

## Widespread production of extracellular superoxide by heterotrophic bacteria

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Superoxide, a reactive oxygen species (ROS), is a powerful and versatile reactant that is toxic to living organisms and can dramatically alter the geochemical landscape through a myriad of redox reactions. (A)biotic reactions that are directly or indirectly coupled to sunlight have been the only recognized sources of environmentally relevant ROS. Phytoplankton, for instance, have previously been shown to produce ROS, yet their abundance and distribution in nature is fundamentally constrained by sunlight. Thus, although ROS production has been frequently observed in the deep ocean and at night, superoxide and other ROS are regarded as pertinent only in sunlit systems, which represent merely ~5% of the habitable environment on Earth.

Here we show that common and abundant heterotrophic bacteria are a vast unrecognized source of ROS. We analyzed extracellular superoxide production by a broad range of ecologically and phylogenetically diverse heterotrophic bacteria using a high sensitivity flow-through chemiluminescence approach. Superoxide production was detected by 27 of 30 environmentally common isolates. Rates of superoxide production normalized to the proportion of metabolically active cells varied a few orders of magnitude, between  $0.02 \pm 0.02$  and  $19.4 \pm 5.2$  amol cell<sup>-1</sup> hr<sup>-1</sup>. Although cell-normalized rates of superoxide production by heterotrophic bacteria are lower than those measured previously for marine phytoplankton, rates normalized to cell surface area are comparable to, and in several cases greater than, those of phytoplankton. Superoxide production by a model bacterium within the ubiquitous *Roseobacter* clade involves an extracellular NADH oxidoreductase, suggesting a surprising homology with eukaryotes.

Our discovery therefore introduces the likelihood of ROS cycling in ~95% of the global habitat that is untouched by light, a paradigm shift which will certainly transform our understanding of the geochemistry, ecology, and health of a wide range of modern and ancient environments.

## Venus crustal plateaus as an analog for Archean cratons and SCLM

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A hypothesis is presented suggesting that Venus' ancient crustal plateaus and their mantle roots represent analogs for Archean cratons and their underlying subcontinental lithospheric mantle (SCLM). Crustal plateaus (~1500-2500 km diameter) are quasicircular features that rise 0.5-4.0 km above Venus' lowlands, supported by low density isostatic roots, and host a distinctive structural fabric called ribbon-tessera terrain (RTT). RTT also occurs as arcuate-shaped exposures in the lowlands, widely interpreted as 'collapsed' or rootless crustal plateaus. Crustal plateaus and RTT inliers represent Venus' oldest preserved features and surfaces. RTT fabrics and their host crustal plateaus are postulated to have formed as the solidified 'scum' of huge lava ponds, formed by large bolide (>25 km diameter) impacts with ancient thin lithosphere. Bolides pierced the lithosphere, leading to massive partial melting in the upper mantle. Melt rose to form huge surface ponds, burying bolide scars; high-Mg depleted mantle melt residuum formed a robust buoyant root, leading to plateau formation, and long-term stability. The roots of lowland RTT were removed, likely due to mantle convection.

On Earth, Archean cratons comprise granite-greenstone terrains (GGTs) and associated high-Mg SCLM. Like crustal plateaus, GGTs are unique—lacking contemporary analogs—and they have been remarkably stable since formation; thus, they too record ancient geologic processes of their host.

Recent studies indicate that Late Heavy Bombardment (LHB) on Earth lasted through the Archean. Therefore, like Venus, early Earth's thin lithosphere would have been bombarded by numerous large bolides (>25 km), with a likely similar first-order response, resulting in massive partial melting of the mantle, escape of high-Mg melt to the surface (komatiites), and formation of a high-Mg residuum root, which protected the new-formed crustal features from younger planetary processes. GGTs that survived retain their roots; GGTs that lost their roots were likely accreted to stable GGTs or recycled by younger plate tectonic processes. The hypothesis suggests that Venus' crustal plateaus and Earth's GGTs both formed during LHB, when both of these young hot planets had relatively thin lithosphere, and record a unique era in the evolution of these sister planets. Large bolides punctured the thin lithospheres, which were strong enough to support the products of massive mantle partial melt; the high-Mg melt residuum roots protected these unique regions from younger planetary processes on both planets.