BIOGEOCHEMICAL PROCESSES IN RIVER SYSTEMS

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Keywords: biogeochemical processes, photosynthesis, decomposition, ammonification, nitrification, denitrification, sulfate reduction, methanogenesis, hyporheic, riparian, geology, climate, hydrology, hydraulics, discharge area, stream characteristic.

Contents

Part 1: Key biochemical processes in river systems (by F. J. Triska)
1. Introduction
2. Redox Environment
3. Carbon: Biosynthesis and Decomposition
4. Nitrogen and Phosphorus Biogeochemistry
5. Biogeochemical processes in Anaerobic Environments
6. Hydrologic Considerations in River Biogeochemistry
7. Synthesis
Acknowledgments

Part 2: Factors affecting biogeochemical processes in rivers (by L.W.G. Higler)
1. Introduction
2. Climate and hydrology.
3. Characteristics of the discharge area.
4. Characteristics of the stream.
Glossary
Bibliography
Biographical Sketches

Summary

Biogeochemical processes in rivers are controlled by biological, chemical, geomorphic and hydrologic interactions. These interactions produce variable redox environments wherein microorganisms derive energy and synthesize tissue using oxidation-reduction reactions associated with several elements including C, N, P, S, and to a lesser extent Fe and Mn. Biogeochemistry of river water and surface sediment is typically dominated by photosynthesis and aerobic decomposition. Deeper within the sediments however, oxygen can become depleted due to bacterial respiration. Under anaerobic conditions alternate electron acceptors substitute for oxygen during decomposition. The sequence of terminal electron acceptors, is theoretically determined by the highest free energy yield, beginning with O_2 then NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-}, and CO_2. Hydrologic processes regulate organic matter deposition and delivery of dissolved oxygen to sediment biota. Organic carbon processing increases with increasing contact with the microbial community. In steep, high-order streams with coarse sediments organic matter

processing is facilitated by surface water exchange beneath the stream. As stream gradient and sediment grain size decrease, subsurface exchange decreases, as connection to riparian floodplains, wetlands, oxbow lakes and other complex features increase. Management of rivers for water quality involves minimizing nutrient and sediment loads while preserving floodplains, wetlands, and other channel features that maximize connectivity between biogeochemically diverse environments, microbiota nutrients and organic matter.

Part 1: Key biochemical processes in river systems (by F. J. Triska)

1. Introduction

The chemical composition of river water at any point along a river's path is an integrated product of a myriad physical, chemical and biological processes that take place in the terrestrial environment, bankside riparian zone, upstream surface water and channel sediments. While many water quality processes are physical (e.g. sorption), or occur chemically, independent of biotic activity, others are biologically mediated and hence "bio"geochemical. Biogeochemical processes can significantly impact element cycles, especially for constituents present at low concentration yet essential for biosynthesis. Thus, "biogeochemistry" describes those processes in element cycles that involve biotic interaction with watershed geochemistry. The processes and consortia of microorganisms involved in river biogeochemistry, are similar to those in terrestrial and groundwater environments. Thus the uniqueness of river biogeochemistry stems not from unique metabolic processes or microbiota; rather it emerges from constraints placed on biogeochemical processes by river hydrology. These hydrologic properties include advective transport into and out of the bed, and during high flows, onto the adjacent floodplain.

2. Redox Environment

As on land, the biogeochemistry of rivers is based on a series of oxidation-reduction reactions by biota to derive energy, synthesize tissue, or fix essential nutrients (e.g. nitrogen fixation). To the extent that the environment is spatially diverse and complex in oxidizing and reducing conditions, so is its biogeochemistry. Under defined environmental conditions use of various electron acceptors proceeds in an orderly sequence related to energy yield, and is controlled by the hydrologic distribution of dissolved oxygen relative to biotic and chemical demand. Biogeochemical element processes most critical to biotic production include: C, H, O, N, P, S and to a lesser extent the metals Mn and Fe. In rivers draining areas of unique geochemistry, or landscapes altered by anthropogenic manipulations such as mining, elements with toxic effects (e.g. Se, Hg) can be important in river biogeochemistry.

Biogeochemical processes in rivers are dependent upon on energy capture to support biosynthesis and respiration from either photosynthesis or degradation of organic matter. The preferred electron acceptor is determined sequentially based on redox state, which is the oxidizing or reducing intensity of the surface water or pore water solution (see Table 1). Aerobic respiration and decomposition (oxygen as the terminal electron acceptor) constitute the most energy-efficient oxidation of organic carbon. Oxygen will

be favored until fully depleted (anaerobic) whereupon nitrate becomes the dominant electron acceptor, a process called denitrification. Following nitrate depletion the process of manganese reduction dominates, then iron reduction, sulfate reduction and finally methanogenesis. Theoretically, the most efficient metabolic pathway dominates to the competitive exclusion of others.

