

Hydrogen and energy flow as “sensed” by molecular genetics

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Perhaps just a quick whiff of the rarified air in Yellowstone Park might lead one to the apparently wrong conclusion; namely, that this is a sulfur-driven ecosystem. With all of that smelly hydrogen sulfide emanating from the hot water, it is easy for a microbiologist to leap to the conclusion that sulfur must dominate this ecosystem. Perhaps even more so since the discovery of the deep sea hydrothermal vents and their remarkable symbiotically driven ecosystems (1, 2), we have become accustomed to the notion of microbial systems powered by sulfide and/or sulfur oxidation and expect them to be operating here. For this reason, it was somewhat surprising to read the conclusion of the Spear *et al.* (3) in a recent issue of PNAS, who reported that these smelly boiling pools were in fact running on hydrogen rather than sulfide metabolism. The implications of this work go beyond this apparently straightforward conclusion.

The ability to identify and classify microbes by using molecular genetics techniques (16S rRNA sequence analysis) ushered in a new era in microbiology, making it possible for the first time to assess “who’s there” even when the organisms could not be cultivated (4–6). Based on previously published results showing that members of the *Aquificales* were abundant (7–11), the authors suspected that hydrogen and not sulfur should be the important nutrient. This logic comes from the knowledge that cultivated members of the *Aquificales* use hydrogen either exclusively or preferentially. To test this hypothesis, Spear *et al.* (3) examined the populations in a variety of Yellowstone ponds, with levels of sulfides ranging from nondetectable to $>200 \mu\text{M}$. They also measured several key chemical variables, including sulfate, hydrogen, oxygen, pH, Eh (reducing potential), and methane. With these data in hand, it was possible to ask, using a thermodynamic modeling approach, whether it was feasible that hydrogen was a major energy source in each environment.

This study showed very nicely how a combination of approaches can lead one to an explanation that is compatible with all of the data and yet in contrast to what might have been expected. Thus, the impact of the work may lie as much as in the implementation of the multifaceted ap-

proach as in the particular nature of the conclusions reached: Molecular genetics, environmental geochemistry, and geochemical modeling are brought together to begin to unravel the workings of the ecosystem. Although none of these three approaches on its own might have been sufficient to lead to this inference, taken together, they make a good case for these boiling sulfurous ponds being examples of hydrogen-driven ecosystems. In essence, such evidence can be used to move us from the “who’s there?” era to the “what’s going on?” era—a move of great importance to biologists and geochemists alike.

The boiling pools in Yellowstone Park are running on hydrogen rather than sulfide metabolism.

But does it really matter whether hydrogen or sulfur metabolism dominates these boiling ecosystems? Yes! There is little doubt that one of the most abundant energy sources on almost any geologically active body is expected to be molecular hydrogen. Hydrogen is not only the most abundant element in the universe, it is also sequestered in many geological reservoirs from which can be released as a function of either magmatic degassing, as in so-called magma-hosted systems, and/or the exothermic reaction of highly reduced magmatic rocks (peridotites) with water to release hydrogen, methane, and some simple organics (12–14).

Furthermore, the idea that hydrogen-driven ecosystems exist at all is one that excites scientists across a wide number of different disciplines, and one of considerable controversy and hyperbole. In large part, this excitement derives from the thought that ecosystems entirely uncoupled from the energy of the sun could exist: geologically powered dark ecosystems. In 1992, Tommy Gold (15) first formulated the notion of the deep, hot biosphere, an extensive subsurface zone where life could exist completely uncou-

pled from photosynthesis and its products. Such a finding set the stage for thoughts of early Earth metabolism (a prephotosynthetic Earth) as well as sites for exploration on and off our own planet. Since Gold’s original hypothesis (15), various reports of potential candidates for such environments have appeared. In the Yellowstone case, several geochemically derived energy sources are available, including hydrogen, sulfide, and methane, all of which are documented here. Given that photosynthetically derived oxygen is the electron acceptor for all of them in this system, it is not altogether analogous. However, there is little doubt that the potential electron donors here are at least in part geochemically derived. Because sulfate-reducing bacteria were identified in some of these waters, one must also consider the possibility that some part of the sulfide was of biological origin.

Geochemically produced hydrogen can arise in two fundamentally different ways: (i) outgassing of mantle-based rocks, releasing magmatic volatiles (CO_2 , H_2 , CH_4 , and H_2S) in fluids that are neutral or slightly acidic; and (ii) interaction of water with highly reduced ultramafic rocks (peridotites) releasing high-pH fluids containing H_2 and CH_4 but containing much less CO_2 because of the high pH (11 or higher; Fig. 1). In the latter case, if the water–rock interaction takes place at high temperature and pressure, the product can be primarily methane, with organic carbon produced as well (16). Although there are many variations on these themes (i.e., based on the water source interacting with the reduced rocks), both are capable of producing hydrogen for subsequent powering of subsurface ecosystems.

To this end, in 1995, Stevens and McKinley (17) proposed the existence of a hydrogen-driven microbial community in the deep subsurface of the Columbia River Basin, a claim that was hotly contested by Anderson *et al.* (18) based on the expected rates of hydrogen production. This latter group then proposed a hydrogen-powered ecosystem of their own (19): a subsurface *Archaea*-dominated microbial community in the groundwater system beneath the Lidy Hot Springs in

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