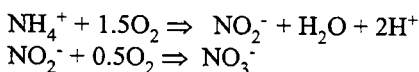


MICROBES AND ENERGY ACQUISITION IN SUBTERRANEAN HABITATS

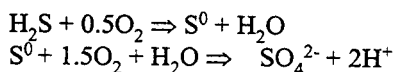
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In subsurface environments, including many caves, life is supported by photosynthetic activity only when light penetrates the cave or when the organic carbon produced by photosynthesis is transported from the surface to the cave in the percolating water. The abundance of life in caves, especially microorganisms, suggests that there are quantitatively important alternatives to carbon fixation by photosynthetic organisms that can support the higher forms of life found there. Chemoautolithotrophic bacteria support a number of ecosystems including caves in which light plays little or no role. Bacterial oxidation of H₂S in geothermal rift vents provides sufficient energy to fix supplies of organic carbon adequate to support clams, crabs, and large worms that thrive in the complete absence of light. The oxidation of metal sulfides emanating from mines and mine waste generate large quantities of organic carbon that exceeds the amount fixed by algae in acid mine drainage. In unlit caves, therefore, the abundance and diversity of life must be limited only by the supply of readily oxidizable substrates that can be used by organisms with the ability to link the energy gained by the enzymatic oxidation of the reduced inorganic compounds to fixation of inorganic carbon (which is usually in abundance) into biomass.

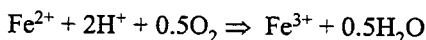
A large number of reduced elements exist that have the potential to be utilized as a source of energy for microorganisms (Ehrlich, 1978). The ones actually employed by microorganisms are a much smaller subset; the ones of general environmental importance (i. e., potential for large amounts of carbon fixation in the present context) are fewer still. Elements that can be oxidized to yield sufficient energy for carbon fixation by microorganisms include nitrogen



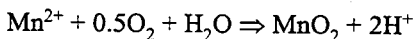
sulfur



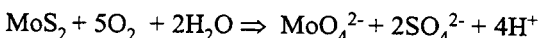
iron



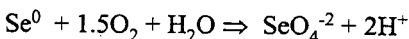
manganese



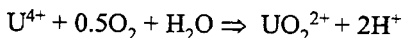
molybdenum



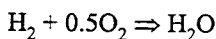
selenium



uranium



hydrogen



Others may exist as well (Ehrlich, 1978). Each reaction yields a different amount of energy to the organism that can be used for the fixation of carbon from CO₂, as well as for all other metabolic processes. The energy yield is based on the number of electrons transferred in the oxidation reaction (n), and the ΔE⁰ of each half reaction according to the relationship

$$\Delta G = -nF\Delta E^0$$

where F is Faraday's constant.

The potential for carbon fixation, therefore, must depend on both the energy yield of the reaction and the supply of the energy source in a specific habitat. Generation of a mole of ATP, the energy transfer compound used in living organisms requires about 10 kcal and fixation of a single mole of CO₂ requires about 335kcal. Exploiting inorganic sources of chemical energy to support a notable biomass of organisms above the bacteria (given that trophic efficiencies are commonly assumed to be about 10%) requires large amounts of the energy source.

Most caves represent oxidized environments. Thus, the supply of reduced materials to fuel carbon fixation might be considered limiting to production. Water seeping from rock pores that are depauperate in oxygen can supply enough reduced materials to allow appreciable local organic matter production at the interface of the oxic-anoxic interface. There are often found mats of bacterial mass that appear as slimy deposits not infrequently referred to by cavers as "snottites," as they hang from surfaces and resemble mucoid stalactites (Northup and Lavoie, 2001). The slime provides a way for the mat to retain its position at the emergence point of its energy supply as well as a means to retain water necessary for the life of the mat organisms. Seepage mats on vertical and roof surfaces probably do not provide a direct food source easily utilized by higher organisms (other than perhaps microinvertebrates such as protozoa). When the mats fall to the floors, or when dripping from snottites causes accumulation of organic matter on the floor or in pools or streams, the particulate organics may be utilized by

heterotrophic invertebrates (e.g., protozoa) which are in turn fed on by higher forms. Dissolved organics are utilized by heterotrophic bacteria which convert the dissolved material to particulate matter that can form the basis of a food chain.

Given the supply of reduced compounds available for energy exploitation by chemoautotrophic bacteria, it is probable that only a few compounds represent major foundations useful for supporting higher organisms. In particular, those compounds already familiar to most cavers, sulfur, iron and occasionally ammonia would be the most important energy sources for life in the unlit caves. Manganese may be important in some limited locations. It is not likely that adequate supplies of uranium, selenium, or molybdenum exist to support an appreciable biomass of higher organisms. Hydrogen is thought to be important in supporting bacterial communities in a number of otherwise energy deficient situations, but there is little evidence that hydrogen supplies from geological sources are adequate to support higher organisms through organic carbon fixation by autotrophic bacteria.

References

- Ehrlich, H. L., 1978, Inorganic energy sources for chemolithotrophic and mixotrophic bacteria: *Geomicrobiology Journal* v. 1, no. 1, p. 65-83.
- Northup, D. E., and Lavoie, K. H., 2001, Geomicrobiology of caves: A review: *Geomicrobiology Journal* v. 18, no. 3, p. 199-222.