PROCESS	Electron Donor	Electron Acceptor	Free Energy (kcal)[a] ΔG^0 (w)
Reduction Processes			
Respiration / Decomposition	Organic Carbon	O_2	-120.0
Denitrification	Organic Carbon	NO_3^-	-113.9
Manganese Reduction	Organic Carbon	Mn^{4+}	-81.3
Iron Reduction	Organic Carbon	Fe^{3+}	-27.7
Sulfate Reduction	Organic Carbon	SO_4^{2-}	-25.0
Methane Formation	Organic Carbon	CO_2	-19.2
Fermentation	Organic Carbon	H_2O	-8.6
Oxidation Processes			
Methane oxidation	Oxygen	CH_4	-97.7
Sulfide Oxidation	Oxygen	HS^-	-95.0
Ferrous Oxidation	Oxygen	Fe^{2+}	-92.3
Nitrification	Oxygen	NH_4^+	-41.4
Manganese Oxidation	Oxygen	Mn^{2+}	-38.6

[a] Change in Gibbs free energy wherein $\Delta G^0(w)=\Delta G^0-RT \ln[H^+]^p$ at pH7 and where p is the stoichiometric coefficient for H^+ in the reaction. (Adapted from Baker et al. 2000)

Table 1. Common biogeochemical processes in river systems

Although biogeochemical processes theoretically occur in an orderly sequence, in actual river sediments some biogeochemical processes can co-occur. For example, the obligately anaerobic process, denitrification, and obligately aerobic process, nitrification, commonly occur in close proximity. The rate of denitrification rate may even depend on the rate of nitrification, wherein the processes are referred to as coupled. Process overlap can also occur between denitrification and Mn reduction. There are several reasons for this co-occurrence. First, some bacteria, which oxidize

organic matter aerobically, also denitrify or reduce Mn. These organisms shift metabolic pathways depending on the availability of suitable terminal electron acceptors. Second, the redox state in the upper sediment layer of rivers is highly dynamic. Hydrologic processes scour and fill surface sediments over short temporal scales altering local redox conditions. Third, presence or absence of organic particulates can drastically alter local redox conditions relative to the scale of microorganisms. Even at the particle level, aerobic processes can dominate at the surface while a reducing environment exists within. In deeper sediments anaerobic processes such as sulfate reduction and methanogenesis proceed in a sediment environment more removed from hydrologic disturbance. After denitrification, energy yield per equivalent drops quickly as the environment becomes more reducing (Table 1). Since many anaerobic biogeochemical processes are not energetically efficient, organic matter often accumulates. Thus sediments with high iron reduction, fermentation, sulfate reduction or methanogenesis are also likely zones of high organic carbon deposition including fermentation by-products such as formate and acetate.

3. Carbon: Biosynthesis and Decomposition

The most common biogeochemical coupling in any ecosystem, including rivers, is between carbon and oxygen through photosynthesis, aerobic respiration, and decomposition. Photosynthesis is the light-required reduction of inorganic carbon into organic matter

$$6 \, CO_2 + 12 \, H_2O \Leftrightarrow C_6H_{12}O_6 + 6 \, H_2O + 6 \, O_2 \tag{1}$$

The reaction is reversible wherein biosynthesis occurs toward the right while respiration and decomposition constitute the reverse. So prevailing is global photosynthesis that atmospheric oxygen composition is controlled by the process. So prevailing is respiration that accelerated oxidation of stored organic matter by industry, agriculture, burning of forest and the internal combustion engine may significantly shift global climate.

Photosynthesis is facilitated by light, in association with specialized photosynthetic pigments (e.g. chlorophyll). Organisms capable of photosynthesis are called "autotrophs" and the production of new biomass from photosynthesis is "autotrophy". The strong atmospheric response to photosynthesis is due primarily to terrestrial, marine and large lake plant production. Oxygen contribution to the atmosphere from photosynthesis in rivers is not well known, but is probably of limited global consequence due to the small area coverage of rivers relative to terrestrial landscapes or the oceans. Nonetheless photosynthesis and associated nutrient uptake in river environments support highly complex food webs, while nutrient regeneration and transport from rivers can be a critical control of primary production in estuarine and coastal environments.

The dissolved oxygen (DO) concentration in river water is a function of photosynthesis and gas exchange with the atmosphere. DO is only marginally soluble in water, diffusing at very slow rates across the water-atmosphere interface. In the absence of hydrologic turbulence oxygen diffusion is 10^4 times slower in water than in air.

