 \cdot 10^6 \text{ S.E. kJ/(m}^2 \cdot \text{yr)} \quad (55)$$

In the denominator, compute the energy inherent in the concentration differential between the physical environment (water and sediment) and the community. This is at least equal to the Gibbs free energy change ΔF associated with the change in concentration (Odum, 1996):

$$\Delta F = R \cdot T \cdot \ln (\text{Conc}_{\text{living}} / \text{Conc}_{\text{physical}}), \quad (56a)$$

where R is the gas constant, T is temperature, $\text{Conc}_{\text{community}}$ and $\text{Conc}_{\text{physical}}$ are the concentrations of Cu in the living community (61.27 mg/g) and in the physical environment (0.0012 mg/g):

$$\Delta F = 8.31 \text{ J/(mole} \cdot \text{°K)} \cdot 298 \text{ °K} \cdot \ln (61.27 \text{ mg/g} / 0.0012 \text{ mg/g}) = 26889.2 \text{ J/mole}. \quad (56b)$$

Multiplying ΔF by the amount of Cu in the community (12.35 $\mu\text{moles/m}^2$) yields the total energy in the concentration differential (in joules):

$$\text{Energy}_{\Delta F} = 26889.2 \text{ J/mole} / 10^6 \mu\text{moles/mole} \cdot 12.35 \mu\text{moles/(m}^2 \cdot \text{yr)} = 332.08 \cdot 10^{-3} \text{ J/(m}^2 \cdot \text{yr)}. \quad (56c)$$

The transformity of Cu is the emery input divided by the energy output:

$$\text{TR}_{\text{Cu}} = 1.74 \cdot 10^6 \text{ S.E. kJ/(m}^2 \cdot \text{yr)} / 332.08 \cdot 10^{-3} \text{ J/(m}^2 \cdot \text{yr)} = 5247.20 \cdot 10^6 \text{ S.E. J/J}. \quad (57)$$

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