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Rethinking Earth's Early Atmosphere

Christopher F. Chyba

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brate species and their population sizes have increased dramatically since 1980. Birds have colonized in lock-step with increased habitat structure, but assemblages remain limited by the lack of forest structure. Yet even in the most disturbed areas, nearly all species of small mammals associated with undisturbed forests have returned. Secondary disturbances have modified pathways of succession. Shifting river channels, small landslides, and mudflows have repeatedly reset succession, enhancing the heterogeneity of vegetation patterns over the volcanic landscape.

Human activities have greatly altered natural ecological processes in many areas affected by the eruption. However, the U.S. Congress established a 43,300-ha National Volcanic Monument where natural processes can proceed unimpeded. Environmental scientists have provided advice concerning protection of natural features; management of erosion, floods, and natural resources; and development of interpretive programs and educational opportunities. During the decision-making process, potential risks to human life or property often outweighed ecological concerns.

A quarter century of ecological studies at Mount St. Helens has produced important lessons. First, living and dead biological legacies (for example, dead trees and rotten logs) are integral to the ecological response, even after severe disturbances. Second, ecological succession is very complex, proceeding at varying paces along diverse paths, and with periodic setbacks through secondary disturbances. Consequently, no single, overarching succession theory provides an adequate framework to explain ecological change. Third, chance factors, such as timing of the disturbance at various scales, can strongly influence survival and the course of succession. Finally, environmental scientists have provided a long-term and broad-scale view of how human actions can affect ecological systems, a requisite but not always integral component of decision-making.

The future at Mount St. Helens will be one of continuing change. The pace of ecological change will be determined by complex processes of ecological succession influenced by landscape position, topography, climate, and further biotic, human, and geophysical forces. The current volcanic activity at Mount St. Helens attests to its dynamic character (*3*). Even so, many biotic, landform, and soil legacies of the 1980 eruption will influence ecological processes for centuries to come.

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ATMOSPHERIC SCIENCE

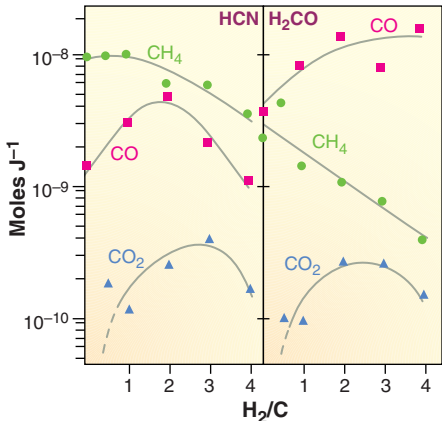
Rethinking Earth's Early Atmosphere

Christopher F. Chyba

In 1952, Stanley Miller, working with Harold Urey, simulated the atmosphere of early Earth with a gas mixture of methane (CH_4), ammonia (NH_3), molecular hydrogen (H_2), and water. When he introduced an electrical spark to represent lightning, he observed the formation of amino acids, the building blocks of proteins (*1*). Miller later showed that the amino acids were the result of reactions in liquid water (representing Earth's ocean) of simple organic molecules such as hydrogen cyanide (HCN) and formaldehyde (H_2CO) formed in the gas mixture (*2*). His experiment turned the study of the origin of life into an experimental science.

However, by the 1960s, the validity of hydrogen-rich (and hence reducing) model atmospheres for early Earth, such as the CH_4-NH_3 atmosphere used by Miller and Urey, was under attack (*3*). Since the 1970s, carbon dioxide (CO_2)–rich atmospheres have been favored (*4*). Miller has shown that the production of amino acids and other organic molecules is orders of magnitude less efficient in such atmospheres (*5*). For this and other reasons, the Miller-Urey approach to the origin of life has fallen out of favor with many researchers. But on page 1014 of this issue, Tian *et al*. (*6*) argue that the early-Earth atmosphere might have been hydrogen-rich after all.

In early models of Earth's evolution, the planet's iron-rich core was assumed to have formed slowly over hundreds of millions of years. Prior to core formation, metallic iron would have been abundant in Earth's mantle, in effect providing a huge oxygen sink. As a result, carbon and nitrogen compounds emitted ("outgassed") into the atmosphere—for example, in volcanic eruptions—would have been saturated with hydrogen (CH_4 and NH_3). Early life would have used the abundant organic molecules produced by Miller-Urey synthesis for energy and raw materials. Core formation would have freed the oxygen, leading to outgassing of CO_2 rather than CH_4 (*7*). Abiotic organic production would have plummeted, whereupon life would have evolved to cope with this change. It was an elegant picture—but probably largely wrong.



Hydrogen lends a helping hand. Yields (in moles produced per joule of input spark discharge energy) of organic molecules thought to be key for the origin of life are lower in CO_2-rich atmospheres than in CH_4-rich ones, although H_2/C ratios >1 maximize organic production in the former case. [Adapted from (*5*)]

It now appears that Earth was hot at the time of its formation, because it accreted from fast-colliding planetesimals. It seems unavoidable that the core formed virtually simultaneously with Earth itself. If the iron was largely sequestered in the core from the start, then there never was a Miller-Urey atmosphere. Even if there ever had been such an atmosphere, modeling suggested that it would be quickly destroyed by solar ultraviolet light. However, this problem would be circumvented by the formation of a high-altitude organic haze, similar to that in the atmosphere of Saturn's moon Titan (*8*). Thus, if Earth ever had a Miller-Urey atmosphere, it could be sus-

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tained. But it remains unclear how to form such an atmosphere to begin with.

