Are microbes better at thermodynamics than geochemists?

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The importance of microbial activity in low-temperature geochemistry is universally recognized. Microbes are dominant drivers of the biogeochemical cycling of carbon, nutrients and metals, they are involved in rock weathering, soil formation, and climate regulation. They assist us in the clean-up of contaminated sites, treat our water supplies, regulate soil fertility, and produce unique chemical compounds, including nano-materials. In order to function, however, microbial cells must acquire substrates that provide them with the necessary chemical elements for biosynthesis and electrons for energy production. In the vast majority of environmental models, microbial activity is represented by mathematical expressions that can be traced back to the classical Monod equation (or the mathematically equivalent Michaelis-Menten equation). Model parameters, such as growth yields and half-saturation constants are usually treated as adjustable coefficients, whose values are assigned based on data determined in batch incubations. Here, observed trends in microbial activity are related to the thermodynamics of metabolic reactions and the mechanisms of cellular energy conservation. The focus is on microbial communities in subsurface environments, where anaerobic repiratory processes play a major role. We review the evidence that the thermodynamic properties of electron donors and acceptors explain the sequence of repiratory pathways according to energetic yields. Particular attention is given to the basic cost-benefit variable for microbial communities – the cellular growth yield. Results from retentostat experiments, designed to simulate the slow growth conditions typically encountered in the deeper subsurface, are used to illustrate the difference between theoretical and empirical growth yields. The results further provide evidence that – as a consequence of the Second Law – the majority of the energy dissipated by subsurface microbes serves to maintain cellular integrity, leaving little room for biomass growth.