Turbulence by river waters facilitates exchange, maintaining high oxygen saturation. In slow moving waters, atmospheric exchange can be greatly reduced. Under conditions of high photosynthesis and low atmospheric exchange dissolved oxygen can become supersaturated during daylight and depleted at night. Severe shifts in DO concentration can have deleterious effects on many aquatic biota. In reaches where daily shifts in DO concentration are sufficient to be accurately measured, the difference between upstream and downstream values and between day and night, can be used to estimate primary production and respiration within a river reach. Other methods, based on photosynthetic oxygen production in light bottles and respiration in dark bottles, have been used to estimate primary production.

The metrics of interest related to photosynthesis are gross primary production (GPP), net primary production (NPP) and respiration (R). Net primary production is the net fixation of carbon into new tissue, while respiration is the metabolic cost associated with primary production. Gross primary production is the sum of net primary production and respiration.

GPP=NPP+R   (2)

NPP can be determined from the net DO produced per unit area per unit time. Respiration is the amount of oxygen depletion per unit area per unit time.

River are generally high in DO as a result of the interaction between photosynthesis and atmospheric exchange, but DO concentration is typically below theoretical saturation. Under-saturated conditions result from respiration by primary producers and other biota, and from the process of decomposition. Oxygen demand from respiration and decomposition is termed "heterotrophy". When production and respiration are simultaneously determined, a ratio of production to respiration (P/R) can be calculated. In rivers where primary production and respiration balance, P/R=1. River reaches where P/R >1 are autotrophic, and where P/R<1 are heterotrophic. System-wide, rivers typically have a P/R<1, i.e. rivers are typically heterotrophic. At the lowest point in the watershed profile, channels collect organic matter from the terrestrial environment, both dissolved and particulate. Biodegradable reduced carbon from outside the system is termed "allochthonous". Allochthonous inputs help support diverse food webs among the world's rivers.

4. Nitrogen and Phosphorus Biogeochemistry

Assimilation of dissolved inorganic nitrogen (DIN) and phosphorus occurs in conjunction with biosynthesis in river biota, and can significantly alter the dissolved loads of these elements, especially under low nutrient (oligotrophic) conditions. Thus Equation 1 for photosynthesis and respiration is highly simplified because both processes simultaneously require nitrogen phosphorus and other trace elements. A more complete representation of biosynthesis must include other major elements relative to their proportion in tissue, a concept called the Redfield ratio. A more representative equation for algal biosynthesis is:

$106\ CO_2 + 16\ NO_3^- + HPO_4^{2-} + 122\ H_2O + 18H^+ +$ (trace elements, energy)

$$\Leftrightarrow C_{106}H_{263}O_{110}N_{16}P + 138 \ O_2 \qquad\qquad (3)$$

In oligothophic settings dissolved N, dissolved P or both may limit biotic production. Nutrient limitation to river production is a function of both concentration and dissolved N/P ratio in the water. Variable estimates of nutrient concentration that saturates the capacity of microorganisms to assimilate an element have been reported in past studies. For soluble reactive phosphorus (SRP), a biologically available form, with concentrations from 1 to 5 μg P/L, usually saturate the uptake process, and maximum biomass accumulates between 7 and 20 μg P/L. DIN concentrations that exceed 50 to 60 μg N/L are usually saturating. Approximately 16 atoms of N are required for each atom of P for tissue synthesis (Equation 3), indicating a limiting N concentration of 16 to 80 μg/L. In oligotrophic waters an N/P ratio <16 indicates N-limitation whereas an N/P ratio >16 indicates P-limitation. Actual limiting ratios vary by species of organism and *in situ* conditions. River N/P ratios usually exceed 20 predicting P-limitation. The nutrient which limits production may also shift temporally. Large daylight depression of nutrient concentration is strong evidence of nutrient limitation coupled to photosynthesis.

P-limitation to biosynthesis is common in oligotrophic systems because its source is primarily geologic weathering, largely outside biologic control. SRP also precipitates with mineral particles during geochemical processes associated with other element cycles. Phosphorus released during mineralization of organic matter, also enters the dissolved pool as phosphate (PO_4^{-3}) which can similarly sorb with iron and aluminum oxides and clay minerals or co-precipitate with calcium or aluminum rendering it unavailable for biotic assimilation. As a result, the total-P load of rivers is usually dominated by biologically-unavailable particulate P. Phosphorus is unusual relative to most biologically essential elements in that it remains in the PO_4^{-3} state in both organic and inorganic forms and thus lacks redox related biogeochemistry.