Tian *et al*. (*6*) may have found a way to sidestep these problems. In their model, the atmosphere is CO_2-rich, not CH_4-rich, but contains as much as 30% H_2. The model uses the current hydrogen outgassing rate, increased by at most a small factor to account for the geologically more active early Earth. What is new is their transonic hydrodynamic escape model: For an atmosphere rich in H_2, the escape of hydrogen to space is hydrodynamic and limited by the availability of extreme ultraviolet light from the Sun. The model yields an escape rate that is much lower than previously found. Because less H_2 escapes, if Earth ever had an H_2-rich atmosphere, it could be sustained.

The figure shows why this matters for the origin of life. HCN and H_2CO are produced at much lower yields in CO_2-rich atmospheres than in CH_4-rich ones, but production is particularly low in CO_2-rich atmospheres when H_2/C ratios fall below 1 or rise above 5 to 10 (*5*). Tian *et al*. (*6*) suggest that they can keep $H_2/C > 1$ in their model, although this also depends on the poorly known CO_2 abundance. Their H_2-CO_2 atmosphere is less favorable for organic production than a Miller-Urey one, but far better than previously preferred model atmospheres with $H_2/C \sim 0.001$.

Many uncertainties and problems remain. Tian *et al*. focus on the oceans as the "birthplace of life," but polymerization of amino acids into proteins (or nucleotides into RNA) is thermodynamically unfavorable in liquid water. Furthermore, in an early ocean as saline as that of today, the salt inhibits key prebiotic reactions (*9*). The bulk ocean may thus have been one of the worst places to try to originate life. After making life's building blocks in the ocean, one needs to look elsewhere to carry the chemistry further. Some authors have abandoned this heterotrophic picture of the origin of life in favor of an autotrophic model, in which metabolic reactions that can fix their own carbon are the first steps on the road to life (*10*).

How does prebiotic organic production in the atmosphere of Tian *et al*. compare to other sources of organic molecules on early Earth? Because of uncertainties in the hydrogen content of the early atmosphere, examinations of this question have considered a range of H_2/C ratios (*11*). As model atmospheres become more hydrogen-rich, production of organic molecules through electrical discharges or ultraviolet light becomes increasingly important relative to delivery of organic molecules by meteorites or comets. Yet shock-tube experiments suggest that in Miller-Urey atmospheres, atmospheric shocks from meteors and impacts could be a dominant energy source for organic synthesis (*11*). Impactors may also have been a major driver of organic production in an early H_2-rich atmosphere.

These are tumultuous times in the study of the origin of life. The early ocean may have been even less hospitable for prebiotic chemistry than previously thought (*9*), and claimed evidence for the earliest signatures of life on Earth is being strongly challenged (*12*). Now a 30-year, albeit shaky, consensus on the nature of the early atmosphere may have to be reexamined, and the geochemical implications of an H_2-rich early atmosphere will need to be scrutinized. This turmoil makes it a great time for young scientists to enter the field, but it also reminds us that some humility regarding our favorite models is in order. As Jacob Bronowski noted, "Science is a tribute to what we can know although we are fallible" (*13*).

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STRUCTURAL BIOLOGY

Flipping Lipids: Is the Third Time the Charm?

Amy L. Davidson and Jue Chen

Gram-negative bacteria such as *Escherichia coli* are defined by the presence of a second or outer membrane bilayer that serves as a unique protective coat. While all cells have a membrane bilayer that forms a barrier to the passage of hydrophilic (water-soluble) compounds, the outer membrane is an asymmetric bilayer whose outer layer (or leaflet) contains a special lipid known as lipopolysaccharide (LPS). LPS decreases membrane fluidity, thereby creating a barrier to the diffusion of potentially toxic hydrophobic compounds (*1*). LPS is synthesized as a precursor known as Ra-lipid A in the inner leaflet of the inner membrane bilayer (*2*). Before it moves to the outer membrane, Ra-lipid A is flipped to the outer leaflet of the inner membrane, where a polysaccharide O-antigen chain is added to form mature LPS.

Two papers by Dong *et al*. (*3*) on page 1023 and Reyes *et al*. (*4*) on page 1028 of this issue shed light on this flipping mechanism. These studies elucidate the structure and dynamics of MsbA, an adenosine triphosphate (ATP)–binding cassette (ABC) transporter believed to accomplish this flipping event. ABC transporters, such as the homodimer MsbA consist of two helical membrane-spanning domains and two nucleotide-binding domains. Two ATP molecules bind along the dimer interface, interacting with residues in two conserved motifs, the Walker A motif from one nucleotide-binding domain and the ABC family signature motif from the opposing domain. Conformational changes in the nucleotide-binding domains, induced by binding and hydrolysis of ATP along the dimer interface, are coupled to conformational changes in the membrane-spanning domains that then mediate transport of substrate. One paper describes the x-ray crystal structure at 4.2 Å of MsbA from *Salmonella typhimurium* and is the third in a series of structures of MsbA from different organisms determined by the Chang laboratory (*4*). Although the first two structures have been criticized as nonphysiologic on the basis of aberrant behavior of the nucleotide-binding domains, it looks as though the third one may be the charm (see the figure). In the new structure, the nucleotide-binding domains appear correctly folded. They face each other across the dimer with an orientation similar to that seen in the ATP-bound dimers observed in the earlier structures (*5*, *6*), except that the dimer interface is more open. In addition, both nucleotide and Ra-lipid A are bound in a configuration suggestive of a "post-hydrolysis" state: Adenosine diphosphate (ADP) is present in one of the two nucleotide-binding domains, and Ra-lipid A

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