The nitrogen and phosphorus cycles are indirectly linked through the process of nitrogen fixation, wherein atmospheric nitrogen (N_2) is fixed into biomass. N-fixation may be autotrophic (cyanobacteria), heterotrophic (some bacteria), or symbiotic (leguminous plants). N-fixation is relatively insignificant in river channels. When N-fixation does occur it is most often mediated by cyanobacteria such as *Nostoc sp.* Since the process requires energy, stream reaches containing *Nostoc* are typically well lighted with very low DIN and ample SRP. Heterotrpohic N- fixation has also been described in association with decomposing wood in streams. Most often N-fixation in rivers is associated with symbiotic N-fixation in riparian plants. In the Pacific Northwest of USA, alder species including *Alnus rubra* and *Alnus tenuifolia*, which contain a symbiont in root nodules, can contribute significant DIN to the N budget of oligotrophic streams.

Nutrient limitation is generally confined to headwater streams in landscapes lacking intensive land use. Agricultural practices and urbanization usually enhance nutrient input from runoff or from discharge of nutrient-enriched groundwater. Anthropogenic nutrient input, particularly in lowland settings, may over-stimulate photosynthesis producing "nuisance" levels of algal biomass. Nuisance growths usually occur at low flow when the hydrologic capacity of the channel to scour attached algae (periphyton) is

low, or in channels with minimal canopy shading, which eliminates light limitation. Nuisance growths commonly consist of filamentous green algae from the genera *Cladophora, Stigeoclonium, Ulothrix* and *Spirogyra*. Nuisance growths can undesirably impact water quality. High primary production can deplete inorganic carbon leading to large shifts of pH and dissolved oxygen concentration caused by alternating daylight production and night consumption. Large accumulations of biomass impede circulation into the bed and degrade habitat for other biota. Habitat degradation caused by over-production demonstrates the need for biogeochemical balance between autotrophy and heterotrophy along river corridors.

Ammonia, usually a minor component of surface water DIN, is favored over nitrate for biological uptake, since it does not have to be reduced for incorporation into biomass. Ammonia is produced in the breakdown of organic matter by the process of ammonification. This breakdown, involving the deamination of amino acids contained in the protein of organic matter, can occur under either aerobic or anaerobic conditions. Deamination usually precedes carbon oxidation. Upon formation, ammonia can be assimilated biologically, ionized to NH_4^+, adsorbed to mineral sediments (especially clays), or oxidized to nitrate. The last fate, nitrification, is a chemoautotrophic process where the energy derived from ammonium oxidation is used to reduce inorganic carbon into biomass (Table 1). The sequential two-step oxidation of ammonium is conducted by different genera of bacteria. The first step, the oxidation of ammonium to nitrite,

$$4\ NH_4^+ + 6\ H_2O \Rightarrow 4NO_2^- + 8\ H^+ + 4H_2O \tag{4}$$

is facilitated by bacteria from the genus *Nitrosomonas*, whereas the oxidation of nitrite to nitrate is facilitated by the genus *Nitrobacter*.

$$4\ NO_2^- + 2\ O_2 \Rightarrow 4\ NO_3 \tag{5}$$

Production of hydrogen ion in the first step of the process can lower pH in highly nitrifying environments. The efficiency of carbon fixation during nitrification varies by species. Nitrification may be inhibited by high concentrations of simple organic substrates such as glucose. The nitrate anion produced is poorly adsorbed to sediments and thus readily transported either downstream or into the bed.

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Biographical Sketches

Frank J. Triska received his PhD from the University of Pittsburgh, USA in 1970. Following two years of military service he obtained a postdoctoral appointment (1973) and eventually a research assistant professorship at the Department of Fisheries and Wildlife, Oregon State University. He accepted a position with the United States Geological Survey (USGS), Water Resources Division in 1979, where he has served as a hydrologist-biologist to the present.

His research in the USGS, National Research Program, has examined biotic processes in streams and rivers, particularly nitrogen cycling in the context of hydrologic transport. Studies in recent years have emphasized nitrogen biogeochemistry in hyporheic river sediments (sites of surface water-ground water exchange).

He has examined nitrogen biogeochemistry in a variety of flowing water environments. These physical settings have included: pristine forested mountain streams (Oregon (USA), California, USA), lowland sand-bed streams (Minnesota, USA), upper Mississippi River (Wisconsin, USA) and tropical rainforest

streams (Costa Rica).

Bert Higler investigated macroinvertebrate associations in relation to vegetation structure in standing waters and in relation to hydraulics in running waters. His primary research took place in The Netherlands. Results are being used by water managers.

His international activities comprise research and education, both in developed and in developing countries. The latter has resulted in a manual on water quality monitoring for use in developing countries.

He has now retired as head of the department of Aquatic Ecology of the Institute for Forestry and Nature Research (now ALTERRA, Research Institute for the Green World), which comprised freshwater and marine research. His present activities as a senior scientist include work for the European Water Framework Directive, nature restoration projects and biodiversity research on macroinvertebrates and